# Disturbance in Forest Ecosystems Caused by Pathogens and Insects

**Philip M. Wargo**[1]

**Abstract.**—Pathogens and insects are major driving forces of processes in forested ecosystems. Disturbances caused by them are as intimately involved in ecosystem dynamics as the more sudden and obvious abiotic disturbances, for example, those caused by wind or fire. However, because pathogens and insects are selective and may affect only one or several related species of trees, or the less vigorous or genetically unfit members within a species, the resulting patterns of disturbance may differ from those caused by abiotic factors. Pathogens and insects may cause disturbance through direct effects on the host species, interactions with abiotic disturbance agents, or interactions with each other. Pathogens and insects can act as ecosystem roguers of weakened trees and sometimes as scavengers, decomposing the killed trees and effecting the release of nutrients essential for ecosystem response. Responses of forests to disturbance by pathogens and insects can range from those that maintain the current domain of species composition, structure, and processes and interactions, and those that favor the development of more successionally advanced species, to those that result in significant changes in species composition, structure, and relationships. The first two responses often are associated with disturbances caused by native pathogens and insects, while the third response is more typical of that to exotic organisms. Pathogens and insects play major roles in ecosystem dynamics; understanding these roles is key to facilitating ecosystem management.

## INTRODUCTION

Pathogens and insects are major driving forces of the disturbance process in forested ecosystems (Castello et al. 1995, Harvey et al. 1993). And disturbances caused by pathogens and insects are as intimately involved in ecosystem dynamics as the more sudden and obvious abiotic disturbance factors of wind and fire. White and Pickett (1985) define disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." Disturbance, then, releases resources that are bound in (nutrients) or restricted by size or structure (light, moisture, space) of aging biomass, and makes them available for new growth by existing or replacement species.

Both abiotic and biotic disturbance agents effectuate the availability of these resources. However, because pathogens and insects are selective and may affect only one or a few related tree species, or the less vigorous or genetically unfit members within a species, the resulting patterns of disturbance may differ from those caused by abiotic factors (Castello et al. 1995).

## DISTURBANCE-RESPONSE RELATIONSHIPS

Pathogens and insects may cause disturbance and subsequent response through direct effects on a host species, interactions with abiotic disturbance agents such as moisture and temperature extremes and air pollutants, or interactions with each other,

[1]*Research Plant Pathologist, USDA Forest Service, Northeastern Forest Experiment Station, Hamden, CT.*

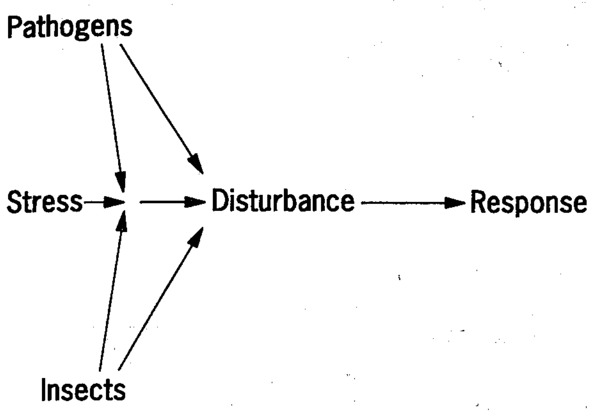


Figure 1.—Pathogens and insects cause disturbance to forest vegetation directly or through interactions with other abiotic stress agents.

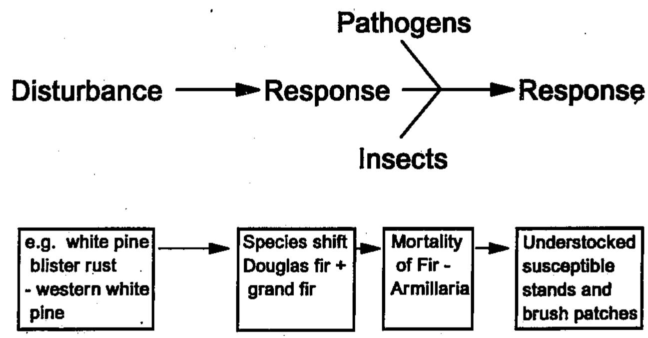


Figure 2.—Response to disturbance by pathogens and insects can result in vegetation changes (response) that are highly susceptible to new pathogens and insects (new disturbance), resulting in different vegetation relationships (new response).

e.g., gypsy moth defoliation and Armillaria root disease (Wargo 1977, 1981) (fig. 1).

In some disturbance relationships, the pathogen or insect may illicit a response to the disturbance that results in an increase in susceptibility of the replacement species to other disturbance agents (fig. 2). An example of this relationship is the effect of white pine blister rust, caused by *Cronartium ribicola*, on western white pine, *Pinus monticola*, forests (Monnig and Byler 1992). In forests of the West, blister rust (the disturbance agent) has killed more than 90 percent of this species in infected stands and has led to major changes in species composition (the response to disturbance) in these forests. Douglas-fir, *Pseudotsuga menziesii*, is now the dominant species along with grand-fir, *Abies grandis*. Both are highly susceptible to Douglas-fir beetle and root disease (the new disturbance agents). Mortality in these stands from root disease occurs long before forest maturation, and the resulting "forests" are understocked root-diseased patches of brush and susceptible trees (the new response) (Monnig and Byler 1992).

## DISTURBANCE REGIMES

Disturbance regimes are used to characterize the spatial and temporal patterns of disturbance and subsequent response of forest communities, i.e., death of dominant individuals in a forest canopy and their replacement (Runkle 1985). Disturbance regimes and response, as indicated by mortality and regeneration, reflect the temporal and spatial distribution of disturbance and its relationship to geographic, topographic, environmental, and plant community gradients or patterns (White and Pickett 1985). Occurrences of disturbance are measured over time: frequency, the mean number of events per time period, is used to express the probability of an event occurring in any given year; return interval (cycle or turnover time) is the mean time between disturbances. Disturbances also vary in intensity. For physical disturbance, this is equivalent to the physical force per area per time; for biological disturbances such as those caused by pathogens and insects, it is closely related if not equivalent to population or inoculum levels. Severity of the disturbance is described as its effects on the organism community or ecosystem, and usually is measured in numbers of trees killed, basal area lost, or biomass destroyed. Host susceptibility has a major influence on severity of disturbance caused by pathogens and insects. Intensity and severity determine the magnitude of the disturbance and consequently the response to it.

The attributes of disturbance regimes, spatial and temporal distribution, frequency of occurrence, and magnitude of disturbance and subsequent response, are influenced by a number of factors (fig. 3). For pathogens and insects, these attributes depend on the whether the host-organ-

| Attributes | Modifiers |
|---|---|
| Spatial Distribution | Native or Exotic |
| Temporal Distribution | Inoculum Potential |
| Frequency | Population Dynamics |
| Magnitude | Susceptible Populations |
| | Forest Maturation |

**Figure 3.—Attributes of disturbances regimes and factors that modify the magnitude of disturbance by pathogens and insects.**

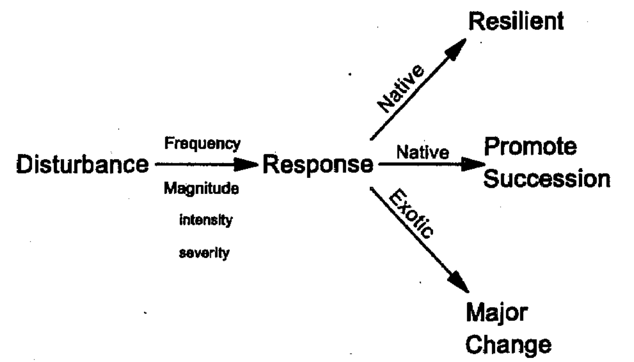


**Figure 4.—Disturbance by pathogens and insects can result in responses that maintain current vegetation, promote successional change, or cause major vegetational changes in forest ecosystems.**

ism relationship is native or exotic, inoculum or population potential and rate of change, and age and distribution of the susceptible host.

## RESPONSE TO DISTURBANCE

Several responses to disturbance are shown in figures 4 and 5. Actual response to disturbance by pathogens and insects depends on the stage of forest development (Oliver 1981) when disturbance occurs, and, of course, the particular organism. Certain pathogens and insects can operate only at specific stages of forest development and maturation, others function at several stages, and still others function only in mature forests that have been predisposed to attack by other disturbance agents. The relationship of forest development and pathogen-induced mortality is illustrated and discussed effectively in Castello and others (1995).

Resilient responses (sensu Holling 1973) are those that usually return to vegetation relationships extant at the time of disturbance (current domain). These resilient responses are typical of native organism/tree associations that have occurred over long periods (Amman 1977).

The interaction of lodgepole pine, *Pinus contorta*, fire, and mountain pine beetle, *Dendroctonus ponderosae*, (MPB) is an example of this relationship (Monnig and Byler 1992). Young lodgepole pine stands are resistant to MPB but they increase in susceptibility as stands mature. Eventually, beetle populations explode and, by mass attack, kill large

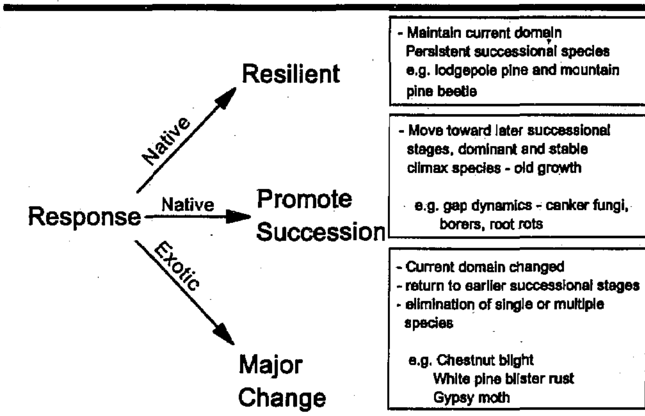


**Figure 5.—Responses to pathogens and insects sometimes depend on whether the organism is native or exotic. Exotic organisms usually cause the greatest disturbance, which can result in the greatest change.**

numbers of lodgepole pine. This mortality provides fuel for fires which recycle the dead trees and open cones for the deposit of seed on the exposed soil. These sites are regenerated as the interaction of fire and beetles create mosaics of lodgepole pine stands of different sizes, ages, and hence susceptiblities. However, fire suppression has affected this relationship and has created vast areas of uniformly susceptible stands that are devastated by massive beetle outbreaks on many of these sites. Later successional species that are typically removed by fire events are replacing lodgepole pine. These stands are not as resilient and probably will be replaced in response to future disturbances.

Another response to native organisms is one that promotes succession in forest stands. Shade-tolerant species in the understory grow into gaps created in the overstory by the selective killing of individual or small groups of trees. Such trees are killed by fungal root pathogens, stem cankers, and borers. In these relationships, gaps tend to be small and successful colonization of the gap is primarily by later successional shade-tolerant species. In forests already dominated by shade-tolerant, later successional species, small gap disturbance maintains these forest types, e.g., beech, *Fagus grandifolia,* and hemlock, *Tsuga canadenis* (Runkel 1984, 1985, Twery and Patterson 1984). Disturbances that cause large gap formation (> 400 $m^2$) allow less shade-tolerant, earlier successional species such as tulip-poplar, *Liriodendron tulipifera,* to colonize the gaps and become part of the canopy (Runkel 1985).

A third response to disturbance can be a major shift in species composition structure and relationships. This type of response can occur when aggressive native pathogens and insects are triggered to outbreak conditions and cause severe disturbance over fairly large areas.

In gaps created by aggressive root pathogens, such as *Armillaria ostoyae* in some interior western conifer forests, shifts in species composition from the susceptible pioneer species of Douglas-fir and lodgepole pine to the more disease-resistant and shade-tolerant western hemlock, *Tsuga heterophylla,* western redcedar, *Thuja plicata,* and subalpine fir, *Abies lasiocarpa* (Shaw and Kile 1991). Van der Camp (1991) referred to these relationships as "root-disease climaxes."

Disturbance from outbreaks of the southern pine beetle, *Dendroctonus frontalis,* also results in a shift from pine forests to hardwood forests as the pine dies (Schowalter 1985). However, the hardwood forests are fire intolerant. Fueled by the abundant dead wood, fire kills them and the forest composition reverts to pine. In the absence of fire, the forests shift to hardwood species (Schowalter 1981, 1985).

## EXOTIC ORGANISMS

This third response is more typical of disturbance by exotic pathogens and insects that historically have caused intensive and severe disturbances over large areas (Haack 1993; Haack and Byler 1993) and which will continue to pose serious threats to forested ecosystems (Liebhold et al. 1995).

The effect of white pine blister rust on western white pine and the subsequent shift in species to Douglas-fir and true firs, as described earlier, (Monnig and Byler 1992) is another example of the severe effects of an exotic pathogen.

The chestnut blight fungus, *Cryphonectria parasitica,* has virtually eliminated American chestnut, *Castanea dentata,* from forests of the East, resulting in forests dominated by oak, *Quercus,* species (Stephenson 1986) that are highly susceptible to defoliation by the gypsy moth, *Lymantria dispar,* also an introduced insect. Indeed, the rate of spread and subsequent effects of gypsy moth probably are related significantly to the effects of the chestnut blight on the oak population.

The gypsy moth has caused considerable disturbance to the oak forests of the Northeast. Introduced to the eastern United States in the 1860's, it has spread southward through the predominantly oak forests of the Appalachian Mountain range. All American oak species are highly preferred food sources and, therefore, highly susceptible to defoliation. Mortality in many areas has been severe, though the ecological consequences of this disturbance are not clear. In some sites, red maple is emerging as a replacement species, but many sites also are regenerating to oak or will regenerate to oak so long as browsing by unusually high numbers of whitetail deer is prevented. Increases in deer numbers are partially the result of increased browse made available by canopy mortality induced by gypsy moth. Ecosystems have complex interactions!

The hemlock woolly adelgid, *Adelges tsugae,* is another introduced insect that is causing significant mortality and that has great potential to change ecosystems. This insect was introduced to the West Coast during the 1920's and again to the East Coast during the 1950's (Annand 1924, McClure 1989). The potential for *A. tsugae* to cause disturbance was not recognized until after there were significant infestations and subsequent mortality of hemlocks in southern New England during the late 1980's. Current hemlock populations have low genetic diversity, possibly related to their decline (pathologically induced) as a species in the Northeast about 4,700 years ago, as indicated by pollen records (Foster and Zebryk 1993). Hemlock is a late successional, highly shade-tolerant species whose demise will result in significant changes in species composition in sites where it is dominant. The potential socioeconomic impact also is great because hemlock is associated with riparian areas that receive heavy recreational use.

## ECOSYSTEM ROGUERS AND SCAVENGERS

Not all pathogens and insects function as major disturbance agents. Many act as ecosystem roguers, alone or synergistically with other disturbance factors. They kill individual trees or small groups of trees that have been stressed by disturbances such as drought, wind, defoliation, and fire. Many trees that become marginal producers as they age or are stressed by disturbance continue to "tie up" or use large pools of resources of light, water, carbon, and nutrients. Pathogens and insects kill these trees, resulting in the release of nutrients and other favorable growth factors for use by the replacement vegetation. Some organisms, such as the *Armillaria* fungus also act as an ecosystem scavenger, decaying the woody substrate that falls to the forest floor. Thus, pathogens and insects can play beneficial roles in stabilizing a site by providing the resources (nutrients, light, moisture) for rapid recolonization of disturbed sites.

## DISTURBANCE AND ECOSYSTEM MANAGEMENT

A concerted effort must be made to identify the physiological, spatial, and temporal conditions that affect risk and hazard from pathogens and insects. Cycles of biotic agents of disturbance are more difficult to determine and predict than physical agents because of the many interrelated biotic and abiotic factors that control their population dynamics. However, many insect outbreaks are keyed to the onset of specific climate and weather changes or to vegetation maturity, all of which can be monitored (Mattson and Haack 1987). Information on distribution, abundance, and potential impacts of pathogens and insects must be linked with information on landscape structure, species composition, potential successional pathways, and other disturbance regimes. This information along with data on the effects of soil, climate, and topography on the ecosystem are needed to accurately predict severity and duration of epidemics, their effects and impacts, and recurrences. Models of biology and impacts for insects such as the spruce budworm, tussock moth, southern pine beetle, gypsy moth, and diseases such as dwarf mistletoe and *Armillaria* and *Phellinus* root diseases are examples of useful information that already is available.

Disturbance by pathogens and insects is pervasive throughout forest ecosystems: it is not a question of whether disturbance will happen but what kind, where, and when. Forest management planners must incorporate information on disturbance by pathogens and insects into the USDA Forest Service's forest plans. Specifically, they must determine the types of pathogens and insects that can be expected within particular ecosystems, develop criteria for determining where disturbances will occur, and calculate the probability of occurrence. This information along with data on the vulnerability of certain areas to particular pathogens and insects and the management objectives for those areas can be used to more accurately assess the impact of disturbance and determine appropriate management alternatives. Incorporating data on disturbance potential by pathogens and insects into land management plans will increase our ability to respond appropriately. An understanding of these disturbance effects is critical to ecosystem management!

## LITERATURE CITED

Amman, G.D. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: impact on succession. *In:* The role of arthropods in forest ecosystems. New York: Springer-Verlag: 3–18.

Annand, P.N. 1924. A new species of *Adelges* (Hemiptera, Phylloxeridae). Pan-Pacific Entomology 1: 79–82.

Castello, John D.; Leopold, Donald J.; Smallidge, Peter J. 1995. Pathogens, patterns, and processes in forest ecosystems. BioScience. 45(1): 16–24.

Foster, D.R.; Zebryk, T.M. 1993. Long-term vegetation dynamics and disturbance history of a *Tsuga*-dominated forest in New England. Ecology. 74(4): 982–998.

Haack, Robert A. 1993. Exotic forest insects and diseases in North America: patterns and recent arrivals. In: North American forestry commission forest insect & disease working group; 1993 October 13–15; Veracruz, Mexico. 1–12.

Haack, Robert A.; Byler, James W. 1993. Insects & pathogens. Regulators of forest ecosystems. Journal of Forestry. 91(9): 32–37.

Harvey, Alan E.; McDonald, Geral I.; Jurgensen, Martin F.; Larsen, Michael J. 1993. Microbes: driving forces for long-term ecological processes in the inland Northwest's cedar-hemlock-white pine forests. *In:* Interior cedar-hemlock-white pine forests: ecology and management symposium proceedings; 1993 March 2–4; Spokane, WA. USDA Forest Service, IMRES: 157–163.

Holling, C.S. 1973. Resilience and stability of ecological systems. Annual Review Ecological Systems 4: 1–23.

Liebhold, Andrew M.; MacDonald, William L.; Bergdahl, Dale; Mastro, Victor C. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. Forest Science Monographs. 30: 1–49.

Mattson, William J.; Haack, Robert A. 1987. The role of drought in outbreaks of plant-eating insects. BioScience. 37(2): 110–118.

McClure, Mark S. 1989. Evidence of a polymorphic life cycle in the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae). Annals of the Entomological Society of America. 82(1): 50–54.

Monnig, Edward; Byler, James. 1992. Forest health and ecological integrity in the northern Rockies. FPM Rep. 92–7. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region. 18 p.

Oliver, C.D. 1981. Forest development in North America following major disturbances. Forest Ecology and Management. 3: 153–168.

Runkle, J.R. 1984. Development of woody vegetation in treefall gaps in a beech-sugar maple forest. Holarctic Ecology. 7:157–164.

Runkle, James R. 1985. Disturbance regimes in temperate forests. In: The ecology of natural disturbance and patch dynamics. London: Academic Press: 17–33.

Schowalter, T.D. 1981. Insect herbivore relationship to the state of the host plant: biotic regulation of ecosystem nutrient cycling through ecological succession. Oikos. 37: 126–130.

Schowalter, Timothy D. 1985. Adaptations of insects to disturbance. *In:* The ecology of natural disturbance and patch dynamics. London: Academic Press: 235–252.

Shaw, C.G., III; Kile, G.A. 1991. *Armillaria* root disease. Agric. Handb. 691. Washington, DC: U.S. Department of Agriculture.

Stephenson, S.L. 1986. Changes in a former chestnut-dominated forest after a half century of succession. American Midland Naturalist. 116: 173–179.

Twery, M.J.; Patterson, W.A. 1984. Variations in beech bark disease and its effects on species composition and structure of northern hardwood stands in central New England. Canadian Journal of Forest Research. 14: 565–574.

van der Kamp, B.J. 1991. Pathogens as agents of diversity in forested landscapes. Forestry Chronicle. 67: 353–354.

Wargo, P.M. 1977. *Armillariella mellea* and *Agrilus bilineatus* and mortality of defoliated oak trees. Forest Science. 23: 485–492.

Wargo, P.M. 1981. Defoliation and secondary-action organism attack: with emphasis on *Armillaria mellea*. Journal of Arboriculture. 7: 64–69.

White, P.S.; Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. In: The ecology of natural disturbance and patch dynamics. London: Academic Press: 3–13.