13. Effects of Climate Change on Forest Insect and Disease Outbreaks

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General circulation models (GCMs) predict dramatic future changes in climate for the northeastern and north central United States under doubled carbon dioxide (CO_2) levels (Hansen et al., 1984; Manabe and Wetherald, 1987; Wilson and Mitchell, 1987; Cubasch and Cess, 1990; Mitchell et al., 1990). January temperatures are projected to rise as much as 12°C and July temperatures as much as 9°C over temperatures simulated at ambient CO_2 (Kittel et al., 1997). Projections of precipitation are quite variable over the region, ranging from 71 to 177% of ambient levels in January and 29 to 153% of ambient in July among several GCMs (Kittel et al., 1997). Such climate changes clearly may affect the growth and species composition of our northern forests directly in ways discussed in previous chapters. In contrast with the discussions in previous chapters, this chapter steps up one trophic level to consider the effects of climate change on the populations of microorganisms, fungi, and insects that feed in and on forest trees.

Interactions at the community level may greatly complicate predictions of the effects of climate change on the dynamics of consumer populations and forests. Climate change may influence the population processes of microorganisms, fungi, and insects directly through the physiology of individual organisms or indirectly through physiological effects on their host plants, competitors, and natural enemies. The resulting population dynamics are difficult to predict because of the complexity and nonlinearities in the responses of physiological processes to climatic factors and interspecies interactions. Feeding by various consumer guilds is just another stress for forest trees, along with climatic and other abiotic stresses, that alters their growth processes. In addition, stresses resulting from climate change may alter the susceptibility or vulnerability of trees to consumers, exacerbating or ameliorating the effects of their feeding unpredictably.

Throughout most of the chapter, the focus is on the direct and indirect effects of climate change and increasing CO_2 levels on microorganisms, fungi, and insects. Such organisms are often referred to as "pests" and "pathogens," reflecting our anthropocentric view as plant pathologists, entomologists, and foresters. At the end of the chapter, the larger question of the effects of changing outbreak dynamics of pest organisms on forests is briefly considered. We have chosen to limit our discussion to the effects of changing climatic variables and CO_2 concentration, ignoring the potential impacts of anthropogenic disturbances. Nevertheless, land use changes by humans and changing forest harvesting regimes may also ultimately affect the frequency and severity of pest outbreaks.

Forest Pests and Climate

Distribution and Abundance of Insects

Climate is an important factor in defining the ranges of most insect species of temperate regions (Andrewartha and Birch, 1954). Climatic variables, notably temperature and precipitation (or another index of moisture), have been used historically in developing climograms that define the limits of favorability for population growth for insect species (Schwerdtfeger, 1935; Gutierrez, 1987). Climatic patterns are a major part of the abiotic setting for the many population and community interactions of a species (Huffaker and Messenger, 1964). Over a species' range, climate may play different roles from the center of the distribution to its margins (Rogers and Randolph, 1986; Hoffman and Blows, 1994). At the poleward margin, climatic factors, in particular low temperature, often define the zone in which recruitment just equals mortality and in which the survival of a population is risky. In the interior of a distribution, climatic factors provide conditions for optimum population growth and mediate interactions with hosts, competitors, and natural enemies. Reasons for limitation at the opposite margin (e.g., the southern margin in the northern hemisphere) are less explored, although they undoubtedly result from biotic interactions (Gaston, 1990).

Across a species' range, climatic factors are important determinants of its abundance through their direct and indirect effects on population increase. As poikilotherms, insects grow as a function of temperature: their growth rates, generation times, fecundity, and intrinsic survivorship are primarily temperature-dependent (Uvarov, 1931; Andrewartha and Birch, 1954). Likewise, temperature and moisture are critical factors in the growth of host plants of herbivorous insects and of their invertebrate predators and parasitoids and pathogens. Indeed, the range of a plant species often determines the distributional limits for a herbivore, and plant abundance provides limits for the herbivore's abundance. Regulation by natural enemies may also change over the climatic gradient of a species' range. Natural enemy activity, coupled with conditions less favorable for intrinsic population growth, may reduce populations to very low levels so as to define that margin of the range. Climatic factors play identical roles, albeit over smaller areas, in species distributed over ranges in elevation (Randall, 1982).

The distribution and abundance of a species are related: local abundance increases directly with range size (Gaston, 1990; Lawton, 1995). In addition, variation in abundance increases with range size. Thus, some of the most common and prevalent insect species also have the highest local populations. Many serious forest insect pests fit this description: they occur over large areas and can produce large, damaging populations. Many also display large variation in abundance, undergoing wide oscillations that result in populations increasing from virtually undetectable levels to outbreak levels over much of their ranges in only a few generations (Berryman, 1987). Such species are the primary subject of this review.

Pest Outbreaks

In the most general ecological sense, an outbreak may be defined as "an explosive increase in the abundance of a particular species that occurs over a relatively short period of time" (Berryman, 1987). Another important characteristic is that outbreaks occur episodically (Myers, 1988)—if not as population cycles, then as approximately periodic oscillations. In addition, outbreaks of some species appear to be synchronized spatially, so that numerous local populations explode almost simultaneously over wide geographical regions. A good example is the eastern spruce budworm, *Choristoneura fumiferana* (Clemens), whose populations may exist at low levels for up to 20 years and then increase through the spruce–fir forests of eastern North America virtually simultaneously in outbreaks that last over a decade (Royama, 1984; Mattson et al., 1988).

Numerous hypotheses have been proposed to explain the onset of outbreaks. They have been thought to result from changes in the physical environment, most typically from changes in weather; intrinsic changes in the genetic or physiological makeup of populations; intrinsic life history characteristics of "pest" species, such as *r* strategies; interactions with higher or lower trophic levels in the case of herbivores, which result in the cycling most often demonstrated in mathematical predator–prey models; changes in host plant physiology or biochemistry as a result of environmental stresses; and escape from regulation by natural enemies (Berryman, 1987; Myers, 1988). In the following, we consider briefly just three hypotheses—specifically, those most influenced by weather and, thus, most likely to be invoked under climate change. They are the plant stress hypothesis, the theory of climatic release, and the Moran effect.

Berryman (1987) broadly classified insect outbreaks into two types: eruptive and gradient. Eruptive outbreaks arise rapidly and, once underway, continue as a self-perpetuating process in space and time that is generally impervious to environmental changes. Eruptive outbreaks are driven by intrinsic population processes and trophic-level factors that operate under time lags. In contrast, gradient outbreaks are driven by changing environmental factors that provide more favorable conditions for population growth. Increases in abundance during gradient outbreaks reflect the opportunistic response of insect populations to increases in their resources. Clearly, gradient outbreaks are very likely to be caused directly by climate change, whereas eruptive outbreaks are much less likely to be affected by it.

Roles of Weather in Pest Outbreaks

Weather As a Stressor: Herbivore–Plant Interactions

Mattson and Haack (1987a,b) proposed several general ways in which plant water stress might increase the likelihood of herbivore outbreaks, including (1) effects on the behavior of herbivores and on their microhabitats, (2) effects on the nutritional quality of plants, and (3) effects on the abilities of plants to regulate herbivores. First, stressed plants may stimulate herbivore feeding through chemical or physical changes. In addition, water stress reduces leaf transpiration, resulting in higher leaf temperatures, which may provide more favorable microhabitats for herbivore growth and development. As a second mechanism, the nutritional hypothesis suggests generally that stress enhances the nutritional quality of plants to insect herbivores (Mattson and Haack, 1987a,b), perhaps because of increased concentrations of nitrogen (N) in stressed tissues (White, 1984). Increased nutritional quality enhances growth and development rates and fecundity of herbivores, increasing the likelihood of outbreaks. Mattson and Haack (1987a) also speculated that plant stress may increase the ability of herbivores to detoxify plant defensive chemicals. Third, water stress may impair a plant's ability to produce defensive compounds, allowing herbivores to feed more readily. In plants that are generally tolerant of insect feeding, particularly by defoliators, water stress reduces growth of new tissues, rendering plants more susceptible to loss (Mattson and Haack, 1987a).

Among forest insects, bark beetles have been frequently cited as good examples of the positive effects of plant water stress on herbivores (Mattson and Haack, 1987b; Waring and Cobb, 1992; Ayres, 1993). In an extensive review of the literature on the impact of plant stress on herbivore dynamics, Waring and Cobb (1992) reported that wood borers, which were usually associated with conifers, responded positively to drought stress in all cases reviewed. However, in a critique of the plant stress hypothesis, Larsson (1989) argued that host water stress may have different effects on different insect herbivore feeding guilds. Similar to reported results for bark beetles, he observed that water stress may have positive effects on sucking insects, such as aphids, presumably due to higher plant nitrogen concentrations under stress. On the other hand, he speculated that gall-forming insects may suffer from host stress, which may reduce the size of the galls that they depend upon for development. He also felt that stress might have negative effects or no effects on leaf chewers. Similarly, Waring and Cobb (1992) enumerated many cases of negative effects of plant stress on herbivores. As an alternative to the plant stress hypothesis, Price (1991) made a case for the positive effects of plant vigor on herbivore attack although his examples emphasized gall formers, which may be special cases among herbivore feeding guilds. Given the multitude of apparently contradictory results in the literature, it clearly will be important to consider the feeding guilds to which particular pest species belong in evaluating potential effects of climate change on them as mediated through their hosts.

The plant stress hypothesis is too simplistic even in the apparently clear-cut situation of southern pine beetle, *Dendroctonus frontalis* Zimmerman, and pine, however. Reeve et al. (1995) suggested a more physiologically realistic model of the interaction based on differential effects of water availability on growth and photosynthetic rates in pine trees. Under that model, higher than normal water levels, that is, beyond those associated with any water stress, may also make trees more susceptible to pine beetles by facilitating rapid shoot growth at the expense of allelochemical production. A similar hypothesis has been proposed for the association of western spruce budworm outbreaks with periods of increased rainfall in chronically dry regions of the southwestern U.S. (Swetnam and Lynch, 1993).

Weather As a Trigger of Outbreaks: The Theory of Climatic Release

The theory of climatic release proposes that weather causes outbreaks through direct effects on insect populations (Greenbank, 1956). Outbreaks are thought to be triggered by several successive years with weather conditions favorable to population growth. The classic case for which the theory was developed were outbreaks of the eastern spruce budworm in Canada (Wellington et al., 1950; Greenbank, 1956). Favorable weather conditions included dry, sunny, or warm weather, or some combination of those factors, during the spring period of larval development. Such conditions favored the survival and rapid growth of larvae, which resulted in increased fecundity. Outbreaks were thought to result from several years of enhanced population growth. Ultimately, the favorable local weather patterns were linked to synoptic, regional storm systems (Wellington et al., 1952).

Martinat (1987) was critical of the theory of climatic release because of the precise timing required between weather events and outbreaks. He stressed that most insect outbreaks display a fairly regular periodicity. Thus, the theory requires that weather phenomena show similar periodicity and that the critical weather variables remain in favorable ranges over several successive years. Martinat (1987) indicated the unlikelihood of such a scenario given current knowledge of long-term weather patterns.

Weather As a Synchronizer of Outbreaks: The Moran Effect

Moran (1953b) proposed an alternate hypothesis for the role of weather in regional outbreaks, which has been called the Moran effect (Royama, 1992). Under this theory, weather does not cause outbreaks directly. Instead, oscillations in abundance result from intrinsic population processes. Within the time series model that Moran proposed, the oscillations are driven by second-order autoregressive processes (Moran, 1953a), which have been interpreted as delayed density-dependent factors, such as the activity of specific parasitoids (Turchin, 1990), or as first-order autoregressive factors that act in a direct density-dependent fashion, such as the activity of generalist predators (Williams and Liebhold, 1995a). An extrinsic factor, such as weather, acts only as a stochastic perturbation in the model. Given similar intrinsic biotic processes to produce oscillations in local populations across a region, exposure to common weather keeps the populations oscillating in synchrony. Thus, weather acts in the Moran effect not to cause outbreaks, but simply to synchronize the oscillations of local populations so as to produce regional outbreaks.

Williams and Liebhold (1995b) applied Moran's technique to explain historical outbreaks of the gypsy moth, *Lymantria dispar* (L.), in the New England states of the U.S. They reported that outbreaks were synchronous among states over a 55-year period. Using time series techniques, they then identified three weather variables that were strongly correlated with gypsy moth defoliation in all four states. The variables, daily minimum temperature and daily rainfall in mid-December during the current gypsy moth generation and daily minimum temperature in mid-July during the previous gypsy moth generation, were also strongly correlated among the states, suggesting that they were common regional factors that synchronized gypsy moth populations.

Direct Responses of Insects and Pathogens to Changing Climate

Direct Effects on Insect Population Processes

Climate change will have both direct and indirect effects on insect populations (Porter et al., 1991; Cammell and Knight, 1992). Direct effects are those mediated through the physiology of individuals, including changes in development, survival, reproduction, behavior, and movement. Although effects of variable temperature and humidity are well documented at the individual level, extrapolating them to changes in dynamics at the population level under large-scale climate changes is the difficult, but essential step in understanding the effects of climate change (Kingsolver, 1989). Indirect effects on herbivores are mediated through the trophic levels surrounding them, in particular, effects on their host plants and natural enemies (Cammell and Knight, 1992).

Several direct effects on herbivores are expected, particularly as a result of rising temperatures. For multivoltine herbivores, more time will be available at the beginning and end of the growing season for population development, especially as winter temperatures are generally expected to increase more than summer temperatures (Porter et al., 1991). With increased accumulation of heat units through the growing season, generation times will decrease and more generations will be possible per season for multivoltine herbivores (Porter et al., 1991; Cammell and Knight, 1992). Overwintering survival is expected to increase, and hence, to allow increased overwintering at higher latitudes. Among migratory species, migration is expected to increase (Sutherst, 1991). At the regional scale, increasing temperature is expected to allow expansion of herbivore populations to higher latitudes and higher elevations (Williams and Liebhold, 1995c; Parmesan, 1996).

Increasing temperatures may alter overwintering patterns of species through changing diapause requirements and increasing overwinter survival. The aphid, *Elatobium abietinum* (Walker), the major defoliator of Sitka spruce in the United Kingdom (UK), produces overwintering eggs on the European continent and in Scandinavia (Straw, 1995). However, it is able to develop continuously in the UK, not producing an overwintering stage. With warmer mean temperatures and fewer extreme cold events, survival is likely to increase, populations will be able to build, and increasing pest problems are anticipated in Sitka spruce plantations (Straw, 1995).

For multivoltine herbivores with the capacity for several generations per year, a relatively modest increase in temperature may permit an additional generation over much of a species range. In a modeling study of European corn borer populations across Europe based on degree day accumulations, Porter et al. (1991) found that, with a 1°C increase, not only were univoltine populations able to shift northward by 165 to 665 km, but also multivoltine populations were able to increase generations incrementally at a given location. Similarly, some generally univoltine bark beetle species can become bivoltine under the variability of current weather conditions, suggesting the potential for multivoltine populations under actual climate change (Heliövaara et al., 1991).

Direct Effects on Pathogen Dynamics

There has been considerable speculation, but little direct experimental evidence, concerning the effects of climate change on the incidence and/or severity of forest pathogens. However, there is much information available about weather and climatic effects on specific host–pathogen systems and this can provide insights regarding possible changes in pathogen dynamics and alteration of geographical ranges.

Increased concentrations of atmospheric CO_2 alone are unlikely to directly affect pathogen life cycles substantially within the range of the predicted doubling of CO_2 (Manning and Tiedemann, 1995). In particular, many root pathogens are accustomed to elevated CO_2 levels commonly found in soils, and most aboveground pathogens, primarily fungi and bacteria, will be unaffected by increases in CO_2 from 0.03 to 0.07% (Manning and Tiedemann, 1995). However, one recent study showed a 20-fold increase in spore production by *Colletotrichum gloeosporioides*, causal agent of anthracnose on a tropical legume, under twice ambient CO_2 (Lupton et al., 1995), so the assumption of no direct effects must be viewed cautiously. Additionally, airborne fungal spores from litter and soil were shown to increase 4-fold under twice ambient CO_2 concentrations in a study conducted with *Populus tremuloides* Michx. grown in open-top chambers (Klironomos et al., 1997). While most of the spores included the common genera of fungal decomposers, *Aspergillus, Penicillium,* and *Cladosporium,* there also was an increase in spores produced by species of *Fusarium* and *Alternaria*. Both of these genera have species that can act as decomposers, weak parasites, or pathogens (Klironomos et al., 1997).

Projected increases in CO_2 may alter temperature regimes and rainfall patterns and thus have significant effects on pathogen survival, reproduction, dissemination, and present geographical distribution. Disease is the result of interactions among a host, a pathogen, and the environment (the disease triangle), since all components are necessary for disease to develop. Pathogen dynamics often vary in response to weather and climatic events. From this knowledge, various predictions about the impacts of global change have been suggested. For instance, the poplar leaf rust pathogen, *Melampsora allii-populina* Kleb., is presently largely confined to southern and central Europe, while *M. larici-populina* Kleb. dominates throughout most parts of Europe. However because it is more thermophilic in some portions of its life cycle than *M. larici-populina* (Somda and Pinon, 1981), and because *M. allii-populina* is wind-dispersed, it may become more common in northern Europe during years with warmer than average temperatures (Lonsdale and Gibbs, 1996).

A widely distributed pathogen that may significantly change its range under altered temperature and climate regimes is *Phytophthora cinnamomi* Rands the cause of Phytophthora root rot on a wide range of tree species (Lonsdale and Gibbs, 1996; Brasier and Scott, 1994). This oomycete, a soil borne root pathogen, is indigenous to the Papua New Guinea region, and requires warm, wet soils to infect roots (Brasier, 1996). It has a very broad host range affecting over 900 mainly woody perennial plants (Zentmyer, 1980). The pathogen has caused extensive dieback in southwestern Australia in jarrah (*Eucalyptus marginata* Sm.) forests (Shearer and Tippett, 1989). *P. cinnamomi* also caused a major epidemic on chestnut (*Castanea dentata* [Marsh.] Borkh.) and chinkapin (*C. pumila* [L.] Mill.) in the southern U.S. resulting in significant mortality in the 1800s and in the 1920s and 1930s though this has only been weakly related to climatic anomalies (Woods, 1953; Crandall et al., 1945). Since the early 1980s, severe decline of oaks across the Mediterranean has involved *P. cinnamomi* as an important factor predisposing trees to drought stress and affecting declines of *Quercus suber* L. and *Q. ilex* L. in southern Iberia (Brasier, 1996; Brasier and Scott, 1994). Besides the interaction of *P. cinnamomi* and drought, this decline involves interactions with changing land use, site factors, and attacks by other organisms (Brasier and Scott, 1994).

Brasier (1996) made several generalizations about *P. cinnamomi* responses to altered climate. First, climatic warming may move the range of the fungus northward and increase the incidence of periods favoring inoculum production and infection. Warmer seasons will increase the rate of spread of the pathogen, increase inoculum production and increase secondary infection rates. Additionally, warmer winters will permit greater pathogen survival while climatic extremes such as drought or waterlogging will reduce host resistance (Brasier, 1996). Because *P. cinnamomi* and drought are major predisposing factors in Iberian oak decline, this predicted alteration in *P. cinnamomi* distribution could increase infection incidence and extend oak decline to new regions. Host stress caused by climatic extremes may further increase the incidence of *P. cinnamomi* and increase attacks by secondary organisms (Brasier, 1996).

Enhanced moisture conditions will favor many fungi and increase spore production and dispersal by rain splash (Lonsdale and Gibbs, 1996). Increased precipitation in some regions will increase the incidence and severity of foliar and root pathogens that are dependent on moisture for development and dispersal (Sutherst, 1996). Alterations in rainfall patterns could also affect fungal development if rainfall events decrease throughout the growing season, or during particular portions of the growing season. This would affect dispersal and decrease incidence of leaf spot fungi such as *Marrsonina* spp. on poplars (Lonsdale and Gibbs, 1996) or *Cristulariella pyramidalis* Wat. & Marsh. on black walnut (*Juglans nigra* L.) (Neely et al., 1976).

Most climate models predict that temperature increases associated with global change will be greatest in the winter (Barron, 1995). Increasing mean winter temperatures will also affect dormant season pathogen activity. Areas in the temperate latitudes where winter dormancy of woody plants occurs simultaneously with periods when temperatures are sufficient for fungal activity are termed "asynchronous dormancy zones" (Lonsdale and Gibbs, 1996). Particularly with perennial species, many pathogens can only breach host defenses and invade host tissues during the dormant season before temperatures become too cold for pathogen growth. Milder winters may allow greater host tissue colonization for perennial stem canker fungi whose growth is temperature-limited. In addition, climatic parameters may affect low-temperature fungi, such as snow molds. These pathogens require a very humid environment that is common under snow cover and that insulates against extreme cold. These pathogens, such as *Phacidium infestans* Karst., would decrease in their incidence in regions where both the amount and persistence of snow cover decrease (Lonsdale and Gibbs, 1996). Other temperature-sensitive pathogens that can only colonize hosts in the dormant season may also be affected. *Gremmeniella abietina*, the cause of Scleroderris shoot blight of conifers, has been shown to have a "conducive" temperature range from −6 to +5°C for disease expression in tree seedlings (Marosy et al., 1989). Insulating snow cover facilitates infection by protecting the pathogen from exposure to cold temperatures. Changes in snow cover patterns would tend to decrease disease incidence of this pathogen.

The ability of pathogens to infect hosts can be controlled by the duration of leaf wetness. For example, the apple scab fungus, *Venturia inaequalis* (Cke.) Wint., requires a long period of leaf wetness and warm temperatures to infect hosts (Weltzien, 1983). Other forest pathogens may have similar requirements, and changes in the duration of leaf wetness will alter infection dynamics. A notable example of this is the defoliation of sugar maple by forest tent caterpillar (*Malacosoma disstria* Hübner) in northern Pennsylvania in 1994. Defoliation was followed by an unusually moist period from July through October. During portions of this period defoliated trees tried to refoliate and young succulent leaves were colonized by the anthracnose fungus *Discula campestris* (Pass.) von Arx, which prevented refoliation (Hall, 1995). High levels of mortality and extensive crown dieback were observed the following spring.

An increase in mean winter temperature in the northern hemisphere could increase inoculum survival over winter and provide higher levels of initial inoculum in the spring (Coakley, 1995). However, the incidence of frost damage may be expected to decrease along with the canker fungi that invade damaged tissues after injury from frost (Lonsdale and Gibbs, 1996). For agronomic crops, disease incidence of rusts and mildews (obligate parasites) are predicted to increase as the assimilate content of host plants increases. It is unknown whether a similar phenomenon will affect the incidence of rusts and mildews in forests. More vigorous growth of host foliage will lead to denser canopies accompanied by a microclimate more favorable for disease development (Coakley, 1995). With increased production of foliage and woody twigs, there will be a potential, depending on the harvesting method, for more residue after harvest and greater survival of saprophytic organisms. Some of these saprophytes are likely to be facultative parasites, and their incidence may increase.

A high degree of uncertainty is associated with predictions about pathogen dynamics because we do not know the magnitude or rapidity with which climate may be altered and because there is little empirical data about how specific hosts and pathogens will interact. Furthermore, climatic change may have a positive effect on one part of the disease triangle and a negative effect on another (Coakley, 1995). A variety of feedback mechanisms may limit effects associated with increasing CO_2 (Coakley, 1995). For instance, while increasing CO_2 may stimulate host growth, this growth could also be limited by increased competition from competing species or by increased weed or woody shrub competition. Similarly, increased temperature could be beneficial to some plant processes, but could also increase evapotranspiration and water loss. A stressed host plant may then be more vulnerable to the effects of infection by primary pathogens or susceptible to secondary pathogens.

Geographical Range Changes of Insects and Pathogens

The expansion of geographical ranges of many insect species to higher latitudes and elevations is highly likely as a result of the combined effects of the previously cited factors (Porter et al., 1991; Cammell and Knight, 1992). That is, overwinter survival will be enhanced, the capacity of increase will be augmented by more and earlier generations in some species, and dispersal may increase (Porter et al., 1991). For herbivores, presence of the host species is also a requisite of range expansion. Agricultural pests may expand distributions quickly with climate change as growers plant crops at higher latitudes and elevations (Porter, 1995). Although a considerably slower process, even with human intervention, tree species may also migrate, facilitating the range expansions of associated forest insect species (Leverenz and Lev, 1987; Davis and Zabinsky, 1992; Franklin et al., 1992; Dyer, 1995).

Perhaps because significant climate change has not yet been definitively discerned, there have been few studies documenting actual range changes in insects. Through a recent survey of established study sites and a comparison with historical records of occurrence, Parmesan (1996) documented changes in the latitudinal distribution of Edith's checkerspot butterfly over the past 30 years in western North America. Her analyses suggested a subtle thinning out at the southern end of the species distribution and an increased occurrence at northern sites, as might be expected with a northward shift of the species. Similarly, Kozár (1991) and Stollár et al. (1993) documented the northward spread of a number of agricultural pest insects in Hungary over the past two decades under the influence of milder winter temperatures.

In the absence of a clear climate signal and unequivocal observed shifts in species ranges, the only available approach to anticipating range changes is through models. Simulation of changes over large regions often entails using models in conjunction with geographic information systems. Observed species distributions, or some approximation to them, such as detectable defoliation in the case of forest defoliators, are fit as functions of environmental variables. Typically, the best information available to characterize distributions is a map of presence or absence of a species (Williams and Liebhold, 1995c). Environmental variables usually include climatic variables, such as long-term averages of temperature and precipitation, and the distribution of the host species in the case of herbivores (Williams and Liebhold, 1995c), or another indicator of habitat suitability (Rogers and Randolph, 1993). Models are fit using ambient conditions, and then they may be used to extrapolate the effects of changes in climate or other environmental factors.

Modeling studies of forest pests have demonstrated potential for considerable changes in distribution under climate change. Using a regression approach, Virtanen et al. (1996) modeled the frequency of outbreaks by the European pine sawfly, *Neodiprion sertifer* (Geoffroy), in municipalities of Finland over the period 1961 to 1990. Outbreak distributions at two spatial scales were most significantly related to minimum winter temperatures. Under an increase in winter temperature of 3.6°C, the best guess prediction for temperature change by the year 2050 according to a Finnish government policy scenario, outbreak frequencies were projected to increase dramatically over the entire country, with the greatest changes in northern regions.

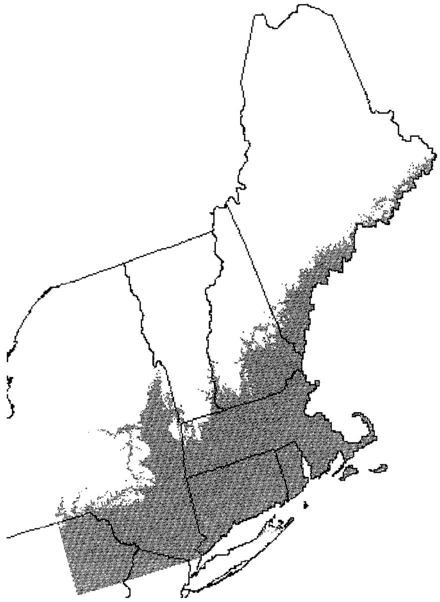
Williams and Liebhold (1995c) investigated potential changes in spatial distribution of outbreaks of the western spruce budworm, *Choristoneura occidentalis* Freeman, and the gypsy moth in the U.S. states of Oregon and Pennsylvania, respectively, using maps of historical defoliation, climate, and incidence of susceptible forest types. Relationships between outbreak incidence and the environmental variables were modeled using a linear discriminant function. With an increase in temperature alone (+2°C), the projected defoliated area decreased relative to ambient conditions for the budworm and expanded slightly for the gypsy moth. With an increase in temperature and precipitation ($+0.5\,\text{mm}\,\text{day}^{-1}$), the defoliated area expanded for both species. By contrast, the defoliated area decreased for both when temperature increased and precipitation decreased. Results for GCM scenarios contrasted sharply. For the GFDL GCM, defoliation by budworm was projected to cover Oregon completely, whereas no defoliation was projected by gypsy moth in Pennsylvania. For the GISS model, defoliation disappeared completely for the budworm and slightly exceeded that under ambient conditions for the gypsy moth. Williams and Liebhold (1995c) interpreted the results as due in part to changes in distribution of the susceptible forest types.

In recent studies, Williams and Liebhold (1997a,b) investigated potential changes in range of eastern spruce budworm and gypsy moth over wide geographical regions in the U.S. Changes in distribution of the susceptible forest types were also projected as functions of climatic variables using a discriminant function model, and those forest scenarios were used in generating the respective defoliator outbreak scenarios.

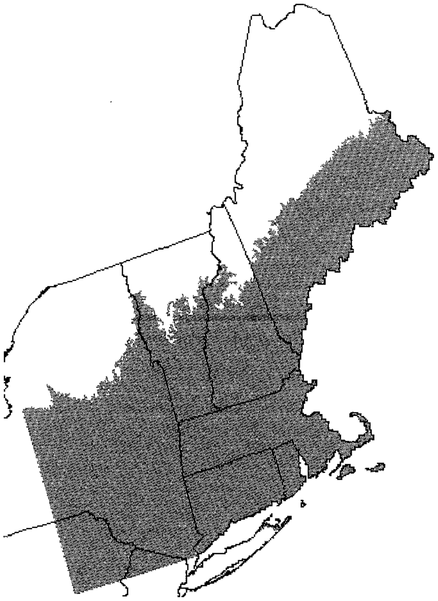
Changes in outbreak distributions of eastern spruce budworm under three climatic warming scenarios were projected over much of the species' range in the northeastern and north central U.S. (Williams and Liebhold, 1997a). In general, predicted areas of defoliation and of the susceptible forests (i.e., the spruce–fir forest type group) decreased in size with increases in temperature. As temperatures increased, the distribution of defoliation exhibited a general pattern of thinning and disappearance at its southern margin, suggesting a northward shift of budworm populations.

Potential range shifts by gypsy moth and the oak forests that it inhabits were projected in the northeastern U.S. (Williams and Liebhold, 1997b). Responses of both susceptible forest (i.e., the oak–hickory and oak–pine forest type groups) and defoliation distributions to rising temperature were projected as increases in area of oak forests and in areas of those forests defoliated by gypsy moth. The gypsy moth outbreak distribution was projected to occupy nearly 29% of the study area under ambient conditions and increased rapidly under three warming scenarios, reaching 100% at +6°C (Fig. 13.1). The defoliation projections exhibited a northward shift with increasing temperature, conforming with the general expectations for latitudinal shifts under climate change.

Changes in pathogen ranges have been predicted by computer modeling or climate matching programs. One such program, CLIMEX, uses climatic data to derive an ecoclimatic index for predicting an organism's potential relative abundance and distribution (Brasier and Scott, 1994). CLIMEX was used with *P. cinnamomi* and appropriate temperature and soil moisture values to predict where the pathogen is currently distributed

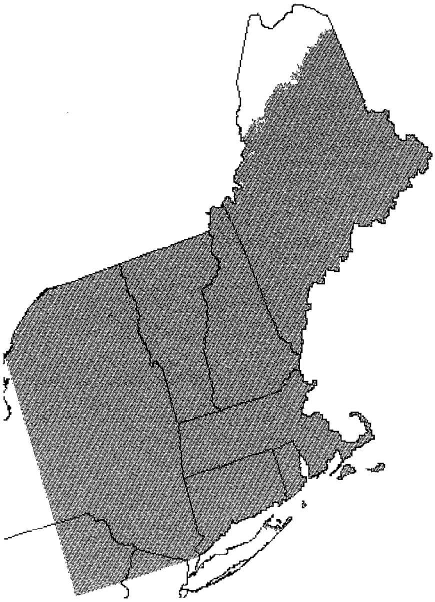


(a)

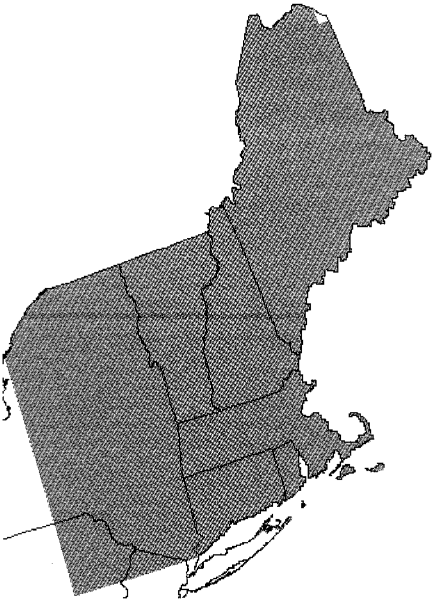


(b)

Figure 13.1. Predicted areas of gypsy moth defoliation in the northeastern United States under ambient conditions and three climate change scenarios: (a) ambient temperature, (b) 2°C increase, (c) 4°C increase, and (d) 6°C increase.



(c)



(d)

Figure 13.1. (*Continued*)

in Europe, thus allowing some verification of the matching process. Various predictions of change in the pathogen's distribution in response to changes in precipitation or temperature inputs can be examined (Brasier and Scott, 1994). The CLIMEX model suggests that given a warming of 1.5 to 3°C, *P. cinnamomi* will increase significantly within its present locations, in southern Europe and western coastal regions, accompanied by some extension of the pathogen's activity into the European continent, but no extension into regions with very cold winters (Brasier and Scott, 1994).

Indirect Effects of Climate Change on Community Processes

Seasonal Synchrony of Insect Herbivores with Host Plants

For insect herbivores, synchrony of hatch or emergence from the overwintering stages with growth and development of host plant tissue may have important consequences for early season growth and survival. Ayres (1993) noted that many forest insect species are specialists on immature plant tissues early in the season. Developing plant tissues, such as expanding leaves, tend to be low in fiber, high in nutritional value, and low in defensive compounds. Higher temperatures narrow the window of availability of such tissues, potentially altering herbivore growth rates and survival. For example, hatch of first instar leaf-eating caterpillars significantly before budbreak may result in starvation or in stunted development due to a delay in feeding (Hunter, 1993). Conversely, delayed hatch may result in caterpillars feeding on older plant tissues, which may reduce growth rates significantly even with a delay of only a few days (Ayres, 1993). Three studies, one using models and the other two controlled field experiments, illustrate this point. Dewar and Watt (1992) compared predictions of temperature-based models for the timing of budbreak in Sitka spruce and larval emergence in the winter moth, *Operophtera brumata* L. In the host model, budbreak timing depended on the accumulation of "chilling time" below a threshold, whereas larval emergence time was based on degree days above a threshold. When daily temperature increases of 0.5 to 2.0°C were simulated, warmer temperatures resulted in the predicted date of budbreak staying about the same, while the date of emergence was advanced. With a 2°C increase, larvae were predicted to emerge 20 days before budbreak in the host, potentially jeopardizing their survival. Alternatively, a recent experimental field study found that an increase of 3°C did not alter the synchrony of winter moth emergence and budbreak in pedunculate oak, a common host of winter moth in the UK (Buse and Good, 1996).

Hill and Hodkinson (1992) compared the synchrony of two psyllid species that occupy separate ranges in a latitudinal gradient. Both species have a common host, dwarf willow, and feed on its catkins, which are available for only a short window in the summer. In field experiments, the researchers increased temperatures by 0.6 to 1.4°C by enclosing trees in clear polyethylene cages. For both psyllid species, synchrony between catkin and nymph development inside the cages decreased as compared with controls. In one case, the asynchrony resulted in significantly smaller adults, while in the other, nymph survival increased and adults were significantly larger.

Using similar methods, Ayres (1993) compared developmental rates of *Epirrita autumnata* (Borkhausen) caterpillars on leaves of mountain birch in the field under ambient conditions and inside greenhouses constructed around trees. Higher temperatures (~+1°C) inside the greenhouses increased caterpillar growth rates, decreased developmental times, and resulted in larger pupae as compared with controls. The overall effect was a rise in the rate of population increase by as much as 2.9 times with a relatively small rise in temperature. The temperature increase apparently affected growth rates of caterpillars much more than those of leaves, allowing caterpillars to benefit from younger leaf tissue longer in the greenhouse treatment.

Over the long run, it is difficult to assess how important seasonal asynchrony resulting from climate change may be. As pointed out by Dewar and Watt (1992), there is considerable natural variability in the timing of budbreak and emergence, and because greenhouse warming likely will be a gradual process, genetic selection by the herbivore may quickly remedy transient asynchrony.

Insect–Plant Interactions under Increasing Carbon Dioxide

Increases in atmospheric CO_2 are likely to alter insect herbivore–plant interactions considerably, primarily through effects on plant growth and development (Ayres, 1993). The projected doubling of CO_2 concentrations over the next century (Houghton et al., 1996) probably will not have direct effects on insect herbivore populations, as insects are known to be able to tolerate CO_2 concentrations far in excess of projections (Graves and Reavey, 1996). Instead, effects will be mediated through changes in the nutritional quality of their host plants. Plants may be affected in several ways by increased availability of CO_2. In general, faster growth rates with increased CO_2 will increase the C/N ratio, resulting in lower tissue concentrations of N. Higher CO_2 levels are hypothesized to increase the potential for producing carbon (C)-based allelochemical defenses (Lincoln et al., 1993; Lindroth, 1996). Higher CO_2 also results in higher starch content of leaves and in increased tissue water content because of increased water use efficiency. Finally, plants grown in higher CO_2 conditions are hypothesized to have leaves with higher specific weight and greater toughness, although the latter phenomenon has been reported in only one experimental study (Lindroth et al., 1993).

Such changes in host plants may have several effects on insect herbivores. Decreasing N concentrations in plant tissues are generally detrimental, decreasing growth rates, increasing developmental time, and decreasing fecundity, all of which involve processes dependent on amino acids (Lincoln et al., 1993; Lindroth, 1996). Increased levels of allelochemicals often may have deleterious effects on growth and survival. In response to lower N and increased starch, herbivores may increase consumption rate, presumably to maintain a relatively constant N intake (Lincoln et al., 1993). In later larval stages, increased consumption may allow a relatively normal growth rate. However, earlier stages may not be able to compensate for lower nutritional quality in that manner, may not be able to eat tougher leaves, and, therefore, may suffer slower growth and increased likelihood of mortality.

Relatively few studies to date have focused on forest insects (Lindroth et al., 1993; Roth and Lindroth, 1994; Herms et al., 1996; Lindroth et al., 1996; Watt et al., 1996; Williams et al., 1997a,b; Williams et al., 1998). Lindroth et al. (1993) investigated changes in plant growth rate and leaf chemistry for three tree species, quaking aspen, red oak, and sugar maple, grown under enriched CO_2. In addition, they investigated consumption and growth parameters for late instar gypsy moth and forest tent caterpillar, *Malacosoma disstria*, fed leaves from the experimental seedlings. Overall, the effects of increased CO_2 were most pronounced on aspen, the fastest growing tree species, and followed the hypothetical patterns just outlined: for both herbivore species, consumption rates were higher, stage durations were longer, and growth rates were lower for larvae fed leaves grown under enriched CO_2. These patterns probably resulted from changes in leaf N concentration and levels of allelochemicals. Results were less clear for the other host species, perhaps reflecting the rather idiosyncratic natures of the differently coevolved plant–herbivore systems. Relative growth rates of forest tent caterpillar were lower on high-CO_2 maple leaves, whereas gypsy moth rates did not differ significantly between treatments and controls on maple. The negative effects on forest tent caterpillar growth were likely due to higher leaf tannin levels, although this effect was ameliorated somewhat under high CO_2. Alternatively, relative growth rates of gypsy moth were higher for high-CO_2 than for ambient CO_2 oak leaves, while forest tent caterpillar rates did not differ significantly on oak. The better performance of gypsy moth resulted from increased levels of starches and decreased levels of tannins in high-CO_2 oak leaves.

Herms et al. (1996) investigated effects of three aspen clones grown under increased CO_2, increased ozone (O_3), and an increase of both gases on first and fourth instars of four forest defoliator species: gypsy moth; forest tent caterpillar; large aspen tortrix, *Choristoneura conflictana*

(Walker); and whitemarked tussock moth, *Orgyia leucostigma* J.E. Smith. The aspen clones differed in their sensitivity to O_3, with one clone susceptible, another resistant, and the third intermediate. Growth and consumption rates and other derived parameters were estimated after feeding caterpillars excised leaves for 48 hours. No effects on larval survival were observed under increased CO_2. Similar to results from previous studies and hypothetical expectations, growth rates were generally lower for all species and instars under enhanced CO_2 (except for first instar forest tent caterpillars grown on the O_3-resistant aspen clone, in which case growth rate increased). Efficiency of conversion of digested food varied with aspen clone, showing a significant increase overall on the O_3-resistant clone under enhanced CO_2 and a significant decrease on the other clones. Unlike results from previous studies and hypothetical expectations, consumption rates were unaffected by increased CO_2, except for the large aspen tortrix, in which consumption rate decreased. Although the effects or air pollutants are beyond the scope of this review, it is interesting to note that Herms et al. (1996) reported significantly increased growth rates for all defoliator species on leaves produced under increased O_3. This increase apparently resulted from an increased efficiency of conversion, probably due to a decrease in concentration of tremulacin, an aspen allelochemical, under the O_3 treatment.

It is difficult to use studies of the effects of increased CO_2 on host plants and herbivores to draw general conclusions about effects at the population level and over long periods. Most studies were carried out in the laboratory and involved effects on individual insect stadia, ignoring effects over the entire life cycle and on fecundity in particular (Lawton, 1995; Watt et al., 1995; Awmack et al., 1997a). Thus, it is difficult to speculate how such effects may affect population dynamics. Potential effects of increased CO_2 on interactions with higher trophic levels are virtually unexplored. The only published study in this area suggests that herbivores may be more vulnerable to their natural enemies under doubled CO_2 concentrations (Awmack et al., 1997b). With chronic exposure to increased CO_2, plants may acclimate to higher levels, potentially altering their interactions with herbivores further over the long term (Watt et al., 1995). A final deficiency of extant studies is that they have tended to look at only one feeding guild, leaf chewers, and generally ignored sucking insects, leaf miners, gall-forming insects, and borers (Watt et al., 1995). Under current theories of the effects of increased CO_2 on plants, the potential effects on these feeding guilds are uncertain.

Pathogen–Plant Interactions under Increasing Carbon Dioxide

Host responses to elevated CO_2 and alterations in host growth, biomass, physiology, and nutrition can be expected to affect interactions with pathogens and diseases. From studies conducted under controlled conditions, only a few generalizations are possible concerning host responses. For instance, most studies have shown an increase in total leaf area due to larger leaves or greater numbers of leaves produced (Ceulemans and Mousseau, 1994). However with yellow poplar, *Liriodendron tulipifera* L., there was a reduction of individual leaf area in response to elevated CO_2, and an increase in fine root production (Norby et al., 1992). Most studies examining woody plant responses to elevated CO_2 have shown that dry weight per unit of leaf area increases and is likely related to increased starch content or additional cell layers (Eamus and Jarvis, 1989). Additional leaf starch may enable some foliar pathogens to increase their colonization of host tissues and increase the area of leaf necrosis, though this has not been demonstrated experimentally. Conversely, under elevated CO_2 leaf N concentrations decrease and secondary compounds, such as tannins and phenolics, increase, which may make leaves less palatable to some insect pests, while the effects on pathogens are unknown (Lindroth et al., 1993).

The shift in production from aboveground components to belowground fine roots indicates that significant C inputs may induce an increase in soil microbial biomass and activity (Zak et al., 1993). This may favor growth of some soil-borne fungal pathogens or mycorrhizae, but, again, experimental evidence is lacking. Pathogenesis in root systems is exacerbated by stresses induced by weather extremes, especially drought during a growing season (Lonsdale and Gibbs, 1996). Root diseases caused by the root-rotting fungi in the genus *Armillaria* can be expected to increase with increasing host stress due to drought or other causes (Wargo and Harrington, 1991). Other diseases are linked to drought or other stressors that may increase in temperate forests under global warming scenarios, though empirical data are lacking. Many of these involve secondary pathogens that usually become pathogenic only when the tree is weakened. Many decline diseases fall into this category and they are discussed in more detail in Chapter 4.

Interactions of Mycorrhizal Fungi and Plants under Increasing Carbon Dioxide

While mycorrhizas are clearly not pathogens, they form mutualistic associations with tree roots that enhance nutrient and water uptake and protect trees from some soil-borne pathogens. These associations are likely to be altered by elevated CO_2. The mycorrhizal association is more efficient since it requires less energy for the host to produce and maintain the mycorrhizal network than it does for the host to produce plant roots (Marshall and Perry, 1987). The fungus provides the host with nutrients, while the host provides the fungus with C (Harley and Smith, 1983). Mycorrhizal fungi protect trees from certain root pathogens (Marx, 1970) and some mycorrhizal species are more effective than others in providing this protection (Malajczuk, 1988). Interspecific competition among mycorrhizal fungi may therefore affect disease incidence (Lonsdale and Gibbs, 1996). Increases in drought frequency will enable other competing fungi to replace established species in mycorrhizal communities due to the death and subsequent regeneration of nonwoody roots (Lonsdale and Gibbs, 1996). These altered mycorrhizal communities may affect disease susceptibility depending on the dominant fungi in the mycorrhizal communities.

Interactions among hosts and mycorrhizal fungi in response to elevated CO_2 may result in a more mutualistic, a less mutualistic, or even a parasitic association (Sanders, 1996). Most recent research has shown inconsistent effects associated with growth in elevated CO_2. The work of Tingey et al. (1995) with ponderosa pine (*Pinus ponderosa* Laws.) and Norby et al. (1992) with yellow poplar show that elevated CO_2 stimulated belowground carbon allocation. This resulted in an increase in mycorrhizal occurrence and a consistent, though statistically nonsignificant increase in root area. With yellow poplar, no significant growth response to elevated CO_2 was found after three years, but there was a sustained increase in leaf-level photosynthesis and lower rates of foliar respiration for trees grown in elevated CO_2 (Norby et al., 1992). There was a consistent trend of a decrease in leaf production and leaf area and an increase in fine root production for trees growing in elevated CO_2. This implies that as CO_2 stimulates aboveground production at least some of the C is allocated to belowground components, such as mycorrhizal production or extraradicle hyphae, in order to enable support of the aboveground production. Similarly, O'Neill et al. (1987) found an increase in mycorrhizal density in response to elevated CO_2 for shortleaf pine (*Pinus echinata* Mill.) and white oak (*Quercus alba* L.).

In addition to the stimulation of belowground C allocation from elevated CO_2, Tingey et al. (1995) found that soil temperature was a key factor influencing seasonal changes in root area density and new root area density. In the summer, when soil temperatures were 15 to 22°C (at 15 cm), new root flushes were produced in ponderosa pine seedlings. Thus, while changes in air temperature will not directly influence root growth, as the soil warms increased root biomass may be produced. However at soil temperatures $>25°C$ ponderosa pine root growth declined significantly (Lopushinsky and Max, 1990). Both the magnitude and duration of soil warming will influence mycorrhizal root growth just as it will affect soil-borne pathogens. Soil warming will have a significant influence on biological activity, including root growth and decomposition, both of which are likely to be accelerated as soil temperature increases (Luxmoore et al., 1993).

At the ecosystem scale, elevated CO_2 could affect the interactions among trees, shrubs, and herbaceous vegetation. The complexity of these interactions is suggested by research in a calcareous grassland (Leadley and Korner, 1996). The percentage of root length in the total plant community that was colonized by mycorrhizal fungi was not significantly affected by elevated CO_2 concentrations of 500 or 650 ppm as compared with ambient levels. However, a significant change in community structure was observed as a result of detrimental growth effects (decreased biomass) on *Prunella vulgaris* L. In elevated CO_2 there was a significant increase in the proportion of the root length being occupied by mycorrhizal fungi for *P. vulgaris*, thus providing a large C sink that may have inhibited growth. A coexisting species, *P. grandiflora* L., showed a significant decrease in mycorrhizal colonization, but no significant change in biomass in response to elevated CO_2. Response of extraradicle mycorrhizal hyphae were not evaluated in this study, but may also account for some of the observed differences. These differential mycorrhizal responses could, over time, lead to a reduction of *P. vulgaris* in the grassland community and a change in the community structure (Sanders, 1996). The effects of elevated CO_2 on interactions among diverse tree and mycorrhizal species have not been studied in forest communities and, therefore, few predictions can be made with any certainty.

Relationships between Insect Herbivores and Their Natural Enemies

Climate change may alter the interactions of herbivores and their natural enemies, resulting potentially in changes in levels of natural control and dynamics of the herbivore (Cammell and Knight, 1992). As with the host plant–herbivore interactions, changes in synchrony between herbivores and their natural enemies during the early season may affect the subsequent levels of control. Dynamics of the interaction during the season may also be affected because critical population parameters, such as the rates of population increase and the functional responses of predators and parasitoids, may vary with temperature. Lengthened growing seasons under a warming climate may increase the time over which overwintering stages of the herbivore are exposed to predation or parasitism. More generally, some natural enemies may be critically limited by specific climatic factors, such that regional climate changes may alter their capacity to attack hosts over large areas.

The potential for seasonal asynchrony between herbivores and natural enemies is apparent in a study by Campbell et al. (1974). They reviewed temperature requirements for several aphid species and their parasitoids, including both the lower thresholds for development and the degree-day sums, or thermal constants, required to complete development. In most cases, hosts had lower thresholds and shorter developmental times, suggesting the potential for varying levels of synchrony under different temperature regimes. Effects of phenological asynchrony were explored by Hassell et al. (1993) and Godfray et al. (1994) using a discrete time host–parasitoid model. The researchers investigated the effects of varying the day of parasitoid emergence from overwintering relative to the host and the level of density dependence on the stability of the two-species system. Increasingly later parasitoid emergence provided a temporal host refuge, permitting host populations to increase successively. At the latest emergence dates, stability was not possible. Simulations run with variable asynchrony, as might be expected with weather variability under climate change, were generally unstable (Hassell et al., 1993).

The potential for increased exposure of overwintering hosts to parasitism with rising temperature is seen with *Ooencyrtus kuvanae* (Howard), an egg parasitoid of the gypsy moth. Gypsy moth overwinters in diapause during the egg stage from about July until April each year (Brown, 1984). The parasitoid attacks host egg masses during the fall and early spring, often inflicting high levels of parasitism depending upon the size of an egg mass (Williams et al., 1990). *Ooencyrtus kuvanae* females are not generally active during the winter months, but are not in diapause. As a result, numbers of fall generations of the parasitoid have been reported to vary from two to five over the its range in North America, apparently in response to climatic differences (Brown, 1984). Increases in fall and winter temperatures clearly may permit additional generations in a specific location, resulting in higher levels of parasitism.

Climatic limitations to natural control of herbivores are generally appreciated (Messenger, 1971), but some natural enemies, such as insect pathogens, may be more definitively limited by critical dependence of their life cycles on temperature and humidity. An example is *Entomophaga maimaiga* Humber, Shimazu & Soper, a fungal pathogen of gypsy moth larvae, whose epizootics decimated host populations over wide areas of the northeastern U.S. in 1989 and 1990 (Hajek et al., 1990). Those epizootics were associated with higher than average rainfall in May, and infection levels of the fungus increased with additional moisture in controlled studies (Hajek et al., 1996). The fungus continues to increase its range, but its ability to produce epizootics under changed climatic conditions likely will depend upon relative levels of temperature and rainfall.

Potential Effects of Changing Climate on Major Forest Insect Pests of the Northeastern U.S.

Because sufficient distribution data, historical time series, and basic ecological knowledge may not be available, it is generally impossible to develop reliable models and make quantitative predictions of the effects of climate change on population dynamics and range changes for even common pest insects. Nevertheless, it may be useful to speculate on relative positive or negative effects of environmental change based simply on qualitative characteristics of insect herbivores and their interactions with trophic levels above and below. Landsberg and Stafford Smith (1992) proposed such a "functional scheme" for predicting the effects of climate change on the likelihood of outbreaks by herbivorous insects. As a conceptual model, they used a tritrophic-level system consisting of host plant, herbivore, and natural enemy complex. They enumerated the various critical trophic-level interactions that may produce density-dependent regulation of the herbivore and then identified the interactions most likely to be sensitive to climate change. For specific systems, they then attempted to identify the interactions most critical for regulation from above or below and predict how climate change may enhance or ameliorate the likelihood of herbivore outbreaks. For herbivores, they considered the plant tissues fed upon, number of generations per season, cues to initiate development in the spring and halt activity in the fall, and shelter locations during winter (e.g., in litter), and speculated how those attributes may be affected directly by change in CO_2 level or climate. Using the larch bud moth, *Zeiraphera diniana* Guenée, as an example, they proposed that the critical factor is the cue to initiate activity in the spring. Warm spring weather may enhance synchrony with host budbreak and increase the likelihood of outbreaks, whereas warm winters may increase overwintering mortality and decrease the likelihood of outbreaks. An obvious shortcoming of this scheme is that a particular system may have multiple critical interactions with conflicting responses to environmental change that confound definitive predictions.

How may climate change affect the most prevalent and damaging forest pests in the northern U.S.? Table 13.1 lists a selection of such species identified as significant forest pests in a recent report by the United States Department of Agriculture (USDA) Forest Service Forest Health Monitoring Program (USDA Forest Service, 1994). Using ideas similar to those of Landsberg and Smith (1992), we speculate on the likelihood of increased outbreak activity for individual species based on the biological and ecological characteristics listed in Table 13.1.

Several species show potential for changing activity given the host tissues on which they feed. The two beetle species may be affected in different ways if precipitation patterns change. If precipitation decreases, spruce beetle, an inner bark feeder, may be favored by the weakening effects of water stress on its host (Ayres, 1993). Alternatively, as a phloem feeder, the white pine weevil is more productive with vigorous growth of host shoots (Hamid et al., 1995), which will be enhanced under an increase in precipitation. Among the leaf feeders, spruce budworm is a specialist on young leaf tissue, and its dynamics may change if increasing temperature alters its synchrony with budbreak of its host (Fleming, 1996).

An increase in the number of generations per season is likely to be relevant for only two species, spruce beetle and hemlock woolly adelgid. Spruce beetle has a biennial life cycle over much of its range, but may

Table 13.1. Ecological Characteristics of Selected Forest Insect Species of the Northern United States

Common name	Species (Order)	Generations per Year	Overwintering Stage	Diapause Physiology	Outbreak Type	Origin	Primary Hosts	Host Tissue
Eastern Spruce Budworm[a]	*Choristoneura fumiferana* (Clemens) (Lepidoptera)	1	Larva	+	Eruptive	North America	Balsam fir	Leaf
Gypsy Moth[b]	*Lymantria dispar* (L.) (Lepidoptera)	1	Embryonated egg	+	Eruptive	Europe	Oak species	Leaf
White Pine Weevil[c,d]	*Pissodes strobi* (Peck) (Coleoptera)	1	Adult	–	Gradient	North America	Eastern White Pine	Phloem
Spruce Beetle[e,f]	*Dendroctonus rufipennis* (Kirby) (Coleoptera)	1, 2, or 3 yr life cycle (2 yr most common)	Larva, Adult	–	Eruptive	North America	Spruce species (mature stands)	Inner bark &phloem
Hemlock[g] Woolly Adelgid	*Adelges tsugae* Annand (Homoptera)	3	Nymph	–	Gradient	Asia	Eastern Hemlock	Parenchyma

[a] Mattson et al. (1987).
[b] Montgomery and Wallner (1987).
[c] Hamid et al. (1995).
[d] Retnakaran and Harris (1995).
[e] Holsten et al. (1991).
[f] Safranyik (1995).
[g] McClure (1996).

complete development in one year or extend to three years dependent on regional temperatures in its range (Holsten et al., 1991). As an example, spruce beetle uncharacteristically completed an entire life cycle throughout Alaska during the unusually warm summer of 1993. Given this flexible life cycle, it seems likely that many populations will reduce to a univoltine condition under a warming climate, allowing more rapid development of outbreaks. Hemlock woolly adelgid produces three asexual generations per year in Connecticut, one during summer and two during fall, winter, and spring (McClure, 1996). Milder winters will favor population growth if they permit another generation. Under the current climate, development time of overwinter generations can vary greatly with weather conditions, suggesting the possibility of further generations under a warmer climate (McClure, 1996).

Three species are endemic (see Table 13.1), with ranges presumably coevolved with their hosts' ranges. Warmer temperatures will increase the potential for northward extension of their ranges, although this is likely to be a long process involving simultaneous movement of insect and host populations (Williams and Liebhold, 1995c). The two exotic species, gypsy moth and hemlock woolly adelgid, are still expanding their ranges (Liebhold et al., 1992, 1995; McClure, 1996). Both appear to be limited currently by cold temperatures at the northern extremes of their distributions, and, thus, warmer winters will favor increased movement into unexploited ranges of their hosts. However, Allen et al. (1993) predicted that gypsy moth will not do well in Florida under that state's warm climatic conditions, suggesting that it soon may encounter the southern limit of its distribution in the U.S.

Several species, such as gypsy moth and spruce budworm, display eruptive outbreaks. Because such dynamics involve complex interactions with hosts and natural enemies (Turchin, 1990; Williams and Liebhold, 1995a), the effects of climate change on, for example, changing outbreak frequency are impossible to predict. Under the Moran effect, however, regional synchrony of outbreaks may be altered if regional climatic patterns change (Moran, 1953b; Williams and Liebhold 1995b).

Overwintering may be variably affected by milder winters. In general, survival will increase with fewer periods of lethal low temperatures. However, in species that overwinter as eggs in obligate diapause, such as gypsy moth, exposure to warmer temperatures may prolong diapause development, resulting in later emergence and possible asynchrony with host development (Williams et al., 1990).

Overall, hemlock woolly adelgid seems most likely to be affected positively by climate change. It may increase numbers of generations, survive better during milder winters, begin activity earlier in spring, and disperse farther north as North America becomes warmer. Spruce beetle is also likely to benefit from warmer temperatures by altering its life cycle to univoltine in wider areas and by responding to host stress conditions if precipitation decreases.

Beyond the effects of climate change on a few serious pest species, there is a real possibility of the development of new pests. In a review of nonoutbreak species of lepidopteran defoliators of mixed fir forests in North America, Mason (1987) noted that for each major outbreak defoliator there are at least nine nonoutbreak species, whose roles in the forest ecosystem are not well known. Under significant climate change and accompanying changes in forest composition and disturbance levels, such defoliators may be released from control and become pests. Another likelihood is the introduction of new exotic pests. Although not a result of climate change per se, such introductions become more likely as a result of the wider scope of global change and increasing levels of international trade in forest products (Liebhold et al., 1995). Invasions of nonnative plant pathogens and herbivorous insects are another component of global change that may alter forest ecosystem function and reduce biodiversity (Vitousek et al., 1996). It is conceivable that climate change may open up new niches for invasion by exotic species after they are established and facilitate their spread.

Consequences of Changing Insect Outbreak Patterns for Forests

Climate change may have profound effects on forests of the northern U.S., as well as those of Europe and Asia (Fanta, 1992; Kobak et al., 1996). Not the least of the influences of a changing climate will be its effects on pest and fire disturbances (Kurz et al., 1995b). In North America, pest disturbances are likely to be more serious than fire in the wetter eastern half of the continent. However, the effects of pest disturbances are more difficult to assess because they often result in growth reduction, rather than mortality, they affect individual species selectively, and they may produce stand replacing mortality (Kurz et al., 1995b).

Despite the general opinion that forests should be net C sinks (Kauppi et al., 1992), the short-term negative effects of disturbances on C storage are likely to be dramatic even in the near future. In trying to assess the effects of climate change on disturbance, Kurz et al. (1995b) emphasized the importance of "asymmetry in the rate of change" of forest processes. That is, forest area and C in forests accumulate through regeneration at a much slower rate than they are lost through disturbance. Thus, forest dynamics are likely to be highly variable in the coming century. Kurz et al. (1995a) noted that aging boreal forests in Canada have become increasingly susceptible to disturbances in recent decades. As a result of a modeling study, Kurz and Apps (1995) reported that increased historical disturbances by fire and insects during the period 1970 to 1990 resulted in none of their scenarios being able to produce a C sink during the decade of the 1990s. Positive C fluxes were projected to resume only after the year 2000 and were not projected to approach recent historical levels until well into the next century (Kurz and Apps, 1995).

Another anticipated effect of climate change is the migration of forests over the long run. How they do so will determine equilibrium forest type compositions and affect the level of transient disturbances. The simplest assumption is that forest ecosystems will shift northward as entire integrated units (Fleming, 1996). Because species compositions and herbivore and natural enemy guilds do not change under such an assumption, the basic community regulatory mechanisms remain constant, and little change is to be expected with climate change beyond a simple relocation of the unit. Obviously, this assumption is too simplistic. More realistically, tree and insect species are likely to move individually (Fleming, 1996), according to their particular dispersion mechanisms and tolerance for conditions in their original ranges (Davis and Zabinski, 1992; Dyer, 1995). Distributions of individual tree species will shift as the result of different population processes over their current range. At the southern end, seedlings are expected to be less tolerant of warmer temperatures and only northward dispersers are expected to survive (Fleming, 1996). Senescence rates of mature trees are expected to increase, and that, coupled with possibility of stress due to climate change, may lead to catastrophic losses to insect herbivores. At the northern end of the range, seedling establishment will be possible increasingly farther north, but slow due to low temperatures (Fleming, 1996). Kurz et al. (1995b) note that population change processes will be asymmetrical at latitudinal extremes. At the northern extreme, change is expected to be slow, whereas at the southern end, change may be very rapid, giving the potential for quite variable transient distributions along the path to equilibrium.

Effects of Climate Change on Forest Decline Diseases

In a seminal paper, Hepting (1963) first summarized the impact of climate and climatic variation on forest diseases. Hepting presented the first comprehensive summary of evidence about climate change and its effects on pathogens and forest diseases. What Hepting termed "physiogenic" diseases are now generally referred to as decline diseases. Manion (1991) defined decline diseases as those "...which are caused by the interaction of a number of interchangeable, specifically ordered abiotic and biotic factors to produce a gradual general deterioration, often ending in the death of trees." In the early 1960s, the importance of decline diseases and the role of climatic fluctuation was just beginning to be appreciated. Pole blight of western white pine (*Pinus monticola* Dougl.) was known to have an edaphic–physiological cause involving fine root deterioration and soil physical properties (Leaphart, 1958). Climatic records indicated that in areas with pole blight there was a period of low precipitation and high temperature from 1917 to 1940 (Leaphart, 1958). Subsequent research (Leaphart and Stage, 1971) indicated that pole blight was triggered by the severe drought of 1936, though more recent research has disputed this claim and proposed that winter thaw–freeze events were the likely triggering factors for the decline (Auclair et al., 1990).

The theory that climatic perturbation is the mechanism that drives widespread forest dieback has been presented for northern hardwoods (Auclair et al., 1992). Region-wide declines of birch (*Betula allegheniensis* Brit., *B. papyrifera* Marsh.) from the 1930s to the early 1950s, and sugar maple (*Acer saccharum* L.) in the 1980s have been correlated with thaw–freeze events (Auclair et al., 1992). Both declines were preceded by a major thaw–freeze event that included two to four weeks of intense cold in the winter and exceptional episodes of early warm weather followed by severe frost in late winter or early spring (Auclair et al., 1992). These coincided with the years 1937 for birch and 1981 for sugar maple. However, this does not account for other maple declines that occurred in Wisconsin in the 1950s and in New England in the 1960s (Giese et al., 1964; Mader and Thompson, 1969).

Five different mechanisms have been proposed to account for changes in tree crown condition in response to these fluctuating climatic factors (Auclair et al., 1992). These include (1) direct injury from exceeding frost resistance by severe cold, (2) soil freezing and root injury due to scant snow cover or open winters, (3) exceeding frost resistance limits for rehydrated tissues following a warm period, (4) xylem cavitation induced by cold temperatures that followed an anomalous warm period, and (5) root injury from deep soil freezing that occurred with saturated soils following the warm period. Because the thaw resulted in saturation of the soil profile from snow melt, this enhanced the vulnerability to deep soil freezing since thermal conductivity of wet soils is 50 times the conductivity of dry soils of the same texture (Auclair et al., 1992). Other research in Quebec has shown that deep soil freezing induced root injury and resulted in increased crown dieback and increased crown foliage transparency for injured sugar maple (Robitaille et al., 1995). More mechanistic studies will be necessary to determine the importance of extreme climatic events on hypothesized region-wide decline scenarios.

While extreme freeze–thaw events are well documented and coincidental with major decline events, they do not account for the differential effects on specific tree species. It is difficult to account for the effects of such events on birch in the 1930s and 1940s and no effects on sugar maple until the 1980s. One current theory is that dieback susceptibility is related to tree maturation (Auclair et al., 1997). Specifically, regional forest dieback is synchronized with maturation of birch and maple populations in northern hardwood forests. The greater susceptibility of mature trees to predisposing stressors makes them more vulnerable to injury from extreme climatic events or other inciting factors (Auclair et al., 1997; Manion, 1991). These ideas are examined in Chapter 4.

The role of climate change, not just variability, is difficult to assess for decline diseases. Perhaps the most suggestive link is decline of yellow cedar (*Chamaecyparis nootkatensis* [D. Don] Spach) in southeast Alaska. For the high latitudes, some GCM models predict that early changes in mean temperatures will be greatest in the late fall/winter and eventually warming will be greatest in midwinter (Kräuchi, 1993). Changes in mean annual temperature are notable in Alaska (Juday, 1984). At Sitka, Alaska, mean annual temperature increased at a rate of 2.08°C in the first half of the century, but moderated to just 0.60°C in the period through 1981 (Juday, 1984). While few pre-1900 climatic records are available for Alaska, there are observations of glacial recessions which report continuous recession in southeast Alaska since 1850 (Heusser, 1952). The initiation of both the warming period and the extensive mortality associated with the decline occur around 1880 (Hennon and Shaw, 1994). Other research implicates the role of extreme freeze–thaw events in this decline (Auclair et al., 1990). Dieback is usually associated with extreme episodes of winter drying, unseasonable frost, summer drought, and heat stress (Auclair et al., 1990). No biotic agents have been found associated with the decline and the primary cause is probably abiotic (Hennon and Shaw, 1994). Climatic warming has likely reduced snowpack, altered decomposition dynamics, and induced soil freezing and root injury, though the exact mechanism of the decline has not been conclusively established (Hennon and Shaw, 1994). In particular, a long-lived species, such as yellow cedar, that does not reproduce often may be especially vulnerable to a moderate climatic shift since it has limited ability to adapt to a changing environment (Hennon and Shaw, 1997).

Conclusions

Even if the extreme GCM climate change projections for the northern U.S. come to fruition, the effects of such changes and accompanying rises in CO_2 on forest insect species are uncertain. The direct effects are likely to be most obvious. Most species will survive more successfully over winter with regional warming. Many will shift their ranges toward higher latitudes and elevations into hitherto unexploited ranges of their hosts. Species with flexible life histories will produce more generations per unit time, increasing their rates of intrinsic population increase. Such direct effects hold the potential to increase the frequency, level, and geographical extent of disturbance by current forest insect pests. The indirect effects are likely to be more subtle to detect and difficult to predict because they involve complex community interactions at multiple trophic levels. Species of defoliators exhibiting eruptive outbreaks, such as gypsy moth and spruce budworm, exemplify the difficulties and uncertainties of indirect effects. There is no consensus among ecologists as to the causes of their population oscillations, although they are likely to arise from complex interactions with their hosts and natural enemies. Anticipating the effects of changing climate on such systems is impossible. Similar difficulties apply to predicting the impacts of changing insect outbreak patterns on forest growth and dynamics. Such uncertainties suggest the need for increased monitoring efforts in future decades as the climate signal becomes stronger.

It is apparent that significant gaps already exist in our understanding of how global change will affect host–pathogen dynamics. The complexity of these interactions involves the many factors mentioned in this review: direct effects of increased CO_2 on hosts and pathogens, indirect effects of altered climate on hosts and pathogens, and interactions among hosts and pathogens in a climate-altered environment. Similar, though larger, gaps exist for ecosystem processes that include the role of pathogenesis in stand dynamics and succession, the role of decomposing organisms in cycling nutrients, and the alteration of C storage dynamics in the ecosystem.

If scenarios associated with increasing CO_2 are correct, then drought frequency will increase in temperate forests and trees and forests may become chronically stressed. Such stresses may lead to progressive deterioration in tree health, increasing susceptibility to secondary organisms (Sutherst, 1996), and perhaps an increase in incidence of decline diseases. Soil-borne pathogens sensitive to soil temperature will spread into new geographical areas from which they are presently excluded due to low temperatures. Alterations in pathogen occurrence and host distribution will alter patterns of disease occurrence both in type and amount (Sutherst, 1996). New disease complexes could emerge with different pathogen and host assemblages. The reproduction rate and number of disease cycles per year may increase under warmer conditions, increasing disease severity and accelerating the evolution of new pathotypes (Sutherst, 1996). The difficulty of studying these numerous interacting factors may account for the paucity of direct experimental data available in the literature. Hopefully, future research will address these issues.

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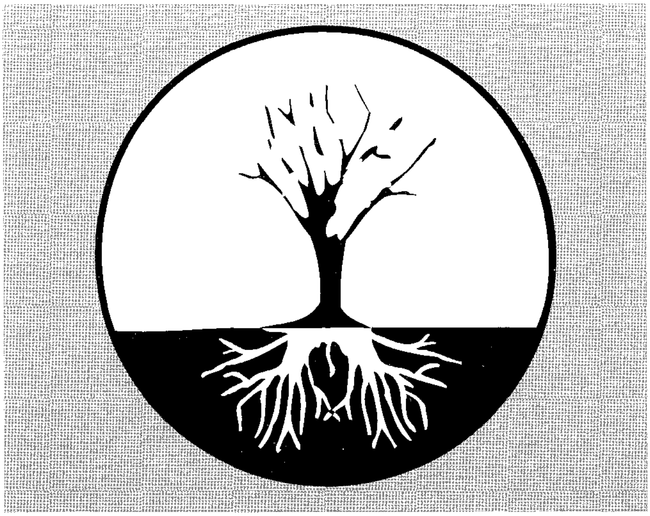

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