CLIMATE CHANGE AND INSECT DISTURBANCE REGIMES IN CANADA'S BOREAL FORESTS

Richard A. Fleming
Great Lakes Forest Research Centre
Canadian Forest Service
P.O. Box 490
Sault Ste. Marie, Ontario P6A 5M7 CANADA

Keywords: Carbon budget, integrated ecosystem response assumption, wildfire promotion, disturbance regime complex, successional pathway

SUMMARY

Natural disturbances are integral processes in the succession, functioning, and carbon-cycling that occurs in most of the world's boreal forests. Insects represent dominating disturbance factors in Canada's boreal forests and during outbreaks trees are often killed over vast areas. This extensive tree mortality shifts the forest toward younger age-classes which contain less biomass and much of the residual carbon is later released to the atmosphere. A fundamental question is whether climate change will increase the frequency, duration, and intensity of natural disturbances and thus accelerate the rate of warming.

Climate change will likely transform the damage patterns caused by many insects and the resulting uncertainties directly affect depletion forecasts, pest hazard rating procedures, and long-term planning for harvest queues and pest control requirements. Because the potential for wildfire often increases in stands after insect attack, uncertainties in future insect damage patterns magnify uncertainties in fire regimes. In addition, insects are important contributors to carbon and nutrient cycling, to biomass decomposition, and to energy flow, and changes in damage patterns can indirectly alter competitive relationships between plants and hence successional pathways, species composition, and forest distribution.

The disturbance regimes associated with three of the most important insects of Canada's boreal forest are described. The assumption of integrated ecosystem response is used to develop scenarios of how the disturbance regimes of a number of boreal forest insects might respond to climate change. Methods for improving the incorporation of insect disturbance regimes in carbon budget estimates for Canada's boreal forests are outlined and concepts underpinning a number of proposed approaches to managing insect disturbance regimes to improve carbon storage and sustain other values and benefits of the boreal resource are briefly discussed. An unresolved issue is the trade-off implicit in any approach, be
it large-scale planting or protection from insects and fire, which uses fossil fuels. Any short-term increase in the sequestration of atmospheric carbon by the forest comes at a cost of additional carbon imported into the modern biospheric system for the long term. Some research approaches for filling key information gaps are briefly suggested.

DISTURBANCE REGIMES

Despite attempts to develop a formal definition of the term disturbance (Rykiel, 1985), none has gained widespread acceptance in the voluminous literature on the subject (Attiwill, 1994). Hence, in keeping with current practice, I use the term disturbance in a general sense to signify an event that destroys biomass and alters resource availability and ecosystem structure (Pickett et al., 1987). Disturbances occur in many forms (e.g., wind, fire, disease, logging) and over a wide range of scales (e.g., compare the area of a canopy gap created by a fallen tree in the forest to the hundreds of millions of hectares of a large spruce budworm outbreak).

The concept of a disturbance regime (Johnson and Gutsell, 1994; Sousa, 1984) is typically used to classify disturbances of a particular type (e.g., insect outbreak) in terms of their areal extent, severity, duration, and frequency. Since many areas are prone to multiple kinds of disturbances (e.g., wind, fire, disease, and insect outbreak), focusing on a single type of disturbance may not lead to a complete analysis of a site's disturbance history (Furyaev et al., 1983). Hence, it is also important to consider how different disturbance regimes interact. In short, it is the disturbance regime complex, or the net effect of each disturbance regime plus their interactions, which is ultimately of interest.

Influence on Ecosystem Succession

It is widely recognized that different kinds of ecosystems are associated with different disturbance regime complexes (Runkle, 1985), and explanations for this association point to the fundamental role that disturbance plays in the development of ecosystem structure and function (Aber and Melillo, 1991; Attiwill, 1994). In sustaining itself at a site, an ecosystem goes through repeated cycles of maturation and renewal. Disturbances are the principal agents in these 'renewal' cycles for releasing the tightly bound accumulations of biomass, energy, and nutrients that characterize an ecosystem at maturity (Holling, 1986). This sudden release produces a pulse of available resources which opportunistic species exploit as they effectively invade the site and launch another successional sequence. This is a critical time. The next successional sequence could retrace previous successional pathways at the site and thus culminate in a mature ecosystem with much the same properties (in terms of species composition, soil qualities [Bever et al., 1997], etc.) as the one which existed.
on the site immediately before the disturbance. In this sense, the original ecosystem has effectively retained the site. On the other hand, if the original ecosystem is not going to retain the site, this is the part of the 'renewal' cycle when another, radically different form of ecosystem is most likely to begin to assert itself (Holling, 1987). Depending on the mix of available resources and micro-environments available at the site, and the variety of species with opportunity to exploit them, the new successional sequence may veer away from the successional pathway leading back to the ecosystem originally situated at the site and veer toward a pathway culminating in a totally new form of ecosystem (Bazzaz 1996; Oliver, 1980) with its own unique disturbance regime complex (Mack and D'Antonio, 1998).

Role in the Carbon Cycle

Disturbances also have an important influence on the carbon cycle in boreal forests. Boreal stands tend to be even-aged, and as they grow towards maturity, the trees within them grow larger, gradually increasing their biomass and net carbon content and that of the stand as a whole. When stands are young, they typically contain relatively little biomass but grow comparatively quickly. When stands reach maturity, they are usually growing very slowly, if at all, but have accumulated large amounts of carbon in their tissues. Disturbances often cause reduced growth and tree mortality over large areas. Reduced growth slows the rate of carbon accumulation and tree mortality can result in an abrupt release of carbon from the dead trees. (If the disturbance is logging, then the carbon can be contained within the dead wood for some time if it is converted to wood products with a long life span [Dewar and Cannell, 1992; Skog and Nicholson, 1998]). A substantial part of the released carbon may be transferred directly to the atmosphere (e.g., after fire [Cofer et al., 1996]) leaving the remainder to decompose as dead organic matter. Decomposition slowly releases additional carbon to the atmosphere (Raich and Schlesinger, 1992; Apps and Price, 1996), but it is also a key process in renewal cycles because it leads to mineralization of nutrients and mobilization of the tightly bound accumulations of biomass and energy in dead tree biomass (Holling, 1986). When disturbances occur frequently, trees have shorter life spans, and hence fewer years of growth to accumulate carbon before it is released back to the atmosphere or transferred to dead organic matter (Cooper, 1983). Thus, in general, the more often disturbances occur in a particular type of forest, the less carbon the forest contains in its living biomass and dead organic matter.

Importance of Response to Climate Change

A key question is whether climate warming will accelerate the accumulation of greenhouse gases in the atmosphere and thus bring on more climate warming, or as Woodwell et al. (1995) bluntly put it: "will the warming speed the warming?" There are at least three mechanisms which
lead to increased plant growth through photosynthetic and 'fertilization' effects (Woodwell et al., 1998) and thus work against this suggestion: (1) increasing mobilization of nitrogen due to a variety of human activities (Kauppi et al., 1995; Moffatt, 1998; Vitousek et al., 1997); (2) faster growth rates and longer growing seasons in a warmer climate; and (3) increasing atmospheric levels of carbon dioxide (Bazzaz et al., 1990), which are also largely responsible for climate warming itself (Keeling, 1960; Houghton et al., 1996). Recent analyses (Cao and Woodward, 1998; Woodwell et al., 1998), however, suggest that as climate warming continues, other mechanisms will begin to predominate. First, after prolonged exposure to an elevated CO₂ concentration, plant growth rates gradually revert back towards their slower, pre-exposure rates (Eamus and Jarvis, 1989; Hattenschwiler et al., 1997; Wullschleger et al., 1997). Second, respiration and decomposition rates are quite sensitive to temperature (Lindroth et al., 1998) so climate warming can be expected to reduce the carbon contained in soils and dead organic matter. Third, since carbon release typically increases more quickly than carbon accumulates in the plant regrowth on a site after disturbance (Houghton et al., 1983; Kurz and Apps, 1996), a major concern is that if climate warming leads to more frequent disturbances, then the warming may indeed speed the warming. This paper deals with this issue in the context of how insect disturbance regimes within Canada's boreal forests can be expected to respond to climate change, which is taken to include increasing levels of atmospheric CO₂ as well as climate variables other than temperature. While it is recognized that climate change is just one aspect of the larger issue of global change which also involves changes in land use/land cover, biological diversity, atmospheric composition in general, and their interactions with each other and with climate change (Walker and Steffen, 1997), these other changes are largely beyond the scope of this paper.

INSECT DISTURBANCE AGENTS
Ecosystem Functioning and Forest Productivity

In all forest biomes, insects play key roles in ecosystem functioning as contributors to carbon and nutrient cycling, to biomass decomposition, and to energy flow (Szújecki, 1987; Haukioja et al., 1988; Haack and Byler, 1993). For instance, insect faeces decompose faster than leaf litter (Fogal and Slansky, 1985; Kimmins, 1972) and, in attacked trees, defoliation hastens nutrient leaching from damaged foliage and litterfall. Defoliation also thins out the canopy, allowing greater penetration of sunlight and rainfall, and the consequent changes in the hydrologic, light, and thermal conditions under the canopy influence future stand development. Hence, Chapin (1993) and Schowalter et al. (1986) argue that chemical elements like nitrogen, calcium, potassium, and phosphorus cycle faster through forest ecosystems than they would if there were no insects present.
Table 1 Average annual depletions (10^6 m³/year) of Canada's productive wood volume and impacts of the major insect disturbance agents in Canada's boreal forest

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Harvest</td>
<td>160.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insects</td>
<td>62.5</td>
<td>51.6</td>
<td>56.6</td>
</tr>
<tr>
<td>Disease</td>
<td>44.9</td>
<td>51.2</td>
<td>48.3</td>
</tr>
<tr>
<td>Fire</td>
<td>36.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>298.8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Major Boreal Forest Insect Disturbance Agents

<table>
<thead>
<tr>
<th>Insect Species</th>
<th>Period</th>
<th>Growth Loss</th>
<th>Mortality</th>
<th>Total Annual Depletion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spruce Budworm</td>
<td>1977-1981</td>
<td>9.7</td>
<td>34.8</td>
<td>44.5</td>
</tr>
<tr>
<td></td>
<td>1982-1987</td>
<td>3.9</td>
<td>23.4</td>
<td>27.3</td>
</tr>
<tr>
<td></td>
<td>weighted average</td>
<td>6.5</td>
<td>28.6</td>
<td>35.1</td>
</tr>
<tr>
<td>Forest Tent Caterpillar</td>
<td>1977-1981</td>
<td>8</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>1982-1987</td>
<td>2.4</td>
<td>0</td>
<td>2.4</td>
</tr>
<tr>
<td></td>
<td>weighted average</td>
<td>4.9</td>
<td>0</td>
<td>4.9</td>
</tr>
<tr>
<td>Jackpine Budworm</td>
<td>1977-1981</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>1982-1987</td>
<td>0.7*</td>
<td>1.6*</td>
<td>2.3</td>
</tr>
<tr>
<td></td>
<td>weighted average</td>
<td>0.4</td>
<td>0.9</td>
<td>1.3</td>
</tr>
</tbody>
</table>

* Sterner and Davidson, 1982  
| Hall and Moody, 1994  
| Weighed averages  
| By comparison, annual 1982-1987 growth = 244.3 - 346.0 x 10^6 m³/year  
| Ratio of growth loss to mortality in jack pine budworm depletions was pro-rated from Ontario data.

In Canada, insect herbivore has substantial impacts on forest productivity (Table 1). Annual forest losses from unrealized growth and tree mortality due to insect attack are estimated at 56.6 million m³ per year. This value represents almost 1.6 times the losses from wildfire and amounts to roughly 1/3 of the annual harvest volume. In addition, because of their vast scales, such disturbances are thought to affect physical climatic processes on a regional and perhaps even on a global level (e.g., Bonan and Shugart, 1989; Price and Apps, 1995).

**In Canada's Boreal Forests**

The boreal forest biome represents two-thirds of Canada's exploitable forest area and covers 3 x 10^8 ha in a continuous transcontinental band extending westward from Newfoundland into British Columbia, the Yukon Territory, and on into the state of Alaska in the northwest (Canadian Council of Forest Ministers, 1997). Spruces (Picea spp.), pines (Pinus spp.), balsam fir (Abies balsamea), white birch (Betula
papyrifera), and trembling aspen (Populus tremuloides) are the dominant tree species and often occur naturally as extensive monocultures (Rowe, 1972).

Despite large-scale harvesting and modern fire control efforts, wildfire is still considered the disturbance which drives succession in most boreal landscapes (Hall, 1995; Weber and Flannigan, 1997). This is particularly true in the drier western regions of the boreal forest, in the wetter eastern parts insects play a larger role. Major insect-caused disturbances are similar to disturbances caused by fire, in that extensive areas of forest are affected on an annual basis, and also like fire (Van Wagner, 1978), insect outbreaks often have a cyclical aspect to their occurrence and play a role in forest succession (Bergeron and Dubuc, 1989). In other respects, there are important differences between the two types of disturbance. Unlike wildfire, insects are host specific and their outbreaks typically result in continuous damage over a period of years rather than in the days to weeks characteristic of fire. Insect outbreaks are also often much more extensive than wildfires and in approximate synchrony over large areas (Candau et al., 1998; Hardy et al., 1986). In addition, even where stand-replacing mortality is not occurring during insect outbreaks, the damage to trees reduces their growth (Table 1) and consequently their sequestration of carbon. Thus, in contrast to the effects of wildfire which are likely offset by photosynthetic uptake elsewhere (McNaughton et al., 1997), even at the largest scales insects, particularly the spruce budworm, are capable of imposing the oscillatory signature of their outbreak cycles on the net carbon fluxes from Canada's boreal forests.

Many insect species can cause damage and localized mortality in Canada's boreal forest, and under certain circumstances many of them will damage large areas of forest. For example, the larch sawfly (Pristiphora erichsoni1) is considered responsible for the destruction of most mature stands of larch in the last century but extensive damage by this insect has not been recorded for 50 years (Jardon et al., 1994). A few insects, however, regularly cause damage over large areas. These include the forest tent caterpillar (Malacosoma disstria) on poplar and other hardwood species such as sugar maple, the jack pine budworm (Choristoneura pinus pinus) on pine species, and the spruce budworm (Choristoneura fumiferana) on spruce and balsam fir.

Forest tent caterpillar

There are many insect defoliators of hardwood trees in the boreal forest (Ives and Wong, 1988; Rose and Lindquist, 1982; Howse, 1995). The most important is the forest tent caterpillar which attacks aspen as its principal host species. Although outbreaks of this insect cause heavy defoliation over extensive areas, the forest tent caterpillar it is not usually responsible for much tree mortality (Moody and Amirault, 1992). Defoliation by this insect might also be beneficial in releasing spruce from
the understory in mixedwood stands (Fitzgerald, 1995). On the other hand, Gross (1991) reported forest tent caterpillar defoliation to be a key factor in the decline of maples that occurred in south western Ontario in 1977-1978. Gross found high dieback in defoliated stands at the end of the defoliation period, 1974-1977, with subsequent mortality of greater than 25% in some stands. The forest tent caterpillar outbreaks are extremely regular and dramatic, with areas affected going from hundreds to millions of hectares in two-to-three years.

Recent work has shown that the population dynamics of this insect might be strongly affected by the spatial structure of the forest. In an analysis of data concerning historical outbreaks in the boreal forest of Ontario, Roland (1993) observed that the amount of forest edge affected the duration of the outbreak. He suggested that the increased fragmentation of aspen forest by both harvesting and land conversion was exacerbating outbreaks of the forest tent caterpillar. Subsequent work (Roland and Taylor, 1997) revealed the cause: the impact of three important natural enemies (parasitic insects) is substantially reduced in fragmented as compared to continuous forest.

- **Jackpine budworm**

Jack pine budworm is the most damaging insect which attacks jack pine in Canada's boreal forest. This insect does not usually cause much mortality to its host over extensive areas, although pockets of mortality are common in defoliated stands. Severe defoliation is most likely in semi-mature to mature stands, and losses to this insect are primarily in the form of reduced tree growth and mortality of intermediate and suppressed trees (Gross, 1992; Hopkin and Howse, 1995). Jack pine budworm outbreaks occur at about ten year intervals and last only two to four years (Volney and McCullough, 1994). Although this insect occurs across the range of jack pine and is found as far east as New Brunswick, there are historical records of large-scale outbreaks only in Saskatchewan, Manitoba and northwestern Ontario. Quebec, New Brunswick, and southern and central Ontario have experienced small, scattered outbreaks (Magasi, 1995).

- **Spruce budworm**

The spruce budworm is the most important biotic disturbance in Canada's boreal forest. The distribution of this insect follows that of white spruce, *P. glauca*, throughout the boreal forest and there are records of severe defoliation within 150 km of the arctic circle (Volney and Cerezke, 1992). Table 1 attributes 62% of all insect-caused losses in forest productivity in Canada to the spruce budworm from 1977-1987. This native insect attacks spruce and balsam fir and, in contrast to the closely related jackpine budworm, often kills most of its host trees, especially when they occur as dense, mature fir stands when outbreaks are not controlled. Mortality also occurs in mature white spruce stands, though it rarely exceeds 40% (MacLean, 1985), presumably because white spruce is better

© 2000 World Resource Review. All rights reserved.
able to recover from several consecutive years of heavy defoliation than balsam fir. Piene (1991) attributes this greater capacity for recovery of white spruce to its more prolific production of epicormic shoots in response to defoliation and the greater life span of its foliage than that of balsam fir. The immediate effect of such outbreaks is to reduce the proportion of balsam fir in the upper canopy. In addition, during outbreaks lasting from 10-15 years, white spruce will usually be badly damaged and often killed. Although white and black spruce are less vulnerable than balsam fir to budworm-induced mortality, their seed production is reduced because spruce budworm larvae attack the female reproductive structures and this results in fewer cones (Blais, 1985). Spruce budworm outbreaks can involve population densities as high as $10^6$ fourth instar larvae/ha and typically last 5-15 years. During the 20-60 years between outbreaks the insect can be difficult to find with densities falling a thousand-fold to $10^4$ fourth instar larvae/m² (Crawford and Jennings, 1989) and this respite permits the spruce-fir forests to regenerate (Mattson et al., 1988).

- Interactions with other disturbance agents: wildfire

Interactions between different types of disturbance are probably the rule rather than an exception. Since insect defoliation and fire are the major disturbances that affect the succession of northern forests, some interaction can be expected. For instance, in the spruce/fir boreal forest a relationship seems to exist between fire and outbreaks of the spruce budworm (e.g., Bergeron and Dansereau, 1993), but the underlying cause of this relationship is uncertain. It is often argued (e.g., Furyaev et al., 1983) that this relationship must be considered in order to understand the role of either kind of disturbance in the boreal forest. A common notion is that heavy defoliation by the spruce budworm can alter successional patterns in mature stands by making the stands more susceptible to crown fires. For instance, Wein (1990) reasoned that increased stress on host trees (e.g., from chronic defoliation or greater insect outbreak frequencies) accelerates host tree mortality. He suggested that greater tree mortality adds to the fuel load and ultimately leads to more frequent and more intense forest fires.

Johnston (1996) discusses the relationship between spruce budworm and fire in Ontario's boreal forests. After severe crown fires, post fire stands can be dominated by birch due to the ability of that tree species to colonize extensive areas by wind-disseminated seed. He suggests that where extensive crown fires have not occurred, shade tolerant species, particularly balsam fir and white spruce are likely to dominate, creating a forest composed largely of tree species susceptible to spruce budworm. Where fire does not occur after a budworm outbreak, the tree mortality resulting directly from the budworm or secondary insects and disease-causing tree pathogens (beetles, root rots) produces gaps in the canopy. Deciduous (non-host) species such as birch and aspen, which require ample light, rarely establish in the smaller openings. Instead, host species of the spruce
budworm such as balsam fir and white spruce, which are more tolerant of shade than birch and aspen, eventually occupy the gaps and thus maintain a forest susceptible to spruce budworm.

Other disturbance-causing insects also interact with wildfire (McCullough et al., 1998). For instance, jack pine is a tree species greatly influenced by both fire and the jack pine budworm. Volney (1988) noted that outbreaks of the jack pine budworm in the prairie provinces have increased in areal extent over time. He suggested that this is the result of improved control of forest fire which allows more jack pine stands to reach the older ages at which they are most susceptible to the insect. Nealis (1995) suggested that the tree mortality resulting from defoliation contributes to fire in affected jack pine stands by producing gaps in the canopy that expose the forest floor and its litter layer to increased direct sunlight and air circulation. The consequent drying probably promotes ground fires which cause the serotinous cones of jack pine to open and deposit their seed on an exposed mineral bed while simultaneously burning back competing tree species (which are less tolerant of ground fire). This scenario concludes with jack pine’s successful regeneration and retention of the site.

- Interactions with other disturbance agents: tree pathogens

Although insect defoliators are generally regarded as the most important group of biotic disturbance agents in Canada’s boreal forest, disease-causing tree pathogens also play an important role (Table 1). Tree pathogens are important in stand development, primarily by eliminating unfit individuals from the over-story, and thus creating openings where new species can gain a foothold. This process is usually less dramatic than the disturbances caused by the major insect defoliators, and as such, receives little attention. Tree pathogens usually cause impacts at the stand level, but occasionally they also affect forests at broader scales. Diseases caused by root rots such as Armillaria spp. and Tomentosus (Inonotus tomentosus) are chronic problems in older stands of both conifers and hardwoods in the boreal forest. These diseases do not cause extensive damage but kill individual trees, or pockets of trees, and cause gaps in the canopy. Such diseases are often most active after prolonged insect defoliation or drought has weakened the trees. In other cases (e.g., hypoxylon canker [Entoleuca mammata] of aspen) insect vectors are crucial to the dispersal of the pathogen (Ostry and Anderson, 1998). Although diseases are less evident than fire or insects as causes of major forest disturbances, they influence the forest landscape by contributing to tree mortality in unfit individuals and regenerating material in natural ecosystems (Castello et al., 1995). For instance, an exotic tree pathogen, white pine blister rust (Cronartium ribicola), has changed the forest landscape by affecting the distribution and abundance of mature eastern white pine (Castello et al., 1995). This is particularly true in the southern portion of the boreal region where the
disease has the greatest impact because of the regional climate (Gross, 1985). In these areas the pathogen kills younger white pine and makes regeneration difficult after harvest, reducing the white pine component of the forest.

- **Interactions with other disturbance agents: extreme weather**

  Next to wildfire, the major abiotic disturbances of the boreal forest involve various types of extreme weather (Weber and Flannigan, 1997). Drought has often been recorded and damage is most noticeable on shallow sites. Drought stress is directly harmful to forest vegetation but more often acts in concert with secondary organisms to cause tree mortality. Drought conditions can also increase the level of stress to which defoliated trees are subjected during insect outbreaks and can result in higher than normal tree mortality. For instance, while drought does not directly predispose jack pine to insect defoliation, drought conditions stimulate flowering on jack pine and this, in turn, increases the survival of jack pine budworm (Nealis and Lomic, 1994), and hence the likelihood of damage during an outbreak (Volney, 1988). There is also evidence suggesting that spruce budworm reproductivity (Sanders et al., 1978) and survival (Lucuk, 1984) increase directly as a result of the warmer and drier conditions of drought (Mattson and Haack, 1987). Indirect effects are also important for the spruce budworm. At high temperatures the vulnerable larval stages can escape many natural enemies because: (a) the larvae develop faster than at normal temperatures (Lysyk, 1989) and thus reduce the duration of their exposure; and (b) they develop more quickly at high temperatures than do many of their natural enemies (Fleming and Candau, 1998).

  Wind-throw, caused by strong surface winds which can uproot extensive areas of forest, is a common feature of boreal forests and plays an important role in determining their structure (Flannigan et al., 1989). Wind-throw is often reported in various parts of the boreal and differs greatly in extent. Because the sudden appearance of many uprooted trees can greatly accelerate fuel accumulation, fire hazard often increases after wind-throw occurs (Flannigan et al., 1989). Ice-storms, late spring frosts, and floods are other kinds of extreme weather which can affect successional pathways in the boreal forest.

**CLIMATE CHANGE EFFECTS ON INSECT DISTURBANCE REGIMES**

Atmospheric CO₂ levels are already about 25% greater than they were at the start of the industrial revolution and may more than double by the end of the next century at present rates of increase (Siegenthaler and Sarmiento, 1993). Research indicates that elevated atmospheric CO₂ concentrations can affect herbivorous insects in terms of their chemical
communication systems (Stange and Wong, 1993; Stange, 1997) and the quality of the plant food they acquire from their host trees (Lindroth et al., 1997, Williams et al. 1997, 1998). The magnitude of the food quality effect, and even whether the effect is beneficial or detrimental to the insect, seems to depend on soil nutrient availability (Kinney et al., 1997) and the particular insect and tree species (Awmack et al., 1997; Lindroth and Kinney, 1998; Lindroth et al., 1993), or even the life stages of those species (Williams et al., 1998), that are involved. In a number of cases, elevated CO₂ had no apparent effect (Awmack et al., 1997; Docherty et al., 1997). The fact that none of these experiments studied the net effects of simultaneous increases in temperature and CO₂ adds to the difficulties in generalizing how herbivorous insect populations will respond to elevated CO₂ in a changed climate.

Kirschbaum and Fishlin (1996) summarize the most plausible scenarios for the changes in climate that Canada's boreal forests are likely to experience up to 2050. In general, temperature increases of 1-2 and 1-3 °C in the summer and winter, respectively; regional changes in annual precipitation, usually of about ±20%; and drier soils as a result of 2-8 mm less water. Weber and Flannigan (1997) emphasize that these generalities hide sharp regional differences that can be expected: reduced frequency of drought in the southeastern boreal, warmer and longer growing seasons and much milder winters from western Ontario westward.

These changes in climate, and the accompanying CO₂ enrichment, may affect a given insect herbivore population directly through its per capita growth rate or indirectly through interactions and feedbacks with other species and abiotic components of the environment. In addition, although climate will probably directly affect the population's survival and fecundity, competitive interactions among individuals of the same species and trophic interactions with other species in the food-web will modify the degree to which these climate-induced effects are realized as changes in the population's net per capita growth rate (Kingsolver, 1989). Competition between individuals during outbreaks of boreal forest insect species such as the spruce budworm, however, often seems to have little impact except among feeding larvae at very high densities (e.g., Sanders, 1991). Therefore, any damping of the degree to which climate affects the growth rate of these populations presumably comes mainly from indirect effects such as those associated with trophic interactions (Fleming, 1996). In the past the net result of these indirect effects for the spruce budworm has been a tendency for per capita growth rates to increase during warm, dry years (Wellington, 1948).

A Life Cycle Perspective: the Spruce Budworm

The life cycle provides a useful framework for exploring how climate change could affect individual insect species (Cammell and Knight, 1992; Landsberg and Smith, 1992). Because it is a native insect with a long
history of study (Morris, 1963), the spruce budworm provides a useful example of an insect from Canada's boreal forest. It has one generation per year. In mid-August, 2-3 weeks after the eggs are laid and most adult moths have died, the first instar larvae hatch and move to overwintering sites on the branches. They overwinter as a tiny second instar larva and resume activity in early May. They then pass through four more instars during which they feed heavily before pupating in late June. Mating, moth dispersal, and oviposition occur in July. The spruce budworm's potential for causing tree mortality and growth loss is due, in part, to its high fecundity (of about 170 eggs per female) and rapid growth rate. A mature sixth instar larva, which weighs about 100 mg (fresh weight) and is about 20-30 mm long, is roughly 1500 times larger than it was as a second instar larva just 6-9 weeks earlier.

Phenological relationships

In its life history, the spruce budworm, has synchronized its greatest nutritional demand with the time when developing, rather than mature, host plant foliage is most available. (This is typical of many herbivores, including close to 50% of forest insect pests [Martineau, 1984]). As balsam fir needles mature, their growth slows but photosynthesis continues, and the result is often increased leaf carbohydrate content relative to nitrogen concentration (Shaw and Little, 1977). Often the surplus carbon is stored as secondary metabolites (Bryant et al., 1983) which either through design (e.g., Rhoades and Cates, 1976; Haukioja, 1980), or accident (Tuomi et al., 1988), can impede herbivore. Moreover, because animal tissue typically requires nitrogen concentrations of 7-14% while plants provide only 0.5-4%, Mattson (1980) and White (1994) have suggested that dietary nitrogen can limit herbivore growth. Hence, developing plant tissue may offer the advantage to the herbivore of being low in fibre (which can limit digestibility), high in nitrogen (nutritional value), and low in secondary metabolites (defensive chemicals).

Foliage will probably develop faster in a warmer climate, and this should reduce the length of the time interval when many herbivores can find young foliage. Poikilothermic herbivores, however, will not need as much time for finding foliage because they feed more actively and also develop faster at higher temperatures. In fact, Fleming and Tatchell (1994) report field evidence that certain northern hemisphere insects have increased their development rates rather steadily from 1965 to 1990. Thus, whether the net advantage in faster development rates will lie with the plants or the insects will probably depend on the specifics of the particular plant-insect herbivore relationship under consideration. For the spruce budworm, simulation of its phenological development in comparison to that of its host tree's foliage suggests that the insect is well synchronized with white spruce (Volney and Cerezke, 1992). The results of a second simulation study suggest that the budworm is so well synchronized with balsam fir that
defoliation is largely unaffected by shifts in weather patterns (Régnière and You, 1991). Thus, the spruce budworm may well remain synchronized in its phenological development with that of the foliage of its host trees in a changing climate. On the other hand, increased CO₂ concentrations may allow host trees to accumulate secondary metabolites to the point where they inhibit herbivore on the leaves at a relatively earlier stage of development than they do now, and this may work against the spruce budworm (but see Lindroth and Kinney, 1998). In general, the net effect of CO₂ enrichment on experimental insect-tree interactions has depended on the species involved (Lindroth et al., 1993).

Of the current theories of budworm population dynamics, the most popular (Royama, 1992) claims that a 'complex' of numerically responding invertebrate natural enemies drives the budworm outbreak cycle, almost as though it were a classic predator-prey relationship. Miller and Renault (1976) found that the prevalence of particular natural enemy species that are part of this complex varies from region to region and from one phase of the budworm's outbreak cycle to another. Because many of these natural enemies will have alternate hosts and various other ecological and physiological constraints to their life cycles which are quite different from those of spruce budworm, there seems little reason to expect the natural enemy complex to be as closely synchronized phenologically with the spruce budworm as the budworm is with its host trees. Thus, some phenological de-synchronization of the spruce budworm with its natural enemies is likely as climate change progresses. The consequences are difficult to predict but the effects of natural enemies on the outbreak cycle could be substantially weakened (Hassell et al., 1993).

**Weather extremes**

Under climate change, North America's boreal forest, especially its most southwestern part, can expect generally drier conditions with an increased probability of heat waves and droughts (Hengeveld, 1995), and there are a number of reasons (see the discussion of drought in the section on 'Interactions with other disturbance agents: extreme weather,' above) why some insect pests may prosper in such a climate (e.g., Solbreck, 1991). Considering spruce budworm in particular, Mattson and Haack (1987) argue that synergistic interaction between drought induced changes in the insect's thermal environment and in host plant quality will permit budworm populations to enhance their survival and fecundity. These authors suggest that given sufficient increase in the insect's survival and fecundity, budworm populations will be able to 'escape' the regulation of natural enemies more easily and rise to outbreak levels more often. This change in insect outbreak patterns can also be expected to aggravate fire regimes.

The populations of a number of insect species fluctuate more violently near the northern edge than they do in the middle of their ranges.
(Thomas et al., 1994). Whittaker and Tribe (1998) attribute this to an increasing importance of the density independent factors (e.g., climate) relative to the density dependent factors (e.g., natural enemies) that affect population dynamics as one moves from mid-range towards the species boundary. This may also be the case with the spruce budworm. For as long as records have been kept, the white spruce forests of western Canada have endured chronic spruce budworm outbreaks. Because the end of these outbreaks is associated with late spring frosts, it is thought that these frosts may contribute to the abrupt collapse of spruce budworm populations on a regional scale (Volney, 1996). The concern is that, as the climate warms, late spring frosts will become less frequent, and as a result, spruce budworm outbreaks will last even longer (Fleming and Volney, 1995).

---

**Natural selection**

There is strong evidence that natural selection continues to 'tune' insect populations to changing environments (Price, 1987, p. 288-289; Stone and Sunnucks, 1993). Many insect species will already have some genotypes preadapted to climate change because of their immense populations. The potential size of spruce populations during outbreak can be estimated from three observations: 'low density' populations have approximately 10 fourth instar larvae/m² (Crawford and Jennings 1989), population densities typically increase about a thousand-fold during outbreaks (Royama, 1992), and the area within which heavy infestation occurs during an outbreak may extend over as much as 0.72 million km² (Hardy et al., 1986). Even if one adopts the conservative estimate that only 0.01% of this area is heavily infested, and ignores other areas which may be moderately infested to not infested, multiplication shows that outbreak populations conceivably can contain as many as $7.2 \times 10^{11}$ insects! When such huge population sizes are considered in terms of mutation rates typical for insects ($10^{-5}$ to $10^{-4}$ [Sager and Ryan 1961]), it is clear that millions of rare genotypes will be produced each generation. Hence, even if all common genotypes, and the vast majority of rare genotypes, prove to be poorly adapted to changes in their ecosystems as the climate warms, by force of numbers alone it is clear that at least a few of these rare genotypes are bound to be 'preadapted' to their new, warmer environment.

The spruce budworm has generally exhibited little geographic genetic variation except for small differences between populations from the eastern and western extremes. This conclusion is based on analyses of mitochondrial DNA (Sperling and Hickey, 1994), isozyme patterns (Stock and Castrovillo, 1981; Harvey, 1983a,b, 1985), and tolerance to insecticides derived from the soil bacterium *Bacillus thuringiensis* (van Frankenhuyzen et al., 1995). The reason for this is presumably extensive gene flow, a consequence of the strong dispersal capabilities of the adult moths, and the weak selection pressure in the case of *B. thuringiensis* (*Bt*) tolerance, a consequence of the extremely limited use in space and time of such
insecticides against the spruce budworm in most of its range. On the other hand, van Frankenhuyzen et al. (1995) found evidence of 'preadaptation' (in Bt tolerance) within populations. They concluded that much of the phenotypic variation in Bt tolerance has a genetic basis and is therefore subject to natural selection if selection pressures become large enough. Because of its much greater spatial extent, which easily exceeds the scales of genetic mixing through moth dispersal, and because of its continuity, forecasts suggest that climate change has the potential to be a considerably stronger selective force than have historical Bt applications.

More common genotypes are also subject to natural selection. For instance, some species with large ranges may be composites of regionally adapted populations (Ayres and Scriber, 1994) so common genotypes in the warmer areas may be able to successfully establish in the cooler areas as the climate warms. Harvey (1983a,b) provides an example from Canada’s the boreal forests. Although he found little genetic variation in spruce budworm populations which had a geographic basis, he did find a genetically-based cline in fecundity and egg weight which he attributed to an adaptation to winter conditions. Females from northern sites tend to lay fewer (150 versus 250 per 100mg moth) but larger (0.22 versus 0.16 mg) eggs than females from southern sites. In the north the larger egg lets the young spruce budworm store enough energy to survive the long winters (Harvey, 1985). If climate warming shortens northern winters, however, one can expect selection in the north gradually to favor the 67% fecundity advantage of the southern genotypes, all else being equal. (One factor which is not equal is photoperiod [Taylor and Spalding, 1986], but the sensitivity of spruce budworm larvae over-wintering in the field to photoperiod is weak and lasts only until December [Régnière, 1990]). Hence, incidents of devastating mortality need not characterize the impact of natural selection in a changed climate. It may be subtle, non-lethal effects that cause many of the predicted shifts in the abundance and distribution of insect populations. Spectacular events of mass mortality, if they do occur, may be relatively trivial to the overall influence of natural selection in a warming climate.

The global circulation models (GCMs) are projecting a protracted trend to a warmer climate (Intergovernmental Panel on Climate Change, 1994). In general, such a trend is likely to allow many generations of directional selection, particularly for insects, since many have at least one generation per year, and this is especially true for those insects (e.g., aphids) which have many generations per year. (If the increased climatic variability that many GCMs are forecasting does occur, it will likely disrupt this process frequently for short periods but seems unlikely to forestall it over the long term). In this situation, those genotypes which are best adapted to warmer environments are expected to constitute an ever growing fraction of insect populations, and the populations are expected to become incrementally better adapted to warmer climates (Fleming, 1996).
adaptation of insect populations in general to a warmer climate could manifest itself in many ways, including increases in the rates and thresholds of phenological development (Fleming and Tatchell, 1994); increases in the number of generations per year (Yamamura and Kiritani, 1998); shifts in geographical (Sutherst et al., 1995) and also possibly host (Niemelä and Mattson, 1996; Tilmont et al., 1998) range; changes in morphology, physiology (Harvey, 1985) and reproductive strategy (Harrington et al., 1995); and possibly even speciation (Orr and Smith, 1998) or extinction (Coope, 1995). This expectation of genetic change has ramifications for closed environment experiments in which organisms of interest are instantaneously placed in conditions imitating future climates. The results may underrate a species’ capability to handle those projected climates because the typically very short duration of the experiments allows little opportunity for genetic changes to occur (Fleming and Volney, 1995).

**Effect of Shifting Climatic Zones**

A key issue is how the species currently assembled together as integral units (Holling, 1992) in different ecosystems will react as climatic zones shift poleward and to higher altitudes as the globe's climate warms. The life cycle perspective suggests that species (Hengeveld, 1990; Davis et al., 1998), or even certain age groups of a particular species (Fleming, 1996) may move north separately rather than as fully integrated components of an entire ecosystem which is moving in unison. In fact, Davis (1981) reports evidence that the conifer species which comprise today's boreal forest in North America migrated northwards separately in the Late Glacial. Separate movement under future climate warming could result from: (a) basic differences in the migratory potential of different tree (e.g., Solomon and Leemans, 1990; Gear and Huntley, 1991) and different insect (e.g., Elias, 1991; Stinner et al., 1989) species; (b) the appearance of 'green bridges' (plants which, once the climate warms, become hosts or provide favorable overwintering sites for exotic animals which previously were incapable of surviving the winter in that region [Porter et al., 1991]); and (c) the destabilization of resident ecosystems (Perry et al., 1990). It follows that chance, historical factors and threshold effects (which have been deduced in many theoretical forest-insect herbivore systems [e.g., Isaev and Khlebopros, 1979], and occasionally reported in North American forest ecosystems [e.g., Bergeron and Dubuc, 1989; Perry et al., 1989; MacDonald et al., 1993]) may determine the nature of the prevailing condition of an ecosystem as climate change progresses (Fleming, 1996). For instance, two sites encountering a similar climate could theoretically be occupied by quite different ecosystems solely because the species composition at each site was different when that climate arrived. Observations (e.g., Payette, 1993) and modelling studies (e.g., Shugart et al., 1980; Pastor and Post, 1988) suggest that such situations should not be unexpected in North America's forests.
The difficulty is that it is almost impossible to predict future species assemblages and the densities and trophic interactions of these species in a different climate. Hence, forecasts of how disturbance regimes might react to climate change invariably rest on an assumption of integrated ecosystem response (Fleming, 1996) at some level.

**Integrated Ecosystem Response Assumptions**

The most fundamental assumption of an integrated ecosystem response is that as climatic zones move poleward (and to higher altitudes), species assemblages, and the ecosystems in which they are embedded, will track suitable environmental conditions from one geographic region to another as complete integrated units (e.g., Farrow et al., 1993). The assumption implies that even if the geographic distribution of a herbivorous insect shifts in response to climate change, its impact (in terms of damage per unit area disturbed) should change relatively little because the species will remain embedded within the same ecosystems (and hence be subject to the same feedback structure and abiotic influences) as before. To some extent this assumption is a basis for various inductive approaches (reviewed by Sutherst et al., 1995) for predicting insect pest responses to climate change. Such approaches predict a species' (or ecosystem's) response to climate warming by matching projected future climates with certain key aspects of the climatic regime observed in the species' (or ecosystem's) present geographical distribution.

The assumption of an integrated ecosystem response to climate change is supported by the Quaternary fossil record which indicates little change in the composition of Coleopteran (beetle) assemblages during the last 2.4 million years (Coope, 1995). On the other hand, the inductive approaches based on this assumption are subject to criticism in two respects. First, such approaches can confuse realized and fundamental niches (Pacala and Hurtt, 1993). Second, in the absence of adequate data, such approaches usually ignore the effects that the predicted increases in ground level CO₂ and other changes in climate and atmospheric chemistry might have.

**Associating climatic patterns with disturbance regime characteristics**

The assumption of integrated ecosystem response can be applied at different levels. At the most fundamental level, statistical analysis of historical data from a certain region reveals associations between short term climatic patterns and disturbance regime characteristics such as frequency, duration, and extent. For example, colder weather was associated with shorter outbreaks of the forest tent caterpillar in central Ontario (Roland et al., 1998) and less frequent outbreaks of the European pine sawfly, *Neodiprion sertifer*, in Finland's boreal forest (Virtanen et al., 1996). Warm, dry summers were associated with outbreaks of a number of other
insect species in Canada's forests (eastern hemlock looper, *Lambdina fiscellaria fiscellaria* [Carroll et al., 1995]; mountain pine beetle, *Dendroctonus ponderosae* [Thomson and Shrimpton, 1984]; western spruce budworm, *Choristoneura occidentalis* [Thomson et al., 1984]; and the spruce budworm [Greenbank, 1963]). Assuming these same statistical associations hold as climate change progresses, one can infer how the characteristics for that disturbance regime might change in response to the climatic changes projected for the region. For instance, Volney and McCullough (1994) found that in north-western Wisconsin, where climatic variation is minor compared to variation in soil moisture, outbreaks of jackpine budworm occurred more frequently on dryer sites. Consequently Volney (1996) suggested "that if global change results in moisture deficit, the sites in Wisconsin that currently experience outbreaks every 10 years will switch to an outbreak frequency of 5 to 6 years currently experienced at the more xeric sites."

• Isolating forest and insect responses

Williams and Liebhold (1997) used a more complex form of the integrated ecosystem response assumption in forecasting how spruce budworm disturbance regimes in the north central and northeastern United States might respond to climate warming. First, they implicitly adopted the assumption in predicting that the distribution of the spruce-fir forests would shift northwards with "a general pattern of thinning" towards the southern end of their range as temperatures warmed. Then, assuming spruce-fir forests are a pre-requisite for defoliation by the spruce budworm, they analyzed the regional historical correlation between spruce budworm defoliation and climate within this forest type. Next, using the climate change projections within the forecasted spruce-fir distribution of the future, they concluded that defoliation would decline in prevalence in the north central and northeastern United States as temperatures increased. This approach rests on the premise that climate induced changes to the spruce budworm's disturbance regime have no effect on the future distribution of spruce-fir forests.

• Associating climatic patterns with disturbance mechanics

At a further level of complexity, the assumption of integrated ecosystem response is applied to dynamic and spatially explicit models of disturbance regimes. In broad terms, such models use probabilities of disturbance initiation, disturbance continuation, and spatial contagion to describe disturbance dynamics on large spatial scales. A rectangular grid of large blocks typically represents the forest in space, and each simulated year a block of forest in this grid which was not disturbed in the previous year will have a certain probability of becoming disturbed. This probability depends on two factors: first, on the conditions within the block (e.g., in terms of its type of vegetative cover, time since last disturbance, etc.) which determine the block's 'susceptibility' to disturbance once exposed (e.g.,
by moths invading from another block), and secondly, on the 'exposure' of the block to sources of disturbance (e.g., the proximity of already infested blocks). Once infested, a block can remain infested for another year and the probability of this occurring depends on the block conditions (including the duration of the infestation up to this point). As long as it is infested, a block also acts as a source of 'exposure' to neighboring uninfested blocks. This approach allows for the 'spread' and development of multi-year disturbances. When historical data are analyzed to determine the climate dependence of these probabilities, and one adopts an integrated ecosystem response assumption that such climate dependence will not itself be affected by climate change, then such models can provide scenarios of the spatial and temporal dimensions of the dynamic evolution of disturbance regimes as the climate changes.

A Scenario for the Spruce Budworm

Research which implicitly adopts the integrated ecosystem response assumption at its two simplest levels provides a consistent composite scenario of how spruce budworm disturbance regimes might react to climate change. In general, this research suggests that outbreaks can be expected to occur more often (Mattson and Haack, 1987) and last longer (Greenbank, 1963) in North America's boreal forests where the climate warms. These forests are expected to shift northwards, 'thinning out' near what is currently the southern edge of the spruce budworm's range, as the climate warms (Williams and Liebhold, 1997). Consequently, as this insect's host trees gradually 'thin out' near the southern edge of its current range, these latter authors expect shorter and less frequent outbreaks there.

The scenarios above are vague about how much more often and how much longer spruce budworm outbreaks are expected to occur. Long term trends in the total annual extent of all insect disturbances in Canada might provide an initial estimate since the spruce budworm alone accounts for over half of this total (Hall and Moody, 1994; Sterner and Davidson, 1982). Thus graphs composed from the aerial survey data (e.g., Kurz and Apps, 1996, Figure 14.2; Walker and Steffen, 1997, Figure 4) show peaks in the extent of all insect disturbances which are synchronized in their timing with those of the spruce budworm's outbreak cycle (e.g., Candau et al., 1998, Figure 2A). These graphs of total area disturbed by insects each year imply that this area has increased many times over since the 1920s. This implication, however, could be misleading. The virtual absence of any insect damage prior to 1938 seems to reflect the initiation of Canada's first large-scale aerial survey programs around that time (Hardy et al., 1986). The fact that the amplitude of the most recent (1978) peak is about twice the size of the next largest peak (1948) in these graphs may reflect the initiation and subsequent build up of aerial survey capabilities in many areas of the country from the late 1930s to the mid 1940s, largely in response to an extensive spruce budworm epidemic (Hardy et al., 1986).
Therefore, the aerial survey data alone are insufficient for determining long term trends in the total annual extent of all insect disturbances in Canada.

Implications for carbon budget analyses of Canada's boreal forests

This concern about the lack of early records of insect damage in the aerial survey data has additional ramifications. To initialize the forest age structure in 1920 in their carbon budget model, Kurz and Apps (1996) used these records and records of fire and harvesting disturbances to work backwards from 1970 inventory data. A more accurate approach to deriving historical insect damage might assume that spruce budworm represented about half of the total during outbreaks and that the timing (and perhaps even the extent and severity) of outbreaks before 1940 could be crudely estimated from analyses of tree ring data (e.g., Krause, 1996; Royama, 1992). While this approach should ultimately result in improved estimates of the 1920 forest age structure, it remains to be seen if such improvements will make any substantial difference to Kurz and Apps’ (1996) analysis of the carbon budget of Canada’s boreal forests.

Spruce budworm impact in a changed climate

Climate change is likely to affect the importance of the damage caused by insects as well as the nature of their disturbance regimes. For the spruce budworm this may be relevant both from an economic perspective and from its interaction with wildfire. Economically, many consider the spruce budworm to be the pre-eminent biotic disturbance agent of North America’s boreal forests, partly because it competes so effectively with industry for the forest resource. Some suspect, however, that the spruce budworm may have less economic impact in a warmer climate. An economic analysis of climate warming impacts on the U.S. forest sector (Mills and Haynes, 1995) suggests that gains in productivity (due to predicted changes in temperature and precipitation patterns, and due to increases in available carbon) could substantially increase the supply/demand ratio for wood products and thus limit prices. In addition, Kruger et al. (1998) argue that CO₂ enrichment might enhance the ability of some tree species to recover from insect attack. Under this scenario, the spruce budworm may cause less annual economic loss in the future than it does now, even if the annual volume lost were greater. But this is only one possible scenario: the assumption of gains in forest productivity is based on a study (McGuire and Joyce, 1995) which explicitly omitted any consideration of how vegetation distributions and disturbance regimes might respond to climate change.

On the other hand, spruce budworm disturbances could become more important in a warming climate because of an increasingly synergistic interaction with fire. In a study of spruce budworm-killed balsam fir, Stocks (1987) noted that the forest fire potential of such stands increases for
just a few years after an outbreak. He suggested that spruce budworm defoliation opens up the canopy and lets understory vegetation proliferate. The moist green layer of understory vegetation effectively prevents fire spread by isolating the dry surface fuels from the crown fuels. After about 5 years of crown breakage and windthrow, however, so much dead and down material has accumulated on the ground that the surface fuel can overcome the dampening effect of the understory vegetation. The potential for summer fires peaks between 5 and 8 years after stand mortality. After that, the potential for forest fires begins to gradually decline as the understory vegetation continues to proliferate and the dead and down surface fuel begins to decompose and absorb moisture.

In a warmer drier climate, especially during drought, this window of increased summer fire potential 5 to 8 years after stand mortality can be expected to widen. The layer of understory vegetation will likely grow more slowly and hold less moisture and thus be less effective at separating surface and crown fuels as stands are defoliated. In addition, the surface and crown fuels themselves will likely contain less moisture. Thus, it will likely take less than 5 years for substantial increases in summer fire potential to occur in spruce budworm killed stands in a warmer and drier climate. In such a climate, the summer fire potential can also be expected to remain high for longer because of the effects described above on the understory vegetation and because the dead and down surface fuel will likely decompose and absorb moisture more slowly.

As well as this expectation that budworm-killed stands are more likely to burn, there are two other factors which suggest that spruce budworm disturbances may promote wildfire in warmer, drier climates. First, in much of the boreal forest, budworm outbreaks currently occur over much greater spatial extents than do fires (Candau et al. 1998, Weber and Flannigan 1997), and second, as outlined above, the best current scenarios suggest that climate warming is likely to increase spruce budworm outbreak frequency in the boreal forest as a whole, and thus the availability of insect-killed stands. (In the very long term, however, increasing fire frequencies could work against the budworm [Bergeron and Dansereau, 1993]). These three factors, when considered together, suggest that spruce budworm disturbances may promote wildfire in warmer, drier climates. It seems likely that this promotion of wildfire could more than offset any reduction in the direct economic impacts of the spruce budworm, itself.

MANAGEMENT CONSIDERATIONS

Management of forest insect outbreaks is one aspect of the larger problem of total forest management. In this context, insect management considerations in Canada's boreal forests are focussed on two problems.
The first is how to manage insect disturbance regimes so as to maximize carbon storage within Canada's boreal forests. The second is how best to manage insect disturbance regimes in order to sustain the benefits currently gained from the forest resource in a future climate change environment. Responses to these problems involve both preparatory activities which anticipate the future and the development of reactive capacity to deal with the unforeseen surprises that are certain to arise as the climate changes. Because of the primitive state of our ability to predict how spruce budworm disturbance regimes will respond to climate change, it is premature to make specific recommendations for a suite of management actions. Consequently, only the general concepts behind some proposed management approaches are commented on below. Specific recommendations are made only in the context of work crucial to advancing our predictive ability.

**Carbon Storage**

Suppression of insect outbreaks is occasionally considered as one way to combat the tendency of insect disturbance regimes to limit the carbon sequestration capacity of Canada's boreal forests. The vast spatial scales involved (Candau et al., 1998), however, make broad-scale suppression prohibitively expensive and environmentally controversial using current conventional insecticides against the spruce budworm.

Using conventional insecticides to protect old growth stands, which store a disproportionate amount of carbon, or areas which have recently been afforested (or reforested) to sequester carbon has also been suggested. This approach must overcome public outcry and demonstrate durability of benefit. For instance, there is little gain in protecting an overmature old growth stand from insect attack only to see it blown down the following year by heavy winds. Nor is there any point in protecting a recently afforested or reforested area if the net greenhouse effect of all gases released in producing, transporting, and applying the insecticide exceeds the net greenhouse effect of the additional sequestration gained through protection.

Protection may also be feasible in conjunction with harvesting. Where harvest rotation lengths exceed the length of the natural disturbance cycle, whether the agent be fire or insect, carbon storage is enhanced by suppressing the disturbances and letting the forest reach the older ages at which it is harvested (Price et al., 1997). Ideally, the economic gains of the harvest alone would justify the expense of protection. A possible additional benefit is that some wood products have very long life-spans and thus further slow the release of carbon back to the atmosphere (Skog and Nicholson, 1998).

The encouragement of suitably pre-adapted non-host tree species in some selected areas is another option. This may involve aerial seeding or other means of planting on a large scale. Genetic improvement of the stock
may also be cost-effective. An unresolved issue is the trade-off implicit in any approach, be it large-scale planting or protection from insects and fire, which uses fossil fuels. Any short-term increase in the sequestration of atmospheric carbon by the forest comes at a cost of additional carbon imported into the modern biospheric system for the long term.

In summary, insect population suppression might possibly be useful for particular species in select areas under certain circumstances to protect stored carbon. The vast scales at which spruce budworm disturbance regimes operate, however, are liable to overwhelm any efforts to manage or alter their course.

**Insect Management for Sustainable Forest Benefits**

Climate change will likely transform the damage patterns caused by many insects and the resulting uncertainties directly affect a number of aspects of forest insect management. As the frequency and duration of outbreaks changes in response to climate change, it will become increasingly difficult to forecast where, and when, and how great the depletions will be. This will make pest hazard rating procedures dated and reduce the predictability in long-term planning for harvest queues and insect control.

In a changed climate, a few of what were once innocuous forest insects may thrive and suddenly become major disturbance agents. Similarly, there is no guarantee that all of today's major insect herbivores will remain significant in the new environment. It may be difficult to distinguish the relatively permanent changes in population density that such scenarios imply from long-term population cycles until long after the fact and this complicates the management of forests for ecological values such as biodiversity (Fleming and Candau, 1998). Changes in disturbance regimes which re-route successional pathways and produce rapid changes in forest landscapes are likely to disrupt certain wildlife species (Thompson et al., 1998) and aboriginal peoples following traditional lifestyles. Such changes may also lead to large unanticipated releases of carbon, especially in the less intensively managed areas of Canada's boreal forests.

The emergence of new insect disturbance regimes also introduces additional difficulties in forecasting future requirements for insect control products. Since such products typically take years to develop and are becoming increasingly target-specific to meet environmental requirements, some companies may become discouraged altogether and shift their research onto items with a more certain future demand. At the same time, demands for insect outbreak suppression may grow, particularly if the potential for wildfire increases further in stands after insect attack as a result of climate change. In that case, uncertainties in future insect damage patterns will magnify uncertainties in future fire regimes.
Research Directions

Other authors have previously proposed shifts in research strategies to gain better insight as to how forest ecosystems in general will respond to climate change and what the consequences of this response will be. These proposals include suggestions for improving the accuracy of predictive models (Kirschbaum and Fishlin, 1996), for improving estimates of the mitigation potential of forestry practices (Brown, 1996), and for improving estimates of the socioeconomic consequences of the response of forest ecosystems to climate change.

A number of key information gaps also limit confidence in forecasts of how insect disturbance regimes in particular will respond to climatic change in Canada's boreal forests, and what the consequences of this response will be. These include the effect of insect outbreaks in a climate change environment on: (a) other disturbance regimes (i.e., those involving different insects or altogether different agents, such as fire), and the reciprocal effects; (b) post disturbance successional pathways and tree growth and carbon sequestration rates; and (c) the rates of net forest decomposition, respiration, and carbon transfer among the soil carbon pools. An ongoing challenge will be to scale-up the innumerable effects of increased CO₂ and temperature on the physiology and ecology of individual insects at various stages of their life cycle beyond the level of population dynamics and to the even larger scales of disturbance regimes.

Another challenge is to wean the forecasting of how insect disturbance regimes might respond to climatic change away from its reliance on the assumption of an integrated ecosystem response (discussed in detail above). At the moment, this seems best served by using a suite of modeling approaches each of which use this assumption in a different way and thus provides a different perspective.

The potential importance of natural selection needs more serious attention. Ricklefs (1989) suggests that genetic changes driven by quantitative selection on populations can affect the structure and diversity of local species assemblages within roughly 7-70 generations. Since many insects can go through seven or more generations a year (e.g., Harrington et al., 1995), natural selection should be considered in developing forecasts of insect responses to climate change. Furthermore, since natural selection in a warmer climate may well increase the number of generations per year (Yamamura and Kiritani, 1998), there is the potential for a positive feedback loop with natural selection speeding further natural selection. For insects such as the spruce budworm, which have just one generation a year and seem unlikely to increase this number, natural selection could still have important, although indirect effects. Royama (1992) suggests that it is a complex of disease organisms which drive the budworm's outbreak cycle. Since many insect pathogens can have many generations each year, they are
subject to the forces of natural selection on short time scales. Hence, through changes to the natural enemy complex, natural selection could bring about changes to the budworm's outbreak cycle and disturbance regime.

Finally, the poor resolution of GCMs and the uncertainties inherent in their performance at regional scales (Smith and Pitts, 1997) present a major difficulty to acquiring suitable scenarios of how future climates will develop. These scenarios will provide the climate input data for the models used to forecast future insect and other disturbance regimes. Because the models will probably be quite sensitive to variations in these scenarios (for reasons discussed above), it is important to improve the realism of these scenarios.

CONCLUSION

Climate change's greatest impact on ecosystem succession and functioning in Canada's boreal forest will likely be brought about by changes in disturbance regimes such as those associated with insect outbreaks and wildfire, and the resulting uncertainties directly affect depletion forecasts, hazard rating procedures, and long-term planning for harvest queues and disturbance control requirements. One practical approach to trying to understand how such changes might develop is to focus on the insect life cycle. A second approach is to adopt the integrated ecosystem response assumption that as climatic zones move poleward (and to higher altitudes), species assemblages, and the ecosystems in which they are embedded, will track suitable environmental conditions from one geographic region to another as complete integrated units. In strict terms, this assumption will almost certainly be violated, but it may provide a useful approximation, especially in the near future while the extent of climate change remains relatively small. This second approach is not necessarily exclusive of the first, but is more immediately practical. Published scenarios which employ this second approach generally suggest that outbreaks of boreal forest insects will last longer and occur more frequently where the climate warms. This does not necessarily mean that the direct economic impact of these insects will increase. On the other hand, indirect effects such as the promotion of wildfire may become extremely important in the warmer, drier climates of the future so uncertainties in future damage patterns of some insects magnify uncertainties in future fire regimes.

A number of questions remain about the role of insect disturbance regimes in the carbon cycle of Canada's boreal forests. The large scale dynamics of spruce budworm outbreaks are poorly understood, but the coupling of geographic information systems with modern computer-based
approaches to conducting spatio-temporal analyses (e.g., Candau et al., 1998) show great promise in this regard. Detailed statistical analysis of historical data is also needed to quantify the large-scale interaction between fire and spruce budworm. Augmentation of these basic analyses of large scale spatio-temporal dynamics of the spruce budworm and of the fire-spruce budworm interaction by including climate data is an obvious next step to identifying important climatic influences. The expectation is that ultimately such analyses will provide scenarios of the spatial and temporal dimensions of the dynamic evolution of spruce budworm disturbance regimes and their interaction with fire as the climate changes. A related research direction involves the analyses of the carbon budget of Canada's boreal forest by using tree ring data to better estimate the annual extent of insect disturbances back to 1920 and beyond. Currently these estimates are based almost entirely on data from survey programs which generally did not become fully operational until the 1940s. Such improvements are important because they reduce biases in the carbon budget analyses and in any apparent long term trends in the extensiveness of insect disturbances. Such improvements to the long term data on spruce budworm disturbances would also benefit the development of models describing the spatio-temporal dynamics of such disturbances and their interaction with fire. Finally, experimental measurement of the effect of disturbance (fire, spruce budworm, and harvesting) on ecosystem carbon budgets is badly needed. One approach might involve placing eddy flux towers on sites experiencing different kinds of disturbance or different times since disturbance to compare CO$_2$ and water vapor fluxes.

Management of forest insect outbreaks is embedded in the larger task of total forest management. In this context, two key goals for the management of insect disturbance regimes within Canada's boreal forests in a future climate change environment are to maximize carbon storage and to sustain the benefits currently derived from those forests. A variety of proposed approaches towards these goals are discussed in terms of their feasibility and likely effectiveness. These approaches involve both preparatory activities which anticipate the future and the development of reactive capacity to deal with the unforeseen surprises that are certain to arise as the climate changes. An unresolved issue is the trade-off implicit in any approach, be it large-scale planting or protection from insects and fire, which uses fossil fuels: any short-term increase in the sequestration of atmospheric carbon by the forest comes at a cost of additional carbon imported into the modern biospheric system for the long term.

**ACKNOWLEDGMENTS:** Useful discussion with Jean-Noel Candau, Buzz Holling, Tony Hopkin, Ted Munn, Mark Tatchell, Jan Volney, and Ian Woiwod over the years have helped in formulating some of the ideas expressed above. I also thank an anonymous reviewer for helpful criticism.
of an earlier draft and Kai Chuah, Christine Leger, Charmane Quinn, and David Rootman for helping me see it all more clearly.

REFERENCES


© 2000 World Resource Review. All rights reserved.


Farrow, R.A., G. McDonald and P.D. Stable, Potential impact of rapid climate change through the greenhouse effect on the pests of pastures in southeast Australia, in E.S. Delfosse (ed.), *Pests of pastures: Weed, invertebrate and disease pests of Australian sheep pastures*, pp. 142-151, CSIRO, Melbourne, Australia (1993).


© 2000 World Resource Review. All rights reserved.


Harvey, G.T., A geographic cline in egg weights in Choristoneura fumiferana (Lepidoptera: Tortricidae) and its significance in population dynamics, *Canadian Entomologist*, 115, 1103-1108 (1983a).

Harvey, G.T., Environmental and genetic effects on mean egg weight in spruce budworm (Lepidoptera: Tortricidae), *Canadian Entomologist*, 115, 1109-1117 (1983b).

Harvey, G.T., Egg weight as a factor in the overwintering survival of spruce budworm (Lepidoptera: Tortricidae) larvae, *Canadian Entomologist*, 117, 1451-1461 (1985).


Stange, G., Effects of changes in atmospheric carbon dioxide on the location of hosts by the moth, *Cactoblastis cactorum*, *Oecologia*, 110, 539-545 (1997).


van Frankenhuyzen, K., C.W. Nystrom and B.E. Tabashnik, Variation in tolerance to *Bacillus thuringiensis* among and within populations of the spruce budworm (Lepidoptera: Tortricidae) in Ontario, *J. Econ. Entomol.*, 88, 97-105 (1995).


