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Climate change and impacts of boreal forest insects

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Abstract

The circum-polar boreal forest has played an important role in the wealth of northern nations since the 15th century. Its natural resources spurred strategic geopolitical developments beginning in the 16th century but intense development of the boreal forest is largely limited to the 20th century. Insects cause considerable loss of wood that has an adverse effect on the balance of carbon sequestered by forests. Current understanding of processes that lead to stand-replacing outbreaks in three insect species is reviewed in this paper. Many of these processes depend on climate either directly, such as reduced survival with extreme weather events, or indirectly, mainly through effects on the host trees. In the boreal zone of Canada, pest-caused timber losses may be as much as 1.3–2.0 times the mean annual depletions due to fires. Pests are thus major, but consistently overlooked forest ecosystem components that have manifold consequences to the structure and functions of future forests. Global change will have demonstrable changes in the frequency and intensity of pest outbreaks, particularly at the margins of host ranges. The consequent shunting of carbon back to the atmosphere rather than to sequestration in forests as biomass is thought to have positive feedback to global warming. Whereas significant progress has been made in developing carbon budget models for the boreal forests of Canada, enormous problems remain in incorporating pest effects in these models. These problems have their origins in the nature of interactions among pests with forest productivity, and problems with scaling. The common problems of verification and validation of model results are particularly troublesome in projecting future forest productivity. The interaction of insects with fires must be accounted for if realistic carbon sequestration forecasts in a warming climate are to be made. These problems make assessments of mitigation and adaptation of pest management alternatives difficult to evaluate at present. Nevertheless, the impacts of stand-replacing insect population outbreaks is important in formulating future resource management policy. Crown Copyright © 2000 Published by Elsevier Science B.V. All rights reserved.

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1. Introduction

The coniferous boreal forest is a circum-polar vegetation belt located between the +13 and +18°C July isotherms. These forest boundaries are modified by precipitation as influenced by oceans and mountains and the influence of maritime and continental climatic patterns (Kuusela, 1990). The productivity of these forests is determined by several additional environmental variables that are subject to change in response to climate and global changes. These include the length of the frost-free season, the depth to perma-frost (which may affect up to 50% of the land base) and day-length. Biotic agents that influence productivity include those that affect trees directly through browsing (mammals), defoliation (mostly

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insects), rots and decays (fungi) and a host of diseases (largely caused by fungi). Indeed the suggestion has been made that insects (and probably fungi) regulate the net primary productivity of forests (Mattson and Addy, 1975).

Boreal forests have long generated economic wealth and have played a strategic role in the historical development of northern countries. Colonization of Siberia by Russians began with their expansion across the Ural Mountains to trap fur-bearing animals in the 16th century. The Russian economy depended on the flow of fur to such an extent that they used pelts as the basis for their currency (Bobrick, 1992). By the middle of the 17th century, the French had established colonies in North America and were exporting furs to Europe from New France. In an effort to prevent the expansion of French interests to the west in North America, the British crown granted a charter to the ‘Governor and Company of Adventurers of England Trading into Hudson’s Bay’ on 2 May 1670. This charter granted the rights to what is now the Hudson’s Bay company to exploit the resources found in all lands drained by rivers flowing into Hudson’s Bay. This act ultimately determined the extent of French settlement in North America, the location of the present border between USA and Canada and had a significant repercussion on the Russian empire’s monopoly in exporting fur to western Europe. More importantly, one could argue that this interference may have delayed the colonization and exploitation of the vast Russian forest resources located in both Europe and Siberia. Exploration of the vast Canadian boreal forest began with the appointment of the first Dominion Forester 100 years ago. Most of the development of the forest resource and extraction of wood products from the boreal forest in Canada did not occur until the latter half of the 20th century although the clearing of forested land in the Nordic countries began in the previous century. By the early 1980s, 21% of the world’s timber products, valued at US$ 48 billion (10^9) annually, came from boreal forests (Kuusela, 1990).

Today, the boreal forest covers 1.02×10^9 ha or 30% of the forested lands on earth. Most significantly, these forests account for 43% of the 958 Pg (10^{15} g) of carbon sequestered in closed canopy forests and their soils worldwide (Brown, 1996). At present rates of withdrawal (by harvesting and land-use changes), boreal forests are thought to sequester 0.5 Pg of atmospheric carbon per annum (i.e. a carbon sink). This positive balance does not offset the total net losses from all forested landscapes combined, which is presently a net source of 0.9 Pg of atmospheric carbon per annum globally. Any increase in withdrawals would further exacerbate this condition. Regionally, some boreal forests may already have become carbon sources (Kurz and Apps, 1999), although this may be offset by global change processes that accelerate biomass accumulation in northern forest stands (Chen et al., in press).

This paper describes the relevant biology, population dynamics and impacts of three forest defoliators in North America that might respond to climate change, adversely affecting the current balance of the boreal forest carbon budget. Their effects must be included in any models that seek to describe the spatial and temporal distribution of carbon in the boreal forest. The three defoliators are the spruce budworm (*Choristoneura fumiferana* (Clem.)), the jack pine budworm (*C. pinus* Freeman), and the forest tent caterpillar (*Malacosoma disstria* Hübner). They were chosen for examination because they provide a range of examples that best illustrate forest depletion processes mediated by insects. Moreover, they cause vast outbreaks which often culminate in extensive replacement of forest stands. Outbreak populations also respond to climatic influences that could change historical outbreak patterns under altered climate regimes. Therefore, their outbreak effects on carbon pools are above those expected from feeding by endemic populations in normal forest stand development.

2. The spruce budworm

The spruce budworm causes considerably more damage than any other insect in North America’s boreal forests, because of this it has been closely studied and monitored over the years. This has produced a richness of information about this insect which substantially exceeds that for the jack pine budworm and forest tent caterpillar, and this difference is reflected in the following descriptions of these three insects.

The spruce budworm is one of the several of closely related Abietoid-feeding *Choristoneura* species whose populations erupt to cause widespread damage. The spruce budworm is a true boreal forest insect whose principal hosts are white spruce (*Picea glauca*

(Moench) Voss) and balsam fir (*Abies balsamea* (L.)). Other species in this group that have been designated as pests include the western spruce budworm (*C. occidentalis* Free.) feeding on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), white fir (*A. concolor* (Gord. and Glend.) Lindl. Ex Hildebr.) and grand fir (*A. grandis* (Dougl. ex D. Don) Lindl.); the Modoc budworm (*C. retiniana* (Wlshm.)) feeding on white fir; and the 2-year cycle budworm (*C. biennis* Free.) feeding on Engelmann spruce (*P. Engelmannii* (Parry ex Engelm.). The latter three pests occur principally in the mountains of western North America (Volney, 1989). The taxonomy of the group remains confused, partly because of nomenclatural problems but also because of the extreme variability within and among populations, overlapping variation among species and hybridization among species in nature (Powell and DeBenedictis, 1995). These problems are further confounded because their host species also vary significantly and often form hybrid swarms where they occur sympatrically (Farrar, 1995). The patterns of geographic variation observed in the distribution of these insects may be exploited to understand how their populations will respond to global change.

2.1. Life history and range

Life history traits and survival functions are among population characteristics critical to understanding the response of pests to changing environments. The life history of the spruce budworm, which is similar to that of the other conifer-feeding species, was described by McGugan (1954). Eggs are laid in mid-July, they hatch in 2 weeks, and the first instar larvae feed on fungi colonizing the phylloplane without causing damage to needles (Retnakaran et al., 1999). The larvae then find a suitable site on branches, spin silken hibernacula in which they moult and overwinter as second instars. In spring, larvae emerge to feed by mining the previous year's needles before they migrate to mine the current year's developing buds. Feeding from then on is usually confined to the newly developing shoots. If the insects deplete this resource, they will then feed on the prior years' needles. The insects pupate in their feeding webs and emerge as moths in 10 days. Females are mated on the evening following their emergence and then lay eggs in masses on needles. Females may disperse from their native stands and be carried by surface winds for several kilometres (Greenbank et al., 1980). There is one generation per year. A variable, but small, proportion of the population may take 2 years to complete this life cycle. This is the defining species characteristic of *C. biennis* (the 2-year cycle budworm) and may be an adaptation to short growing seasons found at high elevations (Harvey, 1967). This second diapause, which occurs in the fourth instar, may also permit the spruce budworm to survive in years when weather extremes, such as the destruction of current year's foliage by late frosts, prevent larvae from completing development in a single season (Harvey, 1985). Although the range maps for the spruce budworm show it surviving as far north as Fort Norman (64°40′N, 125°00′W) in the northwest territories (Harvey, 1996), this is the northern limit of outbreaks (Cerezke and Volney, 1995). Yet these insects can be trapped at Inuvik (68°20′N, 133°35′W) on the Mackenzie River delta at the northern limit of the range of white spruce (Volney, unpublished). It appears, therefore, that survival of the insect in the north is limited by the distribution of its host and not by climate. However, the limitation of outbreaks some 400 km south of this limit has not been explained.

2.2. Temperature requirements and development

Temperature requirements for the insect to complete its development in different parts of its range vary and might explain why northern outbreaks are limited several kilometres south of the known distribution of the insect. Estimates of the cumulative degree-day (DD) (threshold $=$ 6°C) requirements for field populations to develop from 50% second instars to 50% moth emergence in northern Alberta (58°30′N) were found to be 209 DD (Volney and Cerezke, 1992), whereas this value was 345 DD in an Ontario (50°N) population (Lysyk, 1989). Although this suggests a cline in this development parameter, populations collected over a 15° range of latitude showed no variation in development rates when reared in a common environment (Weber et al., 1999). These results suggest that the dispersal capability of moths, which may fly over 450 km per night (Dobesburger et al., 1983), is effective at eroding any selection for locally adapted populations. Hosts have a profound role in determining survival because each instar is adapted to a particular stage of shoot development

(Volney and Cerezke, 1992) and there are morphological and behavioural adaptations to the uncertainty in early spring emergence (Trier and Mattson, 1997). In the more northerly populations some critical stage cannot be completed by a sufficiently large proportion of the population to generate outbreaks.

Spring emergence of spruce budworm larvae is the most variable of all post-diapause developmental processes and may be critical in determining whether populations thrive. Emergence is timed to synchronize at least a fraction of the population with developing host buds (Volney et al., 1983). In comparing post-diapause development rates among *C. occidentalis*, *C retiniana* and hybrid populations, it was evident that spring emergence was the only trait that showed a consistent difference among populations (Volney and Liebhold, 1985). Despite this difference early in the life of the insects, the total development time was essentially the same at moth emergence (presumably this is an adaption to synchronize population for mating). Experiments to determine the optimal emergence time (Lawrence et al., 1997) clearly indicate that the success of *C. fumiferana* in establishing feeding sites is dependent on the proper synchrony between insects and host development. Optimal survival in these experiments was in excess of 60% but fell below 10% when emergence was delayed. Thus, the variation in survival within the generation can be significantly affected by host phenology and may account, in part, for the northern limits of *C. fumiferana* outbreaks.

Heritability of spring emergence is low for populations in pure host stands (Volney and Liebhold, 1985). Low heritability implies that natural selection is unlikely to shift the mean value of the trait concerned easily. This is normal for traits that are critical to survival (Falconer, 1981). This conservatism can be overcome quite rapidly, however, if the populations hybridize in nature. This is precisely what occurs: heritability of this trait in hybrid populations is very high (Volney and Liebhold, 1985). Not coincidentally, this occurs where host species of the insects also hybridize. The evolution of new host relationships is thus rather rapid under such conditions and may afford spruce budworm and its sibling species opportunities for evolution not normally available to less variable species. This appears to have occurred several times in the past, the most recent known case being the hybrids between *C. occidentalis* and *C. retiniana* approximately 7000 y B.P. (Powell and DeBenedictis, 1995). Given the genetic variability of the several *Choristoneura* populations in North America, the apparent lack of strong reproductive barriers among putative species and their dispersal capability, it seems reasonable to conclude that the northern limit of outbreaks could easily outrun the remaining 400 km-wide band of unaffected spruce forest on the continent. Thus, the entire range of white spruce would have to be considered vulnerable to outbreaks, especially under a warming future climate.

2.3. Population dynamics

Spruce budworm population dynamics have been the subject of intense study for several decades (Régnière and Lysyk, 1995). The current understanding is due to recent analyses by Royama (1984, 1992) and is based on a small number of plots in NB, Canada, within the central core of the species range. This work and tree-ring records suggest that populations cycle with a period of 35 years. The simplest model that can describe the observed behaviour is a second order auto-regressive model. Graphical analyses of the New Brunswick data indicate that survival of late-instar larvae and pupae is the factor that is responsible for generating the primary oscillation with this 35-year period. Royama argues that only natural enemies, solely dependent on the budworm host, can potentially contribute to the lagged density dependent effects required to induce this oscillatory behaviour. Mortality from density independent factors and dispersal serve as random perturbations of the population and, if correlated among different localities, serve to entrain populations so that they are regionally synchronous. Unfortunately, Royama's (1992) work was limited to the only such data set available and was based on observations made in selection of four balsam fir stands in northern New Brunswick. In addition, no one has identified the factors that enhance survival in ascending populations. Royama suggests that after the previous outbreak collapses, the effectiveness of natural enemies with a slow numerical response to spruce budworm densities undergoes a gradual but steady decline which eventually becomes so weak that spruce budworm populations begin increasing again.

No general understanding of the dynamics of spruce budworm populations is possible unless meso- and macro-scale processes are surveyed to elucidate the variation in population behaviour within the immense range occupied by the spruce budworm and its relatives. Furthermore, these studies are required to generate current and future impact of the insect under varying climate change assumptions.

The forested area damaged by the spruce budworm can be used as a proxy for population size and has been recorded for varying lengths of time in different parts of Canada. However, the use of proxy data does not permit detailed conclusions regarding the biological causes of population change (Régnière, 1985). Operational defoliation surveys began in 1938 (Hardy et al., 1986) but the quality and extent of coverage improved over subsequent decades as mapping and observational technologies improved (Candau et al., 1998). These data provide the opportunity to examine the meso-scale behaviour of the insect in the eastern half of its range over a 60-year period. Recent work using defoliation maps from Ontario confirm the basic 35-year cycle in budworm population (Candau et al., 1998). Three outbreak areas were identified in Ontario. During the period covered (1941–1996), two outbreaks occurred in each area with those in the eastern one peaking 5–6 years before those in the western area. These authors also found no evidence that outbreak frequencies have increased in the last century as proposed by Blais (1983). Thus, the basic population cycle appears unchanged in this core area despite the warming encountered in the western portions of this area over this period (see Oechel and Vourlitis, 1994).

The reasons for regional asynchrony of outbreaks are still debated. There is a suggestion that outbreaks may be initiated by dispersal between outbreak centres, separated by 475 km, but this is countered by Candau et al. (1998) who reported that outbreaks occurred sooner in eastern Ontario than in western Ontario, opposite to the prevailing winds. This suggestion is also at odds with Royama's (1984) theory which argues that outbreaks are the result of local conditions favouring increased insect densities. In this latter view, dispersal only accounts for a secondary, high frequency, oscillation about the 35-year primary oscillation. Alternatively, outbreak areas may be independent and would be expected to eventually cycle independently. This notion, however, is somewhat at odds with Williams and Liebhold's (in press) macro-scale analyses of the defoliation record between 1945 and 1988. Like Candau et al. (1998), Williams and Liebhold also found that synchrony decreased with distance. Using arbitrarily chosen block locations and sizes (2.56×10^6 ha), Williams and Liebhold estimated that synchrony became negligible at 2080 km. They also concluded that a spatially auto-correlated Moran effect, associated with spatially auto-correlated weather parameters (mean monthly temperature and precipitation) and high, but plausible, dispersal rates accounted for the temporal geographic pattern observed in eastern Canada. They also noted that at the margins of the geographical range of outbreaks (Manitoba and Newfoundland), the temporal pattern of well-defined peaks degenerated into a series of multiple peaks.

Outbreak patterns change dramatically as one proceeds west of the Ontario/Manitoba border. This corresponds to the increasingly dry continental areas that are southwest of the Canadian Shield. Balsam fir becomes less prominent in this western boreal forest leaving white spruce as the predominant spruce budworm host. White spruce stands in the prairie ecoregion and in the boreal forest/prairie ecotone are confined to north facing slopes of ravines. These are the remnants of the forests that colonized these areas following the retreat of the glaciers. Budworm outbreaks in these areas persist for several years. They seem only to be terminated by late frosts that damage the entire crop of current year's shoots thus starving developing larvae (Cerezke and Volney, 1995). Persistent budworm outbreaks interfere with forest stand development, killing trees and opening stands to permit surviving trees to flourish until the next outbreak develops. This is the pattern observed in the Spruce Woods Reserve in southwestern Manitoba where moderate to severe defoliation has been observed in all years (since 1938) when these stands were examined. This forest is essentially a relict of an earlier forest similar to that which now exists further north. These forests persist because fires have not occurred, and white spruce is extremely tolerant to defoliation so the budworm population may take several decades to finally extirpate the stands.

Tree-ring studies have been useful in determining the frequency and duration of outbreaks over large areas (Blais, 1983). Royama (1992) was able to determine that the outbreak return time was approximately 35 years over the last two centuries in New Brunswick and Quebec. Tree-ring studies in New Mexico on the closely related *C. occidentalis* indicate that the regularity of cycles and their synchrony may be a response to land-use changes (Swetnam and Lynch, 1993). Most significantly, they found that periodicity of outbreaks varied from 20 to 33 years indicating that the budworm-forest dynamic is pseudo-periodic in this region. They also found that outbreaks were associated with wet/dry periods and that the extent and severity of outbreaks in the 20th century was a response to land-use changes. Logging, fire and grazing pressures reduced the density, coverage and canopy closure of these forests during the early Anglo-American settlement era. Relaxation of these pressures regenerated a dense, continuous, mixed-conifer forest with an elevated proportion of suitable budworm hosts. In contrast, pre-settlement outbreaks in the spatially and temporally heterogenous forest sustained less severe outbreaks and were not regionally synchronized. These New Mexico forests are close to the margin of the hosts' distribution. The instability in outbreak frequency may be another example of populations at the southern extreme of host ranges deviating from the regular period found in the core of the range.

3. Jack pine budworm

The jack pine budworm (*C. pinus* Free.) feeds primarily on jack pine (*Pinus banksiana* Lamb.). Although jack pine is closely related to lodgepole pine (*P. contorta* Dougl. ex Loud.) and natural hybrids are found in northern Alberta where their ranges overlap, outbreaks have not been recorded in native lodgepole pine or hybrid populations. The insect has damaged plantations of lodgepole pine in the Spruce Woods Forest Reserve of Manitoba.

3.1. Population dynamics

Populations of the jack pine budworm appear to cycle with a 10-year period in the prairie provinces of Canada (Volney, 1988). Thus, the jack pine budworm makes an attractive model to study because of the relatively short period between outbreaks in contrast to the spruce budworm case where one cycle would occupy the entire career of an investigator.

Trends in population densities of the jack pine budworm seem to be determined by survival in the large larval stages (instars 4 and older) when population densities are high (Foltz et al., 1972, Batzer and Jennings, 1980). As with the spruce budworm, factors determining large larva mortality are critical in determining trends in high density spruce budworm populations (Royama, 1992). In contrast to the spruce budworm case where no life table studies exist for rising populations, Batzer and Jennings (1980) reported that survival from the egg stage to establishment of feeding was the critical factor in determining trends in low density populations of the jack pine budworm. It has long been suspected that staminate flowers were important to survival of the early instars (Graham, 1935) but experimental verification of this was only recently provided by Nealis and Lomic (1994). This provides the essential link between the role of host tree performance and the response of the insect population. What is more is that staminate flower production is promoted by water stress (Riemenschneider, 1985) and agents, such as Armillaria root disease, that induces this stress in trees (Mallett and Volney, 1990). Defoliation by the insect causes a cessation of flower production. Not surprisingly, analysis of long-term data sets found strong negative second order effects to be common in all 31 populations examined in northwestern Wisconsin (Volney and McCullough, 1994). The feedbacks necessary to induce oscillations thus come from the combination of host effects and natural enemies in different phases of the population cycle.

Populations in northwestern Wisconsin, which is close to the southern margin of jack pine's range, cycle with frequencies of 5, 6 or 10 years. Moreover, populations that cycle at the higher frequency are found on the drier, nutrient poor sites (Volney and McCullough, 1994). Weather and climate affect the populations indirectly through the response of the trees. The interactions among site, tree nutrition, defensive host chemicals and jack pine budworm performance are complex: the elevated survival of larvae on nutrient-rich (wetter) sites is offset by the elevated fecundity of insects reared on foliage from trees growing on poor (drier) sites (McCullough and Kulman, 1991a,b). The effect of flowering probably over-rides these effects when populations begin to rise from low densities, however.

Jack pine is a seral tree species that relies on fires to open its serotinous cones and release the seed required to regenerate stands. In the absence of fire, jack pine would be replaced by shade-tolerant species but defoliation effectively provides the fuel for ground fires that removes fire-intolerant species (Nealis, 1995). In addition to providing the heat to open cones for seed release (McCullough et al., 1998), fires also prepare the seed bed for jack pine regeneration by removing accumulated needles and woody debris and eliminating seed predators and decay organisms. At the southern margins of its distribution, jack pine becomes an open grown tree, because the jack pine budworm kills more trees than can be regenerated by this process. Surviving trees develop deep crowns without competition, but this is precisely the condition that induces flowering and elevated budworm survival. These conditions are probably the reasons for the frequent outbreaks in northwestern Wisconsin.

The area affected by outbreaks has increased exponentially in the last 60 years (Volney, 1988). By using fire as a proxy for temperature and rainfall in an area where weather stations are sparse, it was determined that drought 7–4 years prior was strongly associated with the onset of defoliation in Canada. In the rapidly cycling populations of Wisconsin, no such lags are possible. These populations may be cycling at the maximum permitted by the insect/host system if at least 1 year's respite from defoliation is required to initiate flower production. It would be difficult for these trees to sustain increased stress from outbreak populations that peak every 5–6 years. With the additional stress from droughts, this system could very well be on the brink of collapse.

4. Forest tent caterpillar

The forest tent caterpillar is an indigenous defoliator of several tree species and has a wide distribution in North America. However, it is a chronic problem in the prairie/boreal forest ecotone located in central Canada (Ives and Wong, 1988). This species faces the same problems as the budworms of synchronising the emergence of neonate larva to successfully colonize developing trembling aspen (*Populus tremuloides* Michx.) buds in spring. However, in this case delay in bud development affects survival and is mediated by adverse weather events such as spring frosts (Blais et al., 1955). Delays in budbreak following insect emergence also increases the effectiveness of parasitoids in reducing survival (Parry et al., 1998). Starvation of the insect can also be induced when late spring frosts damage developing foliage required as food by large larvae (Blais et al., 1955). These spring frosts are thought to be significant events in limiting the duration and extent of outbreaks (Ives, 1973; Volney and Currie, unpublished data). In a study of outbreak origins and associated climatological data, Ives (1973) was able to determine that warm springs 2–4 years prior to the occurrence of severe defoliation were required to trigger outbreaks. Thus, there are climate controls for both the initiation and cessation of forest tent caterpillar outbreaks.

Analyses of defoliation by the forest tent caterpillar in Manitoba and Saskatchewan indicate that there has been an outbreak of this insect in every year since 1924 (Hildahl and Reeks, 1960). Defoliation of individual stands varied from 2 to 5 years. The period between peaks of these outbreaks varied from 6 to 16 years with an average return time of 10 years for most locations. Four of the locations experienced a single outbreak in the 35-year observation period. A striking feature of this history is the apparent movement of outbreaks north from the grassland/forest ecotone in the 1920s to the southern margin of the boreal forest biome in the latter part of their study. One could argue that the drought and warmth of the earlier period (1930s) coupled with increasing forest tent caterpillar attacks in the ecotone essentially extirpated aspen from that region. Hogg (1994) found that the southern limit of the Canadian boreal forest in this region was accounted for by moisture deficits and possibly insect attacks.

Forest tent caterpillar outbreaks are extremely regular and dramatic in Ontario: the affected area can increase from hundreds of hectares to millions in 2–3 years. The outbreaks occur at regular, approximately 10 years, intervals and the duration of outbreak episodes is generally just 2–4 years, although local outbreaks sometimes last as long as 9 years (Sippell, 1962). Population collapse is usually associated with mortality caused by virus epizootics (Myers, 1993) and by parasites (Sippell, 1962). Because the food source of the forest tent caterpillar varies little from year to year, resource depletion is not considered a major contributing factor to population collapses.

Recent work has shown that the population dynamics of this insect may be affected by the spatial structure of the forest. In an analysis of data concerning historical outbreaks in the boreal forest of Ontario, Roland (1993) indicates that the amount of forest edge affected the duration of the outbreak. He suggested that the increased fragmentation of aspen forest caused by both harvesting and the conversion of land from forest to other uses was exacerbating outbreaks of the forest tent caterpillar. Subsequent work (Roland and Taylor, 1997) suggested a cause: the impact of three important natural enemies (parasitic insects) is substantially reduced in fragmented forest, as compared to continuous forest. Roland et al. (1998) examined characteristics of the forest tent caterpillar disturbance regime in central Ontario and tried to relate them to climatic patterns. They reported an association between shorter outbreaks with colder weather. This latter result is at odds with the comments regarding fragmentation and outbreak length because settlement (and hence the degree of forest fragmentation) progressed from north to south which is identical to (and thus confounded with) climate gradients in the region.

5. Impacts

Assessments of impacts have only been made in recent years when the technology to account for damage over large areas was developed. There is considerable variability in the impacts caused by these insects but some appreciation of the magnitudes can be obtained from studies in individual stands. MacLean (1985) summarized the studies on spruce budworm impacts and concluded that over an outbreak cycle the loss of stand volume ranged from 18 to 81% depending on the host species involved and outbreak intensity. By contrast, losses from a single jack pine budworm outbreak varied from 10% in younger stands to 18% in older stands (Volney, 1998). If a stand is repeatedly damaged by several outbreaks these losses become comparable to that sustained by spruce budworm damaged stands. The forest tent caterpillar damaged between 2 and 28% of the basal area of stands studied by Hildahl and Reeks (1960). In their simulation models, Mattson and Addy (1975) suggest that approximately 25% of the standing volume is lost in young aspen stands that sustain a typical outbreak.

The areas affected by these outbreaks historically have been large. In 1975, at the peak of the last spruce budworm outbreak, 71×10^6 ha of forest in eastern North America were defoliated (Hardy et al., 1986). For the jack pine budworm, 5.8×10^6 ha of pine forest in Ontario and the prairie provinces of Canada were defoliated in 1985 (Hall and Moody, 1994). Approximately, 15×10^6 ha of aspen parkland and adjacent boreal forest were damaged by the forest tent caterpillar in the prairie provinces in 1982. In Ontario, the forest tent caterpillar affects the largest area (19×10^6 ha defoliated at moderate to severe levels in 1992) of any hardwood-feeding insect, but typically causes little tree mortality directly (Howse, 1981; Moody and Amirault, 1992). However, Gross (1991) reported that forest tent caterpillar defoliation was an important contributing factor in the general decline of maples that occurred in southwestern Ontario in 1977 and 1978. Gross found high dieback in defoliated stands at the end of the defoliation period (1974–1977) and subsequent mortality of greater than 25% in some stands. By combining the historical patterns of defoliation and the characteristics of the forest affected using a geographical information system, estimates of the total volumes lost to pests can be obtained. The last period for which these estimates are available was 1982–1987. The average annual loss for Canada during this period due to the spruce budworm was $27.3 \times 10^6\,\mathrm{m}^3$, that due to jack pine budworm damage: $2.2 \times 10^6\,\mathrm{m}^3$ and for the tent caterpillar: $2.4 \times 10^6\,\mathrm{m}^3$ (Hall and Moody, 1994).

To put these losses in perspective, the average annual total depletions of Canada's forests in 1982–1987 was $298 \times 10^6\,\mathrm{m}^3$, of which insects and diseases accounted for $106 \times 10^6\,\mathrm{m}^3$, fire for $36 \times 10^6\,\mathrm{m}^3$ and harvest for $160 \times 10^6\,\mathrm{m}^3$. During this period the estimated annual allowable cut, which approximated the growth of this forest, was between 244×10^6 and $346 \times 10^6\,\mathrm{m}^3$. These estimates suggest that we are close to the limits of sustainability. Further, one strategic approach to improve this balance would be to reduce losses due to pests. Experiments to design pest intervention techniques that mitigate these losses and improve the carbon balance in Canada's forests are currently underway (Volney et al., 1999). Although the course of outbreaks can probably not be altered, the principle of preempting pest-caused mortality by harvesting the most vulnerable stands become a possibility with current harvest levels.

6. Conclusions

Populations of the three defoliators on the major forest tree species of the western boreal forest of Canada are all sensitive to climatic effects. The success of the insects in establishing feeding sites in the spring depends on synchrony of their development with that of buds of their hosts. This indirect effect of climate appears to be critical in initiating outbreaks of all three species. The collapse of outbreaks at least for parts of the range is often associated with the catastrophic loss of suitable foliage for these insects, often caused by spring frosts. For the two budworms, the normal collapse of the outbreak in the host's core range is associated with mortality driven by natural enemies late in the larval stage. Life table studies for the tent caterpillar have not been completed but there is evidence of an increasing response by parasitoids as the duration of outbreaks increased (Parry, 1995). The occurrence of outbreaks at a higher frequency toward the warmer margins of the host range seems to be associated with drought in all cases. It is thus quite reasonable to conclude that the insects may be partly responsible for the decline and ultimate extirpation of these stands at the southern margins of the hosts range. In contrast, late spring frosts have a role in terminating outbreaks in the northern reaches of the host range and may be responsible for limiting outbreak areas at these colder extremes. This is a generalization of the theme developed earlier for the spruce budworm (Fleming and Volney, 1995; Fleming, 1996) and applies to the other major defoliators that affect boreal forest tree species.

Any modelling exercise to evaluate the effects of pest on the carbon budget will have to account for these biological processes. The basic biology is sufficiently well known to permit this accounting. Indeed, prototype decision support systems have been developed to manage timber supplies at a forest level (see Erdle and MacLean, 1999). However, these have to be generalized to include the behaviour of the various insects and the variety of conditions encountered over the country. The most difficult outstanding biological question to be resolved is to quantify the basic relationships between the various climate parameters identified above and the processes they drive. Related to this is the reciprocal interaction between fires and insect outbreaks. Fire return frequencies change across this forest both from north to south and from east to west and fire intensities can be modified by insect caused mortality in stands (McCullough et al., 1998). It appears that fire frequencies in the circum-polar boreal forest have declined since the end of the little ice age (1850) and that further decreases will be likely if outputs of global circulation models are to be relied upon (Flannigan et al., 1998). This arises largely because there will be a shift to warmer springs and winters. Under these conditions, the incidence of insect outbreaks will increase and that increase may have already been signalled in the increased outbreak sizes observed in the regions of greatest warming (Oechel and Vourlitis, 1994) such as the prairie provinces and the northwest territories of Canada. Compounding this problem will be the ageing of forests in the absence of stand-replacing fires. Until the interaction of fires with insect disturbances are coupled in carbon budget models, the net effects of decreased fire frequencies and increased incidence of damaging insect outbreaks can only be guessed at.

To evaluate the impact of insects on forest and the consequent feedbacks in the climate system, the current models developed for timber supply analysis will have to be modified to accommodate carbon accounting so that they can be linked to carbon budget models. There are a variety of problems related to the current strategy of taking our understanding developed from intensive studies on small areas and scaling these models to large areas. Any non-linearity in these processes will severely distort outputs, thus affecting the reliability placed in model-generated conclusions (Fleming et al., 1999). Finally, these models will have to incorporate the positive feedbacks that global warming will initiate in these forest/insect systems if they are to be in any sense realistic (Kurz et al., 1995). The present carbon budget model (Kurz and Apps, 1999) includes several aspects of the insect impacts described here but does not account for the feedbacks associated with the interaction of insects and fire, and also the effects of outbreaks that change forests to grasslands are not included. This latter process was specifically not included because the national forest inventory data excludes areas of settlement, where much of this change has taken place from the areas inventoried.

In conclusion, the circum-polar boreal forest's role in geopolitical strategies continues, but has entered a new phase because of the concerns related to carbon cycling. In this phase, however, the commodity, carbon credits, is not only bound to the wealth of the respective countries but is intimately associated with the life-support system of the planet. It is therefore imperative that realistic and accurate forecasts of changes expected under the different future climates be available to policymakers in coming to agreements on the uses to which these northern forests are put. There is a further requirement that adaptation and mitigation considerations be incorporated in the models to guide policy. It would appear that the tenuous positive balance in the carbon budget for Canada's forests may have changed in the last decade mainly due to increases in the incidence of stand-replacing natural disturbances (Kurz and Apps, 1999). The effects of outbreaks of the insects discussed here are a large component of these disturbances. Yet much of the outbreak dynamics seem, to some degree, determined by climate and weather. As a corollary, the reciprocal interaction between climate and insect populations, as mediated by forests and disturbance, has a significant impact on the sustainability of these systems.

In the first attempts to manage natural resources derived from boreal forests, the extirpation of the species on which the economy was based (beaver) had relatively minor long-term effects on the sustainability of the system (demand for fur collapsed before the beaver were driven to extinction). In contrast, forest management policy now has the potential to upset the biogeochemical balance of carbon in the atmosphere unless the equilibrium between harvesting and disturbances can be managed to maintain boreal forests as carbon sinks. Canada's boreal forest may (Kurz and Apps, 1999) or may not be a source of atmospheric carbon (Chen et al., in press). Management of insect population outbreaks, whether they become a substitute disturbance for the fires we prevent with our fire management or become more prevalent because climate change is critical in determining balance in this carbon budget. Given the resource management history of the circum-polar boreal forest in the last 330 years, it seems ironic that the carbon balance to ameliorate conditions in the biosphere may depend on how depletions to the vast Siberian forest will be managed in future.

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