

EFFECTS OF DEFOLIATION BY GYPSY MOTH

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ABSTRACT

Defoliation of trees by the gypsy moth (*Lymantria dispar* L.) has many and varied effects. It causes economic losses through lost forest production and reduced aesthetic qualities of the forest. However, defoliation may improve habitat for many species of wildlife and contribute to increased diversity of eastern forests. Effects on water resources, recreation, and other values differ with different levels of defoliation and different forest types. Primary and secondary effects of defoliation on forested ecosystems are reviewed.

INTRODUCTION

Defoliation of forests by insects is a ubiquitous problem which has been studied in many systems (Kulman, 1971). Assessments of damage caused by forest defoliators must include the many ways in which forests are changed by defoliation (Alfaro 1988, Stark 1987, Schowalter and others 1986). Defoliation of trees by the gypsy moth (*Lymantria dispar* L.) in particular has profound effects on many levels. There are direct effects on the trees themselves, effects on the other components of the forest ecosystem such as animals and other plants, and effects on people, both direct and indirect. Since the gypsy moth was introduced in 1869, its range has been limited to northeastern North America. However, the insect's range has been expanding steadily and nearly all forested areas in North America may eventually be affected to some degree.

The problem is most important on oaks (*Quercus* spp.) in the Northeast, though many other species are affected. In the forests of the region oaks are both the most favored hosts of the gypsy moth and the most valuable hardwood timber species. Mosher's (1915) early work defining feeding preferences of the gypsy moth in North America (Table 1) has been confirmed by more recent studies (Gansner and Herrick 1985, Fosbroke and Hicks 1989). Additional work on host species with a more southerly range indicates that sweetgum and loblolly pine (Barbosa and others 1983, 1986) may be important hosts as the insect invades the South. Oaks in the South certainly remain an important factor in the vulnerability of the forest because there are so many overtopped trees (McGee and Bivens 1984), which are the most likely to die after defoliation (Herrick and Gansner 1987).

EFFECTS ON TREES

The effects of defoliation on trees is due primarily to the reduction of carbohydrate production (Kozlowski 1969, Heichel and Turner 1976), which results in increased vulnerability to pests that kill stressed trees, growth loss, and subsequent indirect changes in the forest. In a multi-layered, mixed-species forest stand, defoliation occurs first on understory trees and later on overstory trees. Similarly, trees in poor condition often are defoliated before their counterparts in good condition. Mortality is most prevalent during and after the initial outbreak of gypsy moth; some stands may experience 80-100% mortality of overstory trees (Campbell and Sloan 1977, Gansner and Herrick 1984). This initial outbreak may last from 3 to 10 years in a region, and individual stands may suffer moderate to heavy defoliation in more than half of those years (Herrick and Gansner 1987). Such extensive damage has not been found in most defoliated stands, however. Even in areas with highly susceptible forest types, many stands experience few defoliations. This phenomenon

results in a majority of the forest suffering minor or moderate levels of mortality (Gansner and Herrick 1984).

Mortality

Losses to mortality necessarily are correlated with frequency and intensity of defoliation, which in turn are correlated with tree species according to gypsy moth feeding preferences (Brown and others 1988, Stephens 1971, 1981b, Hicks and Fosbroke 1987, Campbell and Sloan 1977, Stalter and Serrao 1983, Quimby 1987). However, there are distinct differences among species in their ability to survive defoliation. Hemlock (*Tsuga canadensis*) is among the most vulnerable species despite its status as only a moderately preferred host (Gottschalk and Twery 1989). Hemlock seldom survives even one complete defoliation (Stephens 1988), whereas some oaks on dry sites may survive repeated defoliations indefinitely (Houston and Valentine 1977, Bess and others 1947). The differences are due to many factors, including where the tree's reserve energy is stored, how much energy is required to refoliate, and how much energy is needed to maintain respiration during the refoilation process (Wargo 1981a, 1981b). For example, hemlock's reserves are stored in its needles, so after defoliation there is no available reserve energy, no refoilation occurs, and the tree dies. Which agent causes tree mortality is dependent on locality and other contributing factors (Staley 1965, Starkey and Oak 1989).

Diameter Growth

The standard approach to measuring growth loss for an individual tree has been to record changes in diameter growth at breast height (dbh). Baker (1941) found growth losses directly proportional to the extent of defoliation. Such losses are over and above losses to mortality, and are likely to be the more important component of forest productivity impact after the initial wave of mortality following gypsy moth's first outbreak in an area. Diameter growth loss may, however, overestimate total volume losses by up to 20% because of changes in distribution of wood production. During and shortly after a defoliation episode growth at dbh is reduced by a greater proportion than growth at points higher in the bole (Twery 1987). An additional problem with analysis of growth only at dbh is the difficulty of separating defoliation from other factors such as drought or extreme temperatures (Mott and others 1957).

Volume Growth

Volume growth decreases when a tree is defoliated. In southern New England, Twery (1987) found an average decrease of 20% in stem volume growth of oaks in any year a tree was defoliated compared to the previous, undefoliated year. On average, chestnut oak is affected the most, showing an average growth loss of 33% in such years. Some individual trees, however, showed annual decreases of 50–65% in volume growth when completely defoliated. European studies reported by Gradwell (1974) show similar effects, averaging 59% for heavily defoliated trees.

Growth loss in an individual tree is not confined to the years of defoliation but is evident up to 3 years after a defoliation episode (Twery 1987, Wargo 1981a). Defoliation in a stand of oaks reduces the overall growth of survivors considerably, the effect is carried beyond the year of defoliation, and the growth of the stand recovers after about 3 years. Certainly, some of this effect is a result of reduced leaf area in recovering trees (Heichel and Turner 1976, Wargo 1981a, Picolo and Terradas 1989). For a 2-year defoliation episode that affects forests once each decade, Twery (1987) estimated the average overall reduction in volume increment at 9.7% per year for the stand over the decade, excluding mortality.

Table 1: Categorization of gypsy moth host preferences (adapted from Mosher 1915, Mauffette *et al.* 1983, and Montgomery, this proceedings).

Susceptibile: species readily eaten by gypsy moth larvae during all larval stages.

Overstory: apple, basswood (American linden), bigtooth and quaking aspen, gray, paper (white), and river birch, larch (tamarack), mountain-ash, all oak species, sweetgum, willow.

Understory: hawthorn, hazelnut, hophornbeam, hornbeam, serviceberry, witch-hazel

Resistant: species fed upon when preferred foliage is not available and/or only by some larval stages.

Overstory: beech, black (sweet) and yellow birch, blackgum (tupelo), Ohio and yellow buckeye, butternut, sweet and black cherry, eastern cottonwood, cucumbertree, American and slippery elm, hackberry, all hickory species, boxelder, Norway, red, and sugar maple, pear, sassafras, black walnut, chestnut, eastern hemlock, all pine species, all spruce species.

Understory: blueberries, pin and choke cherry, paw paw, persimmon, redbud, sourwood, sweetfern.

Immune: species that are rarely fed upon.

Overstory: all ash species, baldcypress, northern catalpa, eastern redcedar, balsam and fraser fir, American holly, horsechestnut, Kentucky coffee-tree, black and honey locust, mulberry, sycamore, tuliptree (yellow-poplar).

Understory: all azalea species, dogwood, elderberry, grape, greenbrier, juniper, mountain, silver and striped maple, rhododendron, all rubus species, sheep and mountain laurel, spicebush, sarsaparilla, all viburnum species

Measurements of overall mortality and percentage volume loss per unit land area may not be meaningful, however. The mortality of subcommercial individuals may actually improve the growth of the remaining stand through a thinning effect, or a decrease in growth in an immature stand may be partially recovered by the delay it induces before competitive crowding occurs (Twery and Gottschalk 1988). Twery (1987) found that oaks that remained undefoliated while their neighbors were defoliated actually grew much better than average during the year of defoliation. Similarly, Campbell and Garlo (1982) reported increased growth of pitch pine (*Pinus rigida*) in New Jersey after gypsy moth defoliation of black oaks (*Q. velutina*) in mixed pine-oak stands.

To avoid damage from gypsy moths, Hall (1935) recommended growing pitch pine on Cape Cod, and Behre and others (1936) recommended cutting practices to remove oaks and suggested the planting of conifers. Even earlier, Fiske (1913) and Clement and Munro (1917) were suggesting similar ways to reduce the damage from gypsy moth by stand conversion or maintenance of vigorous stands. This approach is currently impractical in many areas because of the high value of oaks, a lack of alternative commercial timber species, and the large area involved. In areas such as

Cape Cod or the Pinelands of New Jersey, though, stand conversion may be worthwhile for timber production.

Quality Changes

Defoliation and resultant slow growth in oaks have negative implications for wood quality. Growth during years when an oak is defoliated consists almost exclusively of large, earlywood vessels. This wood has a much lower specific gravity than latewood. Because strength is directly related to density, several adjacent rings excessive earlywood may induce manufacturing problems or structural failures in use (Hill 1954, Panshin and de Zeeuw 1970). It is not the low density of the wood, per se, that causes the problems. In fact, very slowly grown oak brings the highest value in parts of Europe. Rather, it is the alternation of layers of unequal density which may cause problems with drying, veneer slicing, or other machining processes. Reduction in wood quality may also result from defoliation via the formation of epicormic branches from latent or adventitious buds. These branches produce knots in previously clear areas of the bole, lowering the production of high-value products like veneer.

Qualitative changes in foliage also result from defoliation. Schultz and Baldwin (1982) found significantly higher quantities of tannins and other phenolics in leaves of red oak trees which had been defoliated previously by the gypsy moth. The regrowth foliage of defoliated trees also has been shown to fix carbon at higher rates per unit area than does primary foliage (Heichel and Turner 1983). However, because the leaf area was smaller and the duration of net production was shorter, no defoliated trees approached the net production of undefoliated trees.

TIMBER VALUES

Mortality, growth losses, and changes in wood quality, all have direct secondary effects on timber values. The standing crop of timber degrades quickly after mortality, causing losses of up to 25% within 5 years (Garges and others 1984, Karasevich and Merrill 1989, Gottschalk and others 1989). Because in some areas as much as 50-90% of the forest is killed, (Herrick and Gansner 1987) these losses can be extremely disruptive to timber markets. The quality of the wood for pulp and papermaking is not degraded substantially in the first 5 years after death of the tree (Kessler and Labosky 1988). The most dramatic effect is the immediate downgrading of potential veneer logs to sawtimber as the tree dies, resulting in value losses of 50% or more. Also affected is the potential growth in value of future crops. Stands that are understocked due to mortality following defoliation cannot utilize the site's growing potential fully, and fully stocked stands with trees that grow more slowly because of defoliation both contribute to the decreased value growth (Gansner and Herrick 1982; Herrick and Gansner 1988). Additionally, the threat of gypsy moth may cause managers to change their land management strategies from faster growing species toward those that are less susceptible to defoliation. For example, although sweetgum (*Liquidambar styraciflua*) grows faster than sycamore (*Platanus occidentalis*) on the coastal plain of Virginia, its higher susceptibility to gypsy moth may result in the management of more sycamore plantations.

LONG-TERM ECOLOGICAL EFFECTS

Further secondary effects on the forest can be found by examining shifts in the ecological balance of affected stands. By removing leaves from some trees and not others, the gypsy moth can change the competitive balance between species and individuals. Decreased leaf area results in decreased carbohydrate production and increased demand for carbohydrate reserves to refoliate. Trees stressed this way lose advantages they may have had in direct competition for growing space, but the effects are also more far reaching. The stresses play a role in allowing secondary organisms such as the two-lined chestnut borer (*Agrilus bilineatus* Weber) and shoestring root rot

(*Armillaria* spp.) to invade and kill a tree (Wargo 1977). Defoliated trees lose seed production capabilities both in the year of defoliation and in at least one subsequent year (Gottschalk 1990). Mortality of trees in a stand also opens more light, space, and other resources to the remaining trees, which are likely to be a different balance of species than those trees which died. In a study of red oak growth in southern New England, Kittredge (1988) found greater growth among oaks that competed with other species compared to those in purer stands. Mixed stands, which are less susceptible to the gypsy moth, thus also may provide faster growing oaks than predominantly oak stands.

Replacement of stands that suffer extensive mortality also is affected by defoliation. Because oak seedlings are also defoliated in extended outbreaks (Shaw 1974), advance regeneration of species that are less susceptible to the gypsy moth is favored. Oaks, which often gain their place in a new stand through stump sprouts, may lose dominance because trees that die from secondary agents after defoliation cannot generate vigorous sprouts. Work by Allen and Bowersox (1989) indicates the extent of this replacement of oak. Stands in Pennsylvania that were dominated by oak before defoliation had only minor proportions of oak in the understory 6-7 years after mortality, especially on the Allegheny Plateau. Although low proportions of oak suggest that it will not be an important component in the next generation of forests, work by Oliver (1978) indicates that a small number of oaks in young stands may gain dominance after the stands reach 50 years of age. In susceptible stands other than oak, such as southern pine-sweetgum stands on the coastal plain of the Southeast, similar selective pressures may shift the species composition toward those species which are less vulnerable to defoliation.

Effects on other forest vegetation may also be great. Shrub and herb density and cover increase dramatically after overstory mortality due to increases in available light, moisture, and nutrients. The increased light also warms the soil sufficiently to induce germination of seeds buried in the forest floor. Short-term changes from defoliation, additional light for the months of June and July, and an extra flush of nutrients from the frass and partially eaten leaf fragments, cause little detectable change in the understory in the absence of tree mortality. Apparently, any response induced in the understory in one growing season is suppressed by the regrowth of the overstory the following season. Collins (1961) found that understory trees that were not defoliated in the same season as their overtopping neighbors had increased growth, but no such effects were found by Twery (1987) or by Hicks and Hustin (1989).

WILDLIFE

Wildlife species are affected by gypsy moths in many ways, primarily through changes in habitat. Many of the forest vegetation changes described above are favorable to many species of wildlife, so the consequences of defoliation by gypsy moth are not uniformly negative. For example, unsalvaged dead trees create more snags for cavity-nesting animals, and limbs and boles that fall to the forest floor provide additional cover or shelter for small mammals and other ground-dwelling animals. The extensive growth of understory herbs, shrubs, and grasses produces a bounty of food and cover for many more wildlife species. The food may be in the leaves of the new vegetation or in the fruits of such shrubs as blueberry (*Vaccinium* spp.) or hazelnut (*Corylus* spp.). The increased vertical stratification of the foliage in the forest benefits many species of birds.

Potentially detrimental effects on wildlife include both the short- and long-term loss of hard mast production, especially acorns. Many wildlife species supplement their diet with acorns, so a loss of this resource reduces the capacity of an area to support some species, especially the gray squirrel (*Sciurus carolinensis*). Increased light reaching the forest floor after tree mortality causes higher stream temperatures and thereby affects a stream's ability to support fish or other aquatic life. Increased woody debris in streams also affects the quality of the aquatic habitat. Increased

patchiness and stratification of the forest resulting from selective tree mortality may improve the habitat for some species of wildlife, but it also may eventually decrease the capacity of a forest to support those species which prefer extensive undisturbed areas. Pileated woodpeckers (*Drycopus pileatus*) are likely to benefit from gypsy moth because they prefer areas with large trees and large quantities of dead woody material, and adjust their territory size in response to changes in such structural variables (Renken and Wiggers 1989).

According to one recent study¹, numbers of species and total abundance of non-game birds increase with the disturbance created by gypsy moth, while other studies have reported inconclusive results (DeGraaf 1987, Cooper and others 1987). As mentioned previously, gray squirrels are adversely affected by gypsy moth through loss of their primary food supply (Gorman and Roth 1989). Other small mammals experience different effects depending on the specific result of a disturbance (Smith 1985). White-footed mice (*Peromyscus leucopus*) seem adaptable in their choice of species of acorns depending on availability (Briggs and Smith 1989), and if other food sources are available they may not be affected by lack of mast in any given year. Gypsy moth pupae and larvae are commonly part of the spring and summer diet of the opportunistic small mammals of the forest floor (Smith 1985). Invertebrates on the forest floor have not been studied in areas disturbed by gypsy moth, but Jennings and others (1988) found increases in abundance and diversity of forest invertebrates after strip cuttings and similar disturbances caused by spruce budworm (*Choristoneura fumiferana* Clem.).

Endangered species of animals also may be affected by the gypsy moth. For example, an endangered salamander in northern West Virginia lives on the floor of oak stands. Destruction of its habitat by defoliation and mortality of the overstory trees and subsequent changes in the temperature regime of the forest floor must be considered among the potential effects of gypsy moth. The Virginia big-eared bat (*Plecotus townsendii virginianum*) also may be affected by gypsy moth and human attempts to control the defoliation. This bat feeds on insects within the forest, often foraging on the tree trunks. Defoliation that results in mortality of trees may perhaps be more likely to deplete the bat's food source than a chemical spray to control gypsy moth, although Doane and Schaefer (1971) did find effects on some non-target species of insects and birds from aerial application of insecticides.

WATER RESOURCES

Another indirect effect of defoliation by gypsy moth extends to water resources. Gypsy moths can influence both the quantity and quality of water in watersheds managed for their yield of supplies of drinking water. The quantity of water yielded from a watershed increases when it is defoliated (Corbett and Lynch 1987) because fewer leaves are available to transpire moisture from the soil. Quality, however, may suffer greatly, as the increased detritus falling to the forest floor decomposes in the warmest part of the year, exporting large amounts of nitrogen and other nutrients in the streams (Swank and others 1981) and increasing amounts of fecal coliform (Corbett and Lynch 1987).

¹Greer, R.D.; Whitmore, R.C.; Smith, H.R.; Twery, M.J. (In Review). Effects of gypsy moth defoliation on wildlife populations: a modelling study.

PEOPLE

Gypsy moths affect people directly through the reduction of aesthetic and recreational benefits from the forest, economic losses, and public health problems. Some of these effects are more easily quantifiable than others, but all can be important factors in assessing the overall impact of defoliation by the insect.

Aesthetic effects can be divided into effects on distant, panoramic vistas and those on interior views of the forest. Scenic overlooks from highways such as Skyline Drive in Shenandoah National Park lose a great deal of their attractiveness when the hillsides are brown in June and July from a current defoliation. However, if mortality occurs the understory will fill in, and the fact that the hillsides are green in the appropriate season prevents many people from noticing any major change in distant views of the forest. If dead trees are salvaged, however, views of mountains with large cutting operations show evidence of the disturbance for a number of years. Interior views, such as those from hiking trails, produce a more complicated reaction in viewers. The unpleasant effect of being pelted with caterpillar droppings during an outbreak is undisputed, as is the negative reaction to walking through a forest of defoliated trees. In the longer term, though, there is not a linear correlation between the amount of gypsy moth-induced mortality and the evaluation of scenic beauty by viewers of the forest.

Freimund (1990) found an increase in scenic beauty in stands with light to moderate amounts of tree mortality after defoliation by gypsy moth, while heavy mortality caused large decreases in the public's estimation of scenic beauty. On the other hand, if an increase in sunlight passing through the open canopy induces significant amounts of flowering of understory plants, some of the negative reaction to overstory mortality may be offset. Within-stand visual preferences generally favor large trees and extended visual penetration (Rudis and others, 1988). If mortality after defoliation is concentrated in the smaller, overtopped trees (Gansner and Herrick, 1984), the net result may be that some forests become more attractive.

Effects on recreation differ from aesthetic effects primarily in high-use areas. In heavily used areas like picnic grounds and camping sites, gypsy moth's primary role is that of a severe nuisance. During its peak, a gypsy moth outbreak can create the effect of rain from frass and leaf fragments. Severe defoliation on the Allegheny National Forest resulted in a 20% reduction in recreational use of affected areas during the outbreak (Goebel, 1987). Longer term effects include the creation of hazard trees in recreation areas when large, defoliated trees die. While snags are a necessary and beneficial part of the forest in general, large dead trees are unwelcome in areas where they might be likely to harm people when they fall.

The public health problems created by gypsy moth are less obvious but nonetheless important secondary effects of gypsy moth infestations. Contact with larval hairs has been documented to cause skin rashes and other allergic reactions (Tuthill and others, 1984, Shama and others, 1982). Although most individuals suffer no serious, long-term health problems, a community-wide outbreak of rashes during heavy infestations can have a significant economic effect.

Residential property also can be affected greatly by defoliation. The same effects related to recreation are applicable to people's back yards. In addition, the loss of yard trees can cause large reductions in home values (Payne and others 1973). Trees help cool a home site in summer and protect a home from winter winds. Loss of yard trees is certain to increase residential energy use. The economic impact on real estate values may well be one of the larger indirect costs of defoliation. The amount spent by homeowners to prevent defoliation of their trees in areas such as southern New England far surpasses the money spent to protect forests.

SUMMARY

The gypsy moth has affected life in the eastern United States for over a century. It has many adverse effects on the ecosystem, but on some sites some components benefit from either the defoliation itself or the ensuing mortality. The loss of leaves causes stress to the trees that becomes evident through decreased growth and increased vulnerability to secondary, mortality-causing organisms. Because the gypsy moth is a selective feeder, the balance of competition between trees and other vegetation changes, inducing long-term ecological changes. Many kinds of wildlife benefit from the kind of forest disturbance the gypsy moth causes, but some are detrimentally affected. Effects directly on people are through changes in recreational and aesthetic values of forested areas and in the form of public health problems. Despite the severe effects of repeated defoliation over many years, there is considerable evidence that the hardwood forests, and oaks in particular, will continue to be an important part of the landscape of the eastern United States (Stephens 1971, 1981a, Stephens and Waggoner 1980, Gottschalk and others 1989).

Much is known about the connections among the effects of defoliation, but much remains to be discovered. Quantification of the effects is easiest where monetary values can be applied directly, such as timber values. Prediction of the reactions of forest ecosystems where the gypsy moth has not yet invaded will require considerable effort, but advance warning can help minimize damage from defoliation. Among the most difficult questions yet to answer are the causal mechanisms involved in many of the aforementioned interactions. Only when we know how changes in the forest ecosystem interact will efficient and effective integrated methods to manage gypsy moth be possible.

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