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Global Climate Change: Disturbance Regimes and Biospheric Feedbacks of Temperate and Boreal Forests

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General circulation models that predict large-scale climatic changes at present account neither for the effects of these changes on terrestrial and aquatic biota nor for feedbacks associated with the effects. This chapter reviews some of the feedback mechanisms through which temperate and boreal forest ecosystems could affect future climatic changes. The effects of changes in forest distribution and changes in growth and decomposition rates are addressed by others in this volume. This chapter emphasizes the role of disturbance regimes and their effects on forest structure and function. We show that changes in climatic conditions have affected forest disturbance regimes in the past and that these changes in disturbance regimes must be considered when assessing biospheric feedbacks to future climate changes. The chapter first identifies indicators of forest ecosystems to be evaluated when assessing feedback potentials. The disturbance regimes in the last 60 years in Canadian forests are reviewed and the potential feedback to climatic changes is discussed. Mitigation options available through forest management and protection are addressed briefly.

FEEDBACK MECHANISMS

To address the issue of biospheric feedbacks to climate change through disturbance regimes, three questions must be answered: Do changes in disturbance regimes affect ecosystem structure and function? Do changes in climate result in changes in disturbance regimes? Will changes in ecosystem structure and function lead to climatic feedbacks?

Terrestrial ecosystems play an important role in the global and regional cycling of carbon, water, and nutrients and interact with climate through these cycles and through albedo, exchange of energy, and other mechanisms. All of these processes are affected

by changes in the structure and function of terrestrial ecosystems. If the changes in ecosystem structure and function are brought about by changes in climate (or environmental change in general) and lead to further changes in climate, positive feedback is said to exist. Negative feedback results from changes in structure and function that reduce the climatic effects that initiated the ecosystem changes.

Forest ecosystems are major reservoirs of carbon and cover a large proportion of the land surface. In this chapter, we focus on feedback mechanisms of forest ecosystems through effects on the carbon cycle, but we emphasize that other feedback mechanisms also exist, as outlined by Bonan et al. (1992).

The effects of forest structure on the carbon cycle can be summarized through four indicators: forest area, forest age class distribution, species composition, and ecosystem carbon density. Changes in forest function (i.e., growth rate, decomposition rate, and other processes) also must considered. These processes affect and are affected by forest structure, and this discussion emphasizes forest structure.

Boreal and temperate forest ecosystems are adapted to frequent stand-replacing disturbances, such as wildfires and insect-induced stand mortality. The spatial heterogeneity and mix of age classes in forest ecosystems reflect past disturbance regimes. The effect of fire frequency on the forest age class structure is well established (Van Wagner 1978; Yarie 1981; Johnson and Larson 1991). Fire cycles (i.e., the average interval between fires at any given point; Van Wagner 1978) in boreal and temperate forests range from a few decades to a few centuries. Estimates of presuppression fire cycles in the boreal forest are 50–200 years and increase from the south to the north and from west to east (Rowe 1983; Bonan and Shugart 1989; Payette 1992). Fire cycles in cold and wet northern ecosystems can be 1000 years and longer (Payette et al. 1989).

Four aspects of disturbances and postdisturbance ecosystem recovery are important: the annual rate of disturbance, the type of disturbance, the rate of postdisturbance forest regeneration, and the rate of biomass and ecosystem carbon accumulation.

Rate of Disturbance

The annual rate of disturbance has a large effect on the forest age class structure. An increase in disturbance rates shifts the forest age class structure to the left, i.e., the proportion of young stands increases. Shifts in age class structures toward younger age classes result in reduced carbon storage because the average biomass decreases and because reductions in the average time between disturbances can affect coarse woody debris and detritus carbon pools (Harmon et al. 1990). A reduction in the length of the fire-free interval also affects species composition, favoring early successional and pioneer species.

Type of Disturbance

The different types of disturbance have significant effects on carbon storage and cycling. All disturbances transfer biomass carbon to soil and detritus carbon pools, where it decomposes in the years following the disturbance. The proportion of biomass carbon transferred to soil and detritus carbon pools is greatest for insect-induced stand mortality, intermediate for wildfires (some release to the atmosphere), and smallest for harvest-

ing (transfer to the forest product sector). These differences in carbon transfer will affect future rates of carbon (and nutrient) cycling and can affect other ecosystem characteristics, such as soil temperatures and water-holding capacity.

Rate of Regeneration

The disturbances discussed here typically are stand replacing. The rate of regeneration and the associated regeneration delay are therefore of great importance to forest structure and function. Regeneration delay refers to a period of time after the disturbance during which the site is occupied by short-lived herbaceous or shrubby vegetation that is not accumulating significant amounts of carbon. The length of the regeneration delay depends on many factors, such as climatic conditions for seedling establishment, and on the presence of seed sources, seed banks, and bud banks. All of these could be significantly affected by climatic change. In some ecotones (e.g., the northern tree line) seed production and regeneration success are temperature limited, and increasing temperatures could reduce regeneration delays. Under present conditions, regeneration failure after (infrequent) major fires occurs in forest tundra ecotones in northern Quebec, resulting in gradual deforestation at the northern tree line (Payette and Gagnon 1985). In other ecotones, such as parts of the southern boreal forest, seedling establishment and survival are limited by soil moisture deficits, and greater evaporative stress associated with climatic changes will increase regeneration delays and favor the northward expansion of grassland (Zoltai et al. 1991).

Boreal forest species are adapted to frequent fires, and some produce serotinous cones that require high temperatures to release their seeds. Boreal tree species require several decades to start seed production (Nikolov and Helmisaari 1992). Regeneration failure could increase if an increased fire frequency results in a fire return interval that is shorter than the time required by boreal trees to reach reproductive age (Heinselman 1973). This would favor a shift in species composition toward species whose seeds are dispersed over longer distances by wind or animals or those species that regenerate vegetatively (Rowe 1983). Increased fire frequency could therefore also increase regeneration delay.

The length of the regeneration delay is of significance to biospheric feedbacks because it reduces the average amount of carbon stored in forest ecosystems in two ways. The area with delayed regeneration has less biomass carbon storage, thus reducing the regional carbon storage. Furthermore, the detritus and soil carbon pools could decrease during the regeneration period because decomposition proceeds while detritus inputs from biomass carbon pools are reduced.

Rate of Carbon Accumulation

Carbon is accumulating in two major pools: the living biomass pool and the soil and detritus carbon pool. In many boreal and temperate forests, biomass carbon pools increase in the first decades after disturbance and decrease in late stand developmental stages (Whynot and Penner 1990; Alban and Perala 1992). There is considerable uncertainty about the dynamics of the soil and detritus carbon pools, and it is not clear whether the reduction in biomass carbon pools in old age classes merely represents a transfer to detritus pools or whether it results in a decrease of total ecosystem carbon.
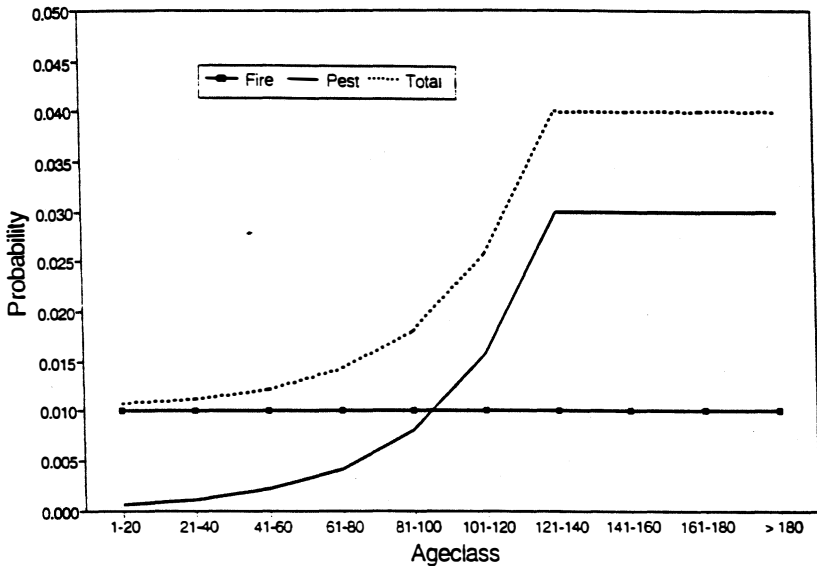
Figure 6.1. Probability of fire and pest disturbances as a function of forest age as used in the simulation model.

BIOSPHERIC FEEDBACKS THROUGH SHIFTS IN FOREST AGE CLASS DISTRIBUTION

The complex effects of disturbance regimes, age class structures, regeneration delays, and carbon accumulation rates on regional carbon storage and biospheric feedbacks are demonstrated through a simple model. The model represents 10,000 forest stands whose probability of disturbance is a function of stand age. It simulates the effects of two disturbance regimes and regeneration delays on forest age class structures. It assumes that the probability (p) of a stand's being affected by the first disturbance is constant with stand age (Figure 6.1, Fire). The probability of the second disturbance increases with stand age (Figure 6.1, Pest). In four sensitivity analysis runs, the fire disturbance rate and the length of the regeneration delay are modified (Table 6.1), whereas the probability of pest disturbance is not altered. After disturbance, the stands experience a regeneration delay (5 years in cases 1 and 3, 10 years in cases 2 and 4). Running the model to equilibrium with the parameters of case 1 generates the age class distribution shown in Figure 6.2 (open bars). Increasing the fire disturbance regime from $p = 0.01$ to $p = 0.02$ and the regeneration delay from 5 to 10 years (case 4) generates the second age class distribution (Figure 6.2, shaded bars). The increase in disturbance regimes shifts the age class structure to the left, i.e., it decreases the average age of the forest.

The forest, in this simple example, has a single biomass accumulation curve. Regional biomass carbon storage is the product of biomass carbon and the area in each age class. Table 6.1 summarizes the results of four sensitivity analysis runs that demonstrate the change in regional biomass carbon storage resulting from changes in disturbance regimes and regeneration delay. The combined increases in the probability of fire and the length of the regeneration delay reduce regional biomass carbon storage by 28%.

Table 6.1. Sensitivity Analysis of a Simple Forest Dynamics Model

Case	Fire probability	Regeneration delay (years)	Regional biomass carbon (percent of case 1)
1. Base case	0.01	5	100
2. More regeneration delay	0.01	10	94
3. More disturbances	0.02	5	78
4. No. 2 and No. 3	0.02	10	72
5. 10% more biomass carbon	0.01	5	110
6. No. 5 and No. 2	0.01	10	103
7. No. 5 and No. 3	0.02	5	86
8. No. 5 and No. 4	0.02	10	79

Note: Age class structure (cases 1 and 4) and biomass-over-age curve are as shown in Figure 6.2.

Increasing biomass storage in each age class by 10%, e.g., as a result of better growing conditions or CO_2 fertilization (Bazzaz 1990), decreases the reduction in regional biomass carbon storage (cases 5–8) but has less effect than the increase in disturbance regimes (cases 7 and 8). Given the age class structure of case 4, biomass carbon storage in each age class would have to increase by 39% to obtain the regional biomass carbon storage of case 1. The conclusions of this analysis are comparable with the effects on regional biomass carbon storage of reducing forest rotation length during the transition from natural to managed forests (Cooper 1983; Dewar 1991).
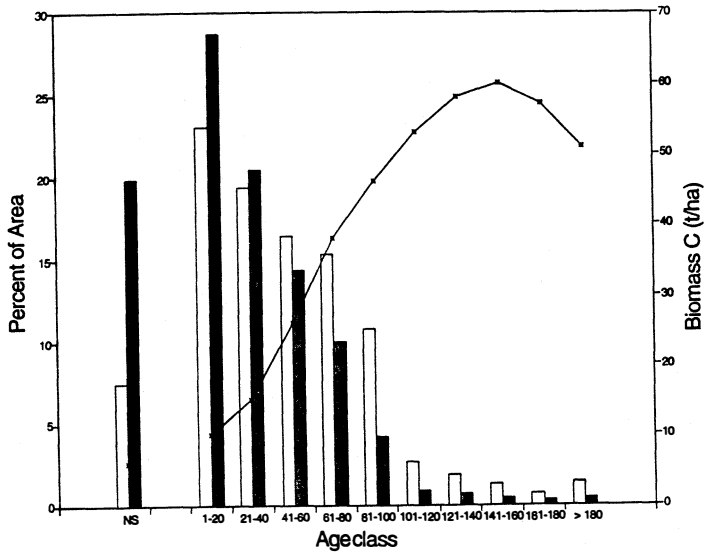

Figure 6.2. Percentage of total area (left axis) and biomass carbon density (C ha^{-1}, right axis) in 20-year age classes of a hypothetical forest. NS represents a nonstocked age class (regeneration delay). Open bars represent area for case 1 in Table 6.1, shaded bars represent case 4.
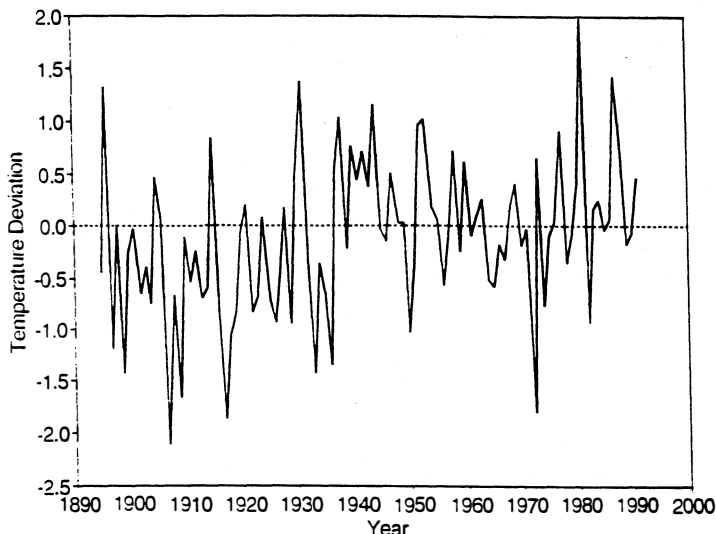
Figure 6.3. Canadian national temperature trend expressed as temperature departures (°C) from the average of the period 1951–1980. (Redrawn from Gullet and Skinner 1992.)

Our analysis ignores the contribution of soil and detritus carbon pools to regional carbon storage. The shift of forest age classes toward a younger age increases the proportion of the area in which decomposition rates are accelerated and detritus inputs reduced, thus decreasing soil and detritus carbon storage. The shift will also decrease the input of coarse woody debris during the stand breakup phases, reducing carbon accumulation in detritus carbon pools. Higher rates of disturbances (other than harvesting) accelerate the transfer of biomass carbon to soil and detritus carbon pools, thus offsetting some of the impacts of changes in age class structure on soil and detritus carbon storage (Kurz and Apps 1994).

HISTORIC EVIDENCE OF CLIMATE IMPACTS ON DISTURBANCE REGIMES

The long-term temperature record (1895–1991) in Canada shows three phases: a warming phase from the late 1890s to the 1940s, followed by a cooling period into the 1970s and a return to warming through the 1980s (Figure 6.3; Gullet and Skinner 1992). The overall warming trend of 1.1°C for the period is statistically significant.

The Canadian Forest Fire Weather Index (FWI) System (Van Wagner 1987), which is used throughout Canada, integrates the effects of temperature, precipitation, wind speed, and relative humidity on the moisture content of forest fuels to predict fire danger. The final component index of the FWI System, the Fire Weather Index itself, is correlated with the monthly area burned in Canadian provinces (Harrington et al. 1983). Long sequences of days without rain strongly influence the monthly provincial area burned in Canada (Flannigan and Harrington 1988). Correlations between the annual temperature deviation and the area annually burned in Canada are statistically significant only for individual regions but not for the entire country. Temperature data alone only account

for a portion of the temporal variation, but detailed long-term precipitation records are not as readily available as temperature data.

Interpretation of the historic relationship between area burned and climatic conditions in Canada is confounded by the impact of organized forest fire protection, which began in the early 1920s. Use of forests for both industrial and recreational purposes has increased steadily over the past seven decades, resulting in significantly more ignition sources and fires. The effect has been somewhat offset by the development of increasingly sophisticated fire protection capability, but the relative impact of both developments on the total area burned is difficult to assess. In addition, the general forest fire management strategy in Canada is to provide intensive protection for high-value recreational and industrial areas, while applying a form of "modified suppression" in remote areas where fire is often allowed to burn naturally. This approach also serves to confound the statistics. Although it is impossible to establish with any accuracy the reduction in areas burned resulting from forest fire protection, it is clear that, at least in the southern parts of Canada, fire control efforts have reduced the area annually burned (Barney and Stocks 1983) and may have contributed to a shift in forest age class structure toward older ages (Blais 1983).

Forest fire protection can have a significant impact on forest age class structures, and many studies have demonstrated that the youngest age classes in regional forest inventories have much less area than older age classes (Heinselman 1973; Yarie 1981; Clark 1990). This deviation from the negative exponential decline in the age class structure (e.g., Figure 6.2) can be achieved through a reduction of the area annually disturbed or through a significant increase in regeneration failure that leads to a reclassification of previously forested land as nonstocked land. None of the studies cited previously addresses this latter possibility and all interpret the shift in age class structure as the result of successful fire protection measures.

Forest harvesting, in particular the clear-cut logging that is predominantly practiced in Canada, has introduced a new type of disturbance. Does it offset the reductions in areas annually disturbed that result from fire protection? Figure 6.4 summarizes the areas burned (10-year running average) and harvested for the period 1930–1989. National harvest area statistics are readily available only for the period after 1975, but harvest volume statistics have been recorded since the late 1920s. In Figure 6.4, the area harvested is approximated from the harvest volume to harvest area ratio established from the statistics for 1975—1990. This approach may lead to an error in the estimate of area harvested in the early part of this century because of changes in harvesting methods and efficiencies (underestimation of area) and the predominant harvesting of old-growth forests with high volumes (overestimation of area).

Figure 6.4 indicates that for the period 1930–1979 the area annually disturbed through fire and harvesting has averaged circa 1.63 million ha yr^{-1}, and that it has increased to circa 3.46 million ha yr^{-1} for the period 1980–1989, largely because of dramatic increases in the area annually burned. The figure also suggests that for the period 1930–1979 the reduction through climatic effects or fire suppression in areas annually burned offsets the increase in areas harvested, resulting in little change in the total area disturbed by fire and harvesting.

The impacts of insect-induced stand mortality on forest dynamics are more difficult to assess because of the nature of insect disturbances. Many forest insects cause growth
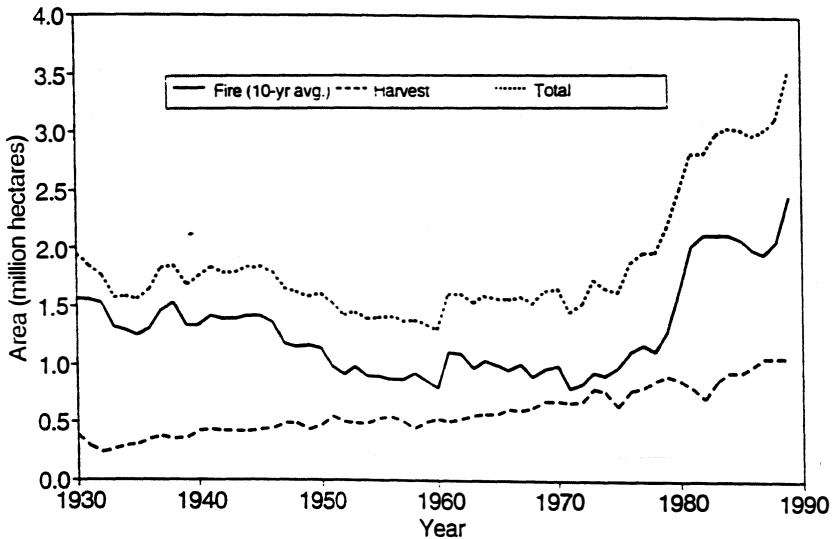
Figure 6.4. The 10-year average of area annually burned and an estimate of the area annually harvested in Canada for the period 1930–1989. Harvesting data are compiled from multiple sources; fire data are from Van Wagner (1988) and Canadian Forest Service.

reductions, selected mortality of host species, or stand-replacing mortality after repeated years of defoliation or bark beetle attacks. Although Canada has a long record of insect outbreak statistics, estimates of stand-replacing mortality are not available for the same period for which fire or harvesting statistics exist.

Regional climatic and forest conditions affect the relative importance of fire and insects as the predominant disturbance regimes. In the drier western boreal forest, fire is the dominant disturbance regime, whereas insects play a much more important role in the wetter eastern boreal forest (Apps et al. 1991; Kurz et al. 1992).

Climatic conditions have long been known to affect insect populations. The association of extreme weather with the occurrence of outbreaks in forest insect populations has been examined by correlating the outbreaks with unusual periods of weather (e.g., Volney 1988). Further indications of climatic controls on insect populations are the frequency of outbreaks and the geographic ranges of insects. Both have been documented for insects associated with northern coniferous forests or species that are likely to become important should climatic conditions permit an expansion of their range to the north. Table 6.2 is a listing of species that fall into the first category: boreal insect species whose outbreaks seem to be associated with extreme weather conditions. One pest species feeding on each major host species is represented in the table. Insect outbreaks are generally distributed in the southern portions of their respective host ranges. Should climatic warming occur, there is every reason to expect that the outbreak areas will expand. Table 6.3 lists insect species whose historical outbreak areas are not in the boreal forest. Yet the outbreak areas are likely to expand to the north if the distribution of the host species change in response to a warmer climate, or if the host range occurs in the boreal forests but the insect outbreaks are currently limited to the southern portion of that range.

Table 6.2. Pest Species of the Boreal Forest Whose Outbreaks Are Associated with Extreme Weather Conditions

Species	Hosts(s)	Factors favoring outbreaks	Reference
Choristoneura fumiferana (spruce budworm)	Spruce/fir	Warm springs	Ives (1974)
		Moderate winter temperatures	
		Dry years	
		Warm dry summers	Greenbank (1963)
Choristoneura pinus (jack pine budworm)	Jack pine	Drought and high temperatures	MacAloney (1944)
		Below average precipitation	Clancy et al. (1980)
		Warm springs	
		Warm, dry periods	Volney (1988)
Malacosoma disstria (forest tent caterpillar)	Aspen	Mild winters	Ives (1981)
		Warm springs	

Major insect outbreaks require a combination of prerequisites that include favorable climate and suitable host conditions. Many insects favor older stands (Volney 1988) and shifts in age class structure resulting from fire suppression can create conditions that are more favorable to insects (Heinselman 1973; Blais 1983; Ritchie 1987). However, the inverse is not necessarily true. Climatic stresses (warm and dry conditions) that lead to shifts to younger age classes because of increased fire activity can also increase host susceptibility to insects (witness insect problems in the southwestern United States during the recent drought conditions). Furthermore, stressed young forest stands may be susceptible to insect problems that are different from those affecting older stands.

FUTURE FEEDBACKS

In the past, disturbance regimes in boreal and temperate forests have been affected by climatic conditions. We must therefore assume that changes in climatic conditions will

Table 6.3. Pest Species of the Cordilleran Forest Whose Outbreaks May Expand to Boreal Regions under Climate Change

Species	Hosts	Factors favoring outbreaks	Reference
Choristoneura occidentalis (western spruce budworm)	Douglas-fir	Low rainfall	Kemp et al. (1985)
		Cool winters	
		Warm springs	
Orgyia pseudotsugata (Douglas-fir tussock moth)	Douglas-fir	Warm spring temperatures	Glendenen et al. (1978)
		Moderate temperatures	Shepherd et al. (1989)
		Dry conditions	
Dendroctonus ponderosae (Mountain pine beetle)	Lodgepole	High overwinter temperatures	Safranyik (1985)
		Low precipitation and warm periods	Thompson and Shrimpton (1984)

continue to result in changes in disturbance regimes that will further affect forest structure and function.

The effects of changes in temperature, precipitation, and relative humidity derived from general circulation models were used to explore the severity of the forest fire season in Canada (Flannigan and Van Wagner 1991). A 46% increase in the seasonal severity rating was predicted "with a possible similar increase in area burned," although much greater increases could not be ruled out. Global warming has also been predicted to lead to greater area burned and a larger number of escaped fires in Northern California (Torn and Fried 1992).

Other studies have predicted changes in forest area and distribution (Rizzo and Wiken 1992; Smith et al. 1992) on the assumption that vegetation and $2 \times CO_2$ climate conditions will reach a new equilibrium. The "transient" responses of vegetation to shifting climatic conditions could result in substantial release of carbon into the atmosphere (King and Neilson 1992).

At present, our ability to predict quantitatively the feedbacks of forest ecosystems to global climatic change is limited, and the analysis is complicated by the wide range of ecological conditions and the likely responses of ecosystem processes (Zoltai et al. 1991; Apps 1993). We are confident, however, in rejecting the assumption that the terrestrial biosphere will not provide feedback in response to changes in climatic conditions. Furthermore, we provide two observations and offer a suggestion about the nature of the feedback.

1. *Asymmetry of rate of change.* Forest ecosystems can remove carbon from the atmosphere or add carbon to it, thus providing negative or positive feedback to climatic warming. The speed at which carbon uptake and release occur can differ greatly because carbon uptake through net ecosystem productivity (the balance between carbon uptake and respiration) occurs much more slowly than the rapid carbon release associated with fires. Moreover, many of the processes that create more favorable conditions for carbon uptake also accelerate other biological processes, such as decomposition, making it harder to achieve large gains through net ecosystem production. On the other side, processes that create ecosystem stress and reduced growth rates, such as extreme temperatures and drought conditions, also favor such disturbances as fire and insect-induced tree mortality.

Changes in forest area are another example of asymmetrical rates of change. The rate at which forest area could expand where growing conditions become more favorable is much less than the rate at which forest area could be lost, e.g., by large-scale forest fires and regeneration failure.

2. *Asymmetry of risk.* To achieve carbon uptake at the regional scale, the sum of the products of carbon density in each age class and the area in each age class (the age class distribution) must increase. This increase can be accomplished through increases in the total forest area, through increases in carbon density in individual age classes, and through shifts in the age class distribution toward age classes with greater carbon density. In any case, though, forest trees must continue to take up carbon at a rate that is greater than ecosystem respiration release while maintaining an age class structure with large proportions of the total area in high-carbon-density age classes.

The factors that determine whether forest ecosystems remain carbon sinks, or at least maintain carbon storage, must all be favorable for many decades, whereas a single extreme year of environmental conditions can lead to tree mortality, insect attack, or loss from fires. As environmental conditions shift away from those to which present vegetation complexes are adapted, the risk of disturbance increases. The asymmetry of risk can be compared with the analogy that the weakest link in a chain leads to breakage. Any one factor that deviates too far from current conditions can induce ecosystem carbon losses, whereas maintenance or increase of carbon storage requires that all factors remain adequate. For example, provenance tests have repeatedly demonstrated that trees are adapted to the prevailing environmental conditions of their origin. Shifting environmental conditions away from that optimum often decreases forest productivity and increases tree stress and susceptibility to insects or other mortality factors (see Chapter 1, this volume).

Changes in forest area are also an example of asymmetrical risk. If environmental conditions shift the boundaries of the climatic zone suitable for boreal forest northward, all that is required to reduce forest area at the forest's warmer and drier limit is one extreme fire year followed by regeneration failure. To expand forest area in the north, however, many different factors (seed sources, soil conditions, disturbance regimes, growing conditions) must be appropriate for many years to ensure successful seedling establishment and survival. Furthermore, the forest area lost in the south will have had greater growth rates and higher carbon storage potential than the area gained in the north.

As a result of these two asymmetries, we suggest that it is more likely that the biospheric feedbacks from temperate and boreal forest ecosystems will be positive feedbacks that further enhance the carbon content of the global atmosphere. Although this discussion focuses on carbon cycling, the conclusion can be extended to all other feedback mechanisms that require that forest area, age class structures, and forest growth be maintained.

The potential to mitigate feedback mechanisms is limited. The success of fire protection measures in the past has contributed in part to calls for further increases in protection efforts to reduce the area annually burned, or at least to prevent future increases. Fire protection is costly and resources are limited. As fire conditions become more severe, a decreasing proportion of the emerging fires is acted upon and the area burned increases in response to climate forcing, albeit at a smaller rate than if no protection measures were in place.

Successful forest fire protection shifts forest age class distribution toward older ages. The structure and function of boreal forests are adapted to frequent natural disturbances, and reducing fire disturbances will increase the forests' susceptibility to insect attacks as the average forest age increases. Fire protection therefore can delay, but not prevent indefinitely, the time at which boreal forests are disturbed.

As already discussed, regeneration delay is one of the important determinants of the role of forest ecosystems in regional carbon cycling and storage. One option to mitigate feedbacks that result from changes in disturbance regimes is to reduce regeneration delays through seeding or planting efforts. Although an analysis of the quantitative implications for the carbon budget has not yet been conducted, seeding and planting

areas disturbed through fire or insect-induced stand mortality might be a viable mitiga-
tion strategy in addition to forest protection efforts. For example, reducing the regener-
ation delay from 5 to 0 years in Table 6.1 increases the regional biomass storage of cases
1 and 4 by 6%.

CONCLUSIONS

Disturbances such as wildfire and insect-induced stand mortality affect forest structure
and function because they influence forest age class distribution, forest area, species
composition, and ecosystem carbon density. Disturbance regimes are affected by cli-
matic conditions as drought and higher than normal temperatures increase fire frequency
and insect outbreaks. Historic evidence suggests that fire regimes are closely coupled
with climatic conditions, and recent temperature increases above long-term averages
have resulted in very significant increases in the area burned annually in Canadian
forests. These increases are large relative to the area burned annually in the period since
1918. A comparison with longer-term, natural fire cycles is complicated by lack of
records and by multiple confounding factors.

Climate-induced changes in disturbance regimes affect forest structure and function,
which in turn influence future climatic conditions through carbon, water, and nutrient
cycling and other feedbacks. Assessing the direction of biotic feedback is a complex task
because of the many nonlinear processes and internal feedbacks.

Assuming no change in forest structure and function under conditions of climatic
change is not justifiable. The potential for feedbacks is significant. We conclude that—
because (1) the potential changes in rates of carbon release from forest ecosystems are
much higher than those of carbon uptake (asymmetry of rates) and (2) the probability of
increased carbon release is much greater than that of increased carbon accumulation
(asymmetry of risk)—positive feedback from temperate and boreal forest ecosystems to
climate change is more likely than negative feedback. Mitigation options through forest
management and protection are limited.

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REFERENCES

Alban, D. H., and D. A. Perala. 1992. Carbon storage in Lake States aspen ecosystems. *Can. J.
    For. Res.* 22:1107–1110.
Apps, M. J. 1993. NBIOME: A biome-level study of biospheric response and feedback to potential
    climate changes. *World Resource Rev.* 5:41–65.
Apps, M. J., W. A. Kurz, and D. T. Price. 1991. Estimating carbon budgets of Canadian forest
    ecosystems using a national scale model. In *Carbon Cycling in Boreal Forest and Subarctic*

Ecosystems: Biospheric Responses and Feedbacks to Global Climate Change, ed. T. Kolchugina and T. Vinson, pp. 241–250. Oregon State University, Corvallis.

Barney, R. J., and B. J. Stocks. 1983. Fire frequencies during the suppression period. In *The Role of Fire in Northern Circumpolar Ecosystems*, SCOPE 18, ed. R. W. Wein and D. A. MacLean, pp. 45–62, Wiley, Chichester, U.K.

Bazzaz, F. A. 1990. The response of natural ecosystems to the rising global CO_2 levels. *Annu. Rev. Ecol. Syst.* 21:167–196.

Blais, J. R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. *Can. J. For. Res.* 13:539–547.

Bonan, G. B., and H. H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. *Annu. Rev. Ecol. Syst.* 20:1–28.

Bonan, G. B., D. Pollard, and S. L. Thompson. 1992. Effects of boreal forest vegetation on global climate. *Nature* 359:716–718.

Clancy, K. M., R. L. Giese, and D. M. Benjamin. 1980. Predicting jack pine budworm populations in northwestern Wisconsin. *Environ. Entomol.* 9:743–751.

Clark, S. J. 1990. Fire and climate change during the last 750 yr in Northwestern Minnesota. *Ecol. Monogr.* 60(2):135–159.

Cooper, C. F. 1983. Carbon storage in managed forests. *Can. J. For. Res.* 13:155–166.

Dewar, R. C. 1991. Analytical model of carbon storage in the trees, soils, and wood products of managed forests. *Tree Physiol.* 8:239–258.

Flannigan, M. D., and J. B. Harrington. 1988. A study of the relation of meteorology variables to monthly provincial area burned by wildfire in Canada 1953–1980. *J. Appl. Meteorol.* 27:441–452.

Flannigan, M. D., and C. E. Van Wagner. 1991. Climate change and wildfire in Canada. *Can. J. For. Res.* 21:66–72.

Glendenen, G., V. F. Gallucci, and R. I. Gara. 1978. On the spectral analysis of cyclical tussock moth epidemics and corresponding climatic indices, with a critical discussion of the underlying hypotheses. In *Time Series and Ecological Processes, Proceedings of the S.I.M.S.-S.I.A.M. Conference*, ed. H. H. Shugart, pp. 279–293, Society for Industrial and Applied Mathematics, Philadelphia.

Greenbank, D. O. 1963. Climate and the spruce budworm. In *The Dynamics of Epidemic Spruce Budworm Populations*, ed. R. F. Morris, *Mem. Entomol. Soc. Can.* 31:174–180.

Gullett, D. W., and W. R. Skinner. 1992. The state of Canada's climate: Temperature change in Canada 1895–1991. SOE Rep. No. 92-2. Environment Canada, Atmospheric Environment Service, Ottawa, Ontario.

Harmon, M. E., W. K. Ferrell, and J. F. Franklin. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 247:699–702.

Harrington, J. B., M. D. Flannigan, and C. E. Van Wagner. 1983. A study of the relation of components of the Fire Weather Index to monthly provincial area burned by wildfire in Canada 1953–80. Inf. Rep. PI-X-25. Canadian Forestry Service, Petawawa National Forestry Institute, Chalk River, Ontario.

Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quat. Res.* 3:329–382.

Ives, W. G. H. 1974. Weather and outbreaks of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Information Report NOR-X-118. Canadian Forestry Service, Northern Forestry Centre, Edmonton, Alberta.

Ives, W. G. H. 1981. Environmental factors affecting 21 forest insect defoliators in Manitoba and Saskatchewan. Information Report NOR-X-233. Canadian Forestry Service, Northern Forestry Centre, Edmonton, Alberta.

Johnson, E. A., and C. P. S. Larson. 1991. Climatically induced change in fire frequency in the southern Canadian Rockies. *Ecology* 72(1):194–201.

Kemp, W. P., D. O. Everson, and W. G. Wellington. 1985. Regional climatic patterns and western spruce budworm outbreaks. Technical Bulletin 1693. United States Department of Agriculture Forest Service, Washington, D.C.

King, G. A., and R. P. Neilson. 1992. The transient response of vegetation to climate change: A potential source of CO_2 to the atmosphere. *Water Air Soil Pollut.* 64:365–384.

Kurz, W. A., and M. J. Apps. 1994. The carbon budget of Canadian forests: A sensitivity analysis of changes in disturbance regimes, growth rates, and decomposition rates, *Environ. Pollut.* 83:55–61.

Kurz, W. A., M. J. Apps, T. M. Webb, and P. J. McNamee. 1992. The carbon budget of the Canadian Forest Sector: Phase I. Information Report NOR-X-326. Forestry Canada, Northwest Region, Northern Forestry Centre, Edmonton, Alberta.

MacAloney, H. J. 1944. Relation of root condition, weather, and insects to the management of jack pine. *J. For.* 42:124–129.

Nikolov, N., and H. Helmisaari. 1992. Silvics of the circumpolar boreal forest tree species. In *A Systems Analysis of the Global Boreal Forest*, ed. H. H. Shugart, R. Leemans, and G. B. Bonan, pp. 13–84. Cambridge University Press, Cambridge.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. In *A Systems Analysis of the Global Boreal Forest*, ed. H. H. Shugart, R. Leemans, and G. B. Bonan, pp. 144–169, Cambridge University Press, Cambridge.

Payette, S., and R. Gagnon. 1985. Late Holocene deforestation and tree regeneration in the forests-tundra of Quebec. *Nature* 313:570–572.

Payette, S., C. Morneau, L. Sirois, and M. Desponts. 1989. Recent fire history of the northern Quebec biomes. *Ecology* 70(3):656–673.

Ritchie, J. C. 1987. *Postglacial Vegetation of Canada*. Cambridge University Press, Cambridge.

Rizzo, B., and E. Wiken. 1992. Assessing the sensitivity of Canada's ecosystems to climatic change. *Climat. Change* 21:37–55.

Rowe, J. S. 1983. Concepts of fire effects on plant individuals and species. In *The Role of Fire in Northern Circumpolar Ecosystems*, SCOPE 18, ed. R. W. Wein and D. A. MacLean, pp. 135–154, Wiley, Chichester, U.K.

Safranyik, L. 1985. Effect of climatic factors on development, survival, and life cycle of the mountain pine beetle. In *Mountain Pine Beetle Symp. Proc.*, Pest Management Report #7, pp. 14–24, British Columbia Ministry of Forests, Smithers, British Columbia.

Shepherd, R. F., G. A. Van Sickle, and D. H. L. Clarke. 1989. Spatial relationships of Douglas-fir tussock moth defoliation within habitat and climatic zones. In *Proceedings, Lymantriidae: A Comparison of Features of New and Old World Tussock Moths*, ed. W. E. Wallner and K. A. McManus, pp. 381–400. General Technical Report NE-123. United States Department of Agriculture Forest Service Northeastern Forest Experiment Station, Broomall, Pa.

Smith, T. M., R. Leemans, and H. H. Shugart. 1992. Sensitivity of terrestrial carbon storage to CO_2-induced climate change: Comparison of four scenarios based on general circulation models. *Climat. Change* 21:367–384.

Thomson, A. J., and D. M. Shrimpton. 1984. Weather associated with the start of mountain pine beetle outbreaks. *Can. J. For. Res.* 14:255–258.

Tom, M. S., and J. S. Fried. 1992. Predicting the impacts of global warming on wildland fire. *Climat. Change* 21:257–274.

Van Wagner, C. E. 1978. Age-class distribution and the forest fire cycle. *Can. J. For. Res.* 8:220–227.

Van Wagner, C. E. 1987. The development and structure of the Canadian Forest Fire Weather Index System. Canadian Forestry Service Technical Report 35. Agriculture Canada, Canadian Forest Service, Ottawa, Ontario.

Van Wagner, C. E. 1988. The historical pattern of annual burned area in Canada. *Forestry Chronicle*, June, pp. 182–185.

Volney, W. J. A. 1988. Analysis of historic jack pine budworm outbreaks in the Prairie provinces of Canada. *Can. J. For. Res.* 18:1152–1158.

Whynot, T. W., and M. Penner. 1990. Growth and yield of black spruce ecosystems in the Ontario Clay Belt: Implications for forest management. Information Report PI-X-99. Forestry Canada, Petawawa National Forestry Institute, Chalk River, Ontario.

Yarie, J. 1981. Forest fire cycles and life tables: A case study from interior Alaska. *Can. J. For. Res.* 11:554–562.

Zoltai, S. C., T. Singh, and M. J. Apps. 1991. Aspen in a changing climate. In *Aspen Management for the 21st Century,* ed. S. Navratil and P. B. Chapman, pp. 143–152. Forestry Canada, Northwest Region, Northern Forestry Centre and Poplar Council of Canada, Edmonton, Alberta.

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