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Effects of *Lymantria dispar*, the Gypsy Moth, on Broadleaved Forests In Eastern North America

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Lymantria dispar (L.) (the gypsy moth), a species native to Eurasia, was introduced to North America in the late 1800's. Since its introduction, *L. dispar* has plagued the eastern deciduous forests causing severe defoliation, and sometimes subsequent disease and/or death. Many efforts have been made to eradicate the leaf-munching caterpillar. These efforts include biological control using parasites, fungi, and viruses, silviculture methods, insecticide application, as well as public education about *L. dispar* transport. Some management techniques have been shown to reduce population numbers, but most just aim at preventing future dispersal and growth. New populations, however, are introduced or reintroduced as others are being eradicated requiring an ongoing effort to monitor and manage the exotic species.

Restoration ecologists are also plagued by *L. dispar*'s propensity to reoccur. Forest restoration may be achieved with satisfaction only to find that the moth has returned for yet another round of defoliation. The species' life cycle and the context in which the population exists presupposes the timing and type of restoration attempted. With its capacity to destroy large forest stands and its evasiveness to complete eradication, *Lymantria dispar* poses an indefinite problem to the restoration ecologist, forester, or conservationist that strives to protect the health, balance, and survival of eastern broadleaved forests in North America.

Lymantria dispar: An Overview

Life History

Lymantria dispar goes through four stages of development: the egg, larva (caterpillar), pupa (cocoon), and moth phases (Figure 1). These stages occur over the course of a year, with eggs overwintering for eight to nine months attached to trees, rocks, or other stationary objects. Each egg mass is approximately 1-1/2 inches long (3.8 cm) by 3/4 inches wide (1.9 cm). Smaller egg masses usually indicate that a population of the species is in decline (Katovich and Haack 1991). Inside of each egg mass, 300 to 1,000 eggs lay within a thin covering of yellowish hairs (setae) from the abdomen of the female moth (USDA 1990). In this egg stage, the first three weeks consist of embryonation followed by a period of dormancy, which is characterized by diapause development mediated by cold and warm conditions (Keena and ODell 1994). Eggs can withstand temperatures below –22 to –25° F (-30 to -31.7 C) if insulated by snow or laid in protected conditions.

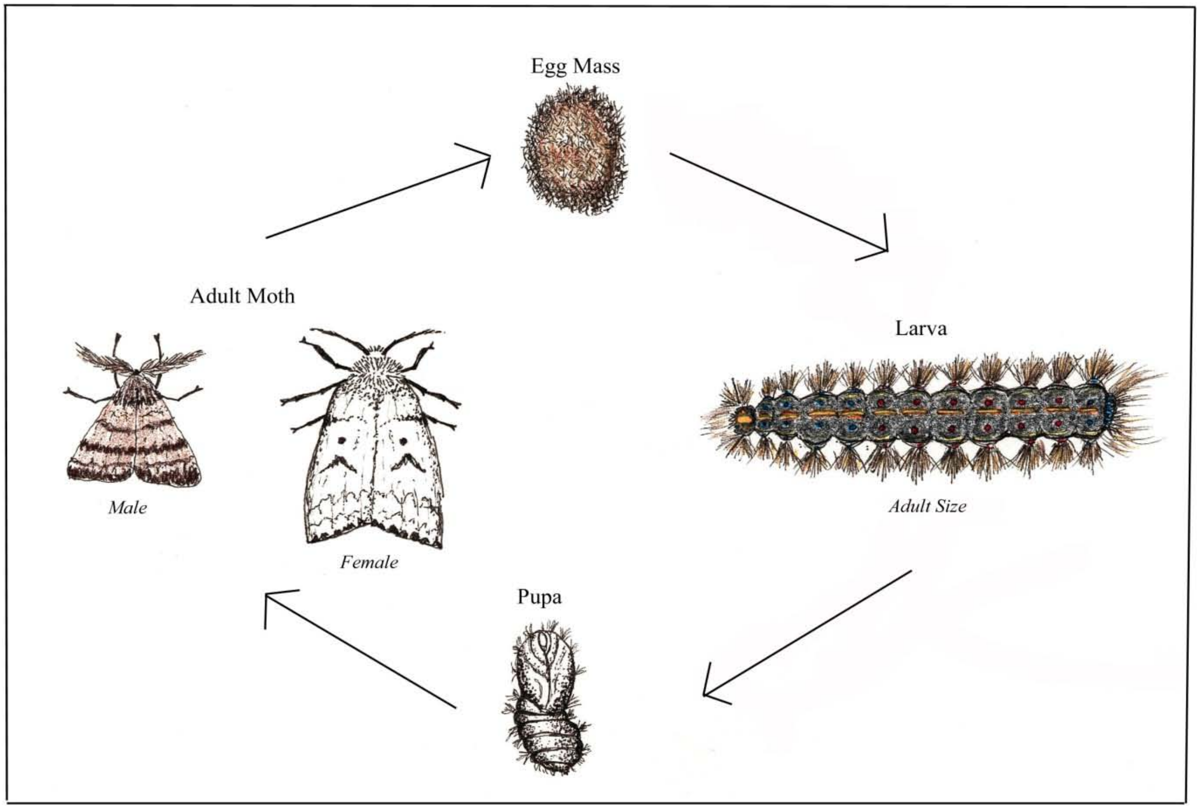

Figure 1- The four stages of development of *Lymantria dispar* (adapted from Mollenhauer, 1990, pg. 24)

Eggs hatch in early spring to mid-May, coinciding with leaf bud of most hardwood trees. After hatching, the caterpillars feed for six to eight weeks on leaves from trees in urban settings, rural areas, and forest stands. In this stage, *L. dispar* can be clearly identified by its six raised pairs of red spots and five raised pairs of blue spots on its dark colored back, as well as being quite hairy (Fig. 1). It is important to note the difference at this stage of *L. dispar* versus two other common tree-feeding caterpillars, *Malacosoma americanum* (Eastern Tent Caterpillar) and *Malacosoma disstria* (Forest Tent Caterpillar).

Larvae progress to adult stage by going through a series of molts, increasing in size through each molt. In between each molt is a stage called instar. Male larvae will usually go through five instars, whereas females will go through six (McManus et al. 1999). Keena and Odell (1994) have observed that as many as eleven instars may be reached before pupation. At the end of their last instar, both male and female larvae will reach a final length of 1-1/2 to 2-1/2 inches (3.8 to 6.4 cm) long (McManus et al 1999).

McManus et al. (1999) described the instar stages in their relation to levels of leaf foraging. In the first three instars, larvae will stay within the crowns of host trees and chew small holes in leaves. The feeding, during these instars, takes place on the outer edge of the leaf and moves toward the center. In the fourth instar stage, and when larvae counts are high, larvae feed continuously day and night until the host tree is completely defoliated. However, when populations of *L. dispar* are sparse, light intensity determines movement of the larvae up and down the tree. For example, when the sun comes up the larvae crawl down the trunk of the host tree to rest during the daylight. They may hide in crevices, under branches, or underneath leaf litter providing an opportunity to predators. When the sun has set, larvae then climb back to the top to resume feeding on host leaves. It is during this final instar stage that the most leaf consumption occurs (roughly 85% of total consumption) (Katovich and Haack 1991).

Following a series of molts and feeding, the larva enters the pupal (cocoon) stage, where it resides for ten to fourteen days. Upon emerging from dark-brown pupal cases (about 3/4 to one inch long; 1.9 to 2.5 cm), the male moth flies away on grayish-brown wings with a 1-1/2 inch (3.8 cm) wingspan. Male moths are smaller in size than females and are brown in color with conspicuous, feathery antennae. Both male and female moths have dark wavy bands across their forewings. Female moths emerge and immediately begin emitting a chemical attractant, or pheromone, which attracts male moths. The females are white-winged, although North American and European varieties are unable to fly. In contrast, the female *L. dispar* of Asia has the capability to fly, and therefore travel many miles in the mating phase (Liebhold 1998).

In their adult stage, the moths focus on mating and laying eggs. In fact, mating often takes place on the day of emergence from the cocoon, followed immediately by egg deposition. No feeding occurs during this final stage. Typically, this completion of the life cycle takes place between July and September on branches and trunks of trees, or any other sheltered location.

Outbreaks in populations of *L. dispar* usually last two to four years and then collapse. Collapses usually result from viral or fungal disease, parasitic attack, predation, starvation, or unfavorable climatic conditions (McCullough and Bauer 2000). Currently, the strategy used by most government agencies is to prevent population outbreaks in the first place by monitoring and managing populations.

Geography

Lymantria dispar is native to most of temperate Eurasia, where it has existed for thousands of years (Liebhold 1998). Because of its interesting life history, *L. dispar* has been studied by many entomologists, including Leopold Trouvelot. Trouvelot brought the moth from Paris to Massachusetts in the late 1800's. While studying the exotic in his home, in 1869, the moth was accidentally released in various stages of life. Its first notable outbreak occurred in 1889 around the Glenwood and Medford areas of Massachusetts, resulting in a complete destruction of foliage (Forbush and Fernald 1896). Since then, *L. dispar* has progressed to the south and west at a rate of five to fifteen miles (8 to 24 km) per year (Katovich and Haack 1991).

Dispersal of *L. dispar* occurs both naturally and artificially. With natural dispersal, newly hatched larvae hang from silken threads tied to host trees and are carried off by the wind for distances of up to a mile (1.6 km). Caterpillars can disperse numerous times before settling down to feed. With artificial dispersal, which has been more successful for the moth, people inadvertently transport egg masses up to thousands of miles on infested cars, firewood, household items, and other possessions (McManus et al. 1999). As a result, moths have been trapped in states such as Washington, Oregon, California, Utah, and Florida. Both dispersal methods have been monitored and subsequently incorporated into control strategies.

L. dispar has been found throughout North America, including all of the northeastern United States, parts of eastern Canada, the southeast, the midwest, and in Michigan and Ontario (Liebhold 1998). Most populations of the exotic species are of European origin, although recently there have been introductions of the Asian population (Liebhold 1998). The Asian variety is, of course, more of a concern since its females are capable of flight and therefore have the potential to spread populations much more rapidly and over greater distances.

Impacted ecosystems

L. dispar larvae feed on more than 500 plant species worldwide, and many indigenous to North America. Susceptible overstory species include *Malus sylvestris* (apple), *Tilia spp.* (basswood), *Populus grandidentata* (bigtooth aspen), *Populus tremuloides* (quaking aspen), *Betula spp.* (birches), *Acer negundo* (boxelder), *Larix spp.* (larch), *Sorbus americana* (American mountain ash), *Quercus spp.* (oaks), *Liquidambar styraciflua* (sweetgum), and *Salix spp.* (willow) (Liebhold et al. 1995). Preferred understory species include *Alnus spp.* (alder), *Crataegus spp.* (hawthorn), *Corylus spp.* (hazelnut), *Carpinus sp.* (hornbeam), *Amelanchier spp.* (serviceberry), and *Rhus spp.* (sumac) (Ravlin and Stein 1999). Some species are considered resistant to the caterpillar unless associated with susceptible species. These include *Tsuga canadensis* (eastern hemlock), *Betula alleghaniensis* (yellow birch), and *Pinus strobus* (eastern white pine). If a preferred species is not available, the caterpillars may even feed on *Acer rubrum* and *Acer saccharum* (red and sugar maple), *Fagus grandifolia* (American beech), and *Ulmus americana* (American elm). Katovich and Haack (1991) have found that early successional stages of northern hardwood forests that have large populations of *Populus spp.* (aspen), *Betula papyrifera* (paper birch), and *Quercus spp.* (oak) are more likely to sustain damage than later successional stages.

The effects of *L. dispar* are largely dependent on the amount of foliage that has been consumed, the status of the tree prior to defoliation, the number of consecutive defoliations, the host species, as well as the amount of available soil moisture (McManus et al. 1999). McManus et al (1999) describes a few circumstances. If only 50 percent of the host tree's crown has been defoliated, the majority of hardwoods will have only a slight loss in radial growth. However, if more than 50 percent of the crown is defoliated, most hardwood species will refoliate or produce follow-up foliage by midsummer. Trees that are healthy prior to defoliation can survive a few repeated defoliations of greater than half the foliage cover.

When *L. dispar* populations are high, defoliation can occur on up to 13 million acres in just one season (USDA 1990). Defoliation of susceptible trees usually does not instantly kill them, but it does sacrifice their health. Trees that are weakened by defoliation show signs of dying back twigs in the upper crown and sprouting old buds on larger branches (McManus et al. 1999). If weakened by consecutive defoliations, secondary pests, such as twolined chestnut borer and armillaria root rot, are the more common cause of death (Katovich and Haack 1991). Once forests have been defoliated, beautiful summer landscapes turn over to a barren winter-like scene.

Hollenhorst et al. (1993, in Rosenberger and Smith 1998) assessed the impact of *L. dispar* and its management on scenic beauty in eastern hardwood forests. In one study area in Somerset County, Pennsylvania, sample plots with tree mortality ranging from six to 98 percent were chosen for photographic representation (Hollenhorst et al. 1993, in Rosenberger and Smith 1998). It was discovered that with up to 30 to 40 percent tree mortality, scenic beauty actually increased. Reasons for an increase in scenic beauty are likely due to the increased amount of sunlight reaching into the stands. With increased sunlight, vegetative regrowth occurs that includes flowering species such as *Kalmia latifolia* (mountain laurel). A gain in visual penetration into the forest stand was also noted to increase its scenic beauty. However, scenic beauty rapidly diminishes beyond 30 to 40 % tree mortality.

The moth can also be an annoyance for people living in infested areas. Short-term damage from tree defoliation includes the presence of leaf fragments, barren trees, the abundant presence of caterpillars, and frass (caterpillar droppings). Exposure to *L. dispar* hairs can also cause allergic reactions, such as skin or eye rashes and respiratory problems (McCullough and Bauer 2000).

One final point to consider with *L. dispar* defoliation is its impact on water quality and quantity. With severe forest defoliation there will be a reduction in interception by forest canopies as well as transpiration losses. Reduced interception leads to an increase in soil moisture and streamflow, along with an opportunity for increased nutrient leaching. Corbett (1992) has noted that an increase in water yield by as much as 5.4 inches (13.7 cm) on strongly defoliated watersheds, which is equivalent to 146,000 gal/acre (138,175 cu-m/sq km).

Nutrients are also transferred more efficiently to the soil floor with the defoliating effects of *L. dispar*. Corbett (1992) stated that nitrogen return was 68 percent greater, potassium 82 percent greater, phosphorus 21 percent greater, and calcium 27 percent greater on defoliated landscapes versus unaffected areas. Therefore, nutrients are much more susceptible to leaching and are also much more available to plants in the understory.

Monitoring Methods

There are several ways foresters and researchers monitor new infestations of *L. dispar* to determine population trends and set thresholds for management. One method is the use of sticky traps baited with female pheromones. The number of males caught by this method, however, has not been a reliable factor in predicting actual population numbers. Katovich and Haack (1991) suggest a more reliable tool of counting the number of egg masses per acre.

The "five-minute walk" and "fixed radius plots" are two common ways to count egg masses (Katovich and Haack 1991). With the "five-minute walk," a surveyor walks casually without stopping and counts all egg masses from that year as time is recorded. Egg masses per acre are then calculated using regression equations determined by Eggen and Abrahamson (1983). The simplicity of this method only gives a rough estimate of population numbers. With the "fixed radius plots," small trees on two sides, large trees on three sides, ground cover and understory of a 1/40-acre parcel are searched for egg masses. The number of egg masses counted is then multiplied by forty to determine the total number of egg masses per acre.

There have been modeling programs created to describe population dynamics of *L. dispar*. These models have been described by Colbert (1999) and include the Stand-Damage Model, the Gypsy Moth Life System Model (GMSLM), the Reduced Gypsy Moth Life System Model, the Ordinary Differential Equations Model, and the Gypsy Moth Phenology Model (GMPHEN). Colbert and Racin (1995) describe the Stand-Damage Model as a way to simulate the growth of a mixed-hardwood forest stand and coincide it with the effects of various defoliation episodes by *L. dispar*. With the GMSLM, *L. dispar* dynamics can be modeled and coupled with simulated management techniques, such as viral, stand manipulations, or mating disruption (Colbert 1999). The GMPHEN Model can predict *L. dispar* growth from egg hatch to pupal emergence, while matching weather data to the model (Colbert 1999).

Modeling can be a useful tool to aid in understanding population dynamics in association with management techniques, climatic factors, and any other variables that can factor in to the prediction of *L. dispar* propensity for defoliation. Modeling is a tool, not a source for answers, and should be used as a supplement to other research and field studies.

Management Techniques

L. dispar continues to move throughout the United States at a rate of about five to fifteen miles (8 to 24 km) per year (Katovich and Haack 1991). Although this rate does not seem alarming, the ability of the species to disperse by artificial means is astounding. *L. dispar*'s dispersal capabilities have spurred governmental and educational institutions to investigate every possible technique available to manage and control its growth and subsequent spread. Management techniques are continually reexamined and new methods are currently being investigated. However, management and control of *L. dispar* is not a recent endeavor.

Early methods

When initial outbreaks of *L. dispar* were observed in the late 1800's, their impacts were so great that commissions were established to deal specifically with the exotic pest. These commissions outlined plans for the removal of the caterpillar from infested areas, as well as the control of its spread to other unaffected neighborhoods. One such plan was the guarding of roads that lead out of the most infested districts of Massachusetts (Forbush and Fernald 1896). At these road barricades, police inspected all horses and vehicles leaving the area, recording all information about the destination of the traveler, as well as destroying any caterpillars found.

Spraying with various insecticides was also explored early on. Arsenical poisons, such as "Paris green," were sprayed throughout infected areas, with only preliminary lab work assessing the impact of such insecticides on the long term health of humans and other species. Even though there arose much opposition to the control method, spraying continued under government order and police enforcement.

Other chemicals were applied directly to egg masses. Such treatments included the use of carbolic acid, followed by a jet of nitric acid, and the use of creosote. One method was simply to gather the eggs and then kill a large mass of them with the use of a cyclone burner (Forbush and

Fernald 1896). It was also at this time that research on biological control with natural agents began.

Natural control agents

Biological control is the way in which natural enemies maintain lower population densities of *L. dispar*. There are entomopathogens, such as bacteria, fungi, and a nucleopolyhedrosis virus (NPV), that act as biological control agents by causing infectious diseases in the species. One particular fungal species, *Entomophaga maimaiga*, has been isolated as an especially effective natural control agent causing 95 percent mortality of large caterpillars (Reardon and Fuester 1999). *E. maimaiga* is not applied as a direct control. Rather, the spores are spread naturally or collected by hand and spread to new locations. The spores, once released, affect *L. dispar* by landing on and penetrating the skin of larvae. Once inside the caterpillar, the fungus nurses from nutrients in the blood to aid in its reproduction (Reardon and Hajek 1998). Larvae infected with *E. maimaiga* die within a week after invasion.

E. maimaiga is also particularly effective at reducing populations of *L. dispar* because it spreads so rapidly and may be used for large parcel application (Reardon and Hajek 1998). This advantage, however, has questioned the host specificity of *E. maimaiga*. Studies have been performed that tested the effects of the fungus on different insect species in the Lepidoptera (moths and butterflies), Orthoptera (grasshoppers), and Coleoptera (beetles). *E. maimaiga* was found to only affect species of Lepidoptera within the superfamily Noctuoidea, which also contains *L. dispar* (Reardon and Hajek 1998).

A popular biological control agent used to manage *L. dispar* is *Bacillus thuringiensis* var. *kurstaki* (Bt or Btk), a native bacterium found in soil and on plants. Btk HD-1 strain, which has not been genetically modified, is the strain of Btk used with *L. dispar*, since 1961, because of its specificity to caterpillars (McCullough and Bauer 2000). It is a widely accepted control method due to its effectiveness, ease of use, and low toxicity to other animals and the environment. Btk produces spores and protein crystals that when eaten by *L. dispar*, become toxic within the caterpillar's digestive tract. Caterpillars then die two to three days later because of starvation and damage to their system (McCullough and Bauer 2000). Btk is only effective if eaten by the caterpillars and if applied soon after egg hatch, since young caterpillars are more sensitive to Btk than older ones.

Btk is usually sprayed on host tree species in the spring during *L. dispar* outbreak. It is effective for a few days until inactivated by sunlight and microbial activity (McCullough and Bauer 2000). Btk is also different than conventional insecticides, in that it is not man-made and does not affect a multitude of leaf-consuming insects, such as honeybees, lacewings, ladybird beetles, and other beneficial species (McCullough and Bauer 2000). It has also been studied with regards to its impacts on mammals, birds, fish, and humans. The Environmental Protection Agency uses regulatory safeguards and requires toxicology testing on a variety of species, and currently states that the technique poses no significant human health hazards (EPA document #EPA738-R-98-004 1998, in McCullough and Bauer 2000). Although Btk is much more selective than other insecticides, it still harms many foliage-consuming native caterpillars, making its use critical only during peak outbreak times.

The nucleopolyhedrosis virus (NPV) is the final natural control agent causing widespread mortality of *L. dispar*. NPV is a naturally occurring disease that is often referred to as "wilt" since it causes the caterpillar to look soft and limp (Reardon and Fuester 1999). NPV outbreaks coincide with increased population densities of *L. dispar*. As infected caterpillars die, they become inocula for other feeding caterpillars making the spread of this natural agent most effective. NPV transmission can also occur when egg deposition occurs on virus-contaminated surfaces (Reardon and Fuester 1999). Other transmitters of the virus include birds, mammals, parasites, and invertebrates, such as *Cotesia melanoscela* (a braconid wasp) which was shown by D'Amico et al. (1998) to cause early mortality in *L. dispar*.

Reardon and Fuester (1999) found that NPV can cause up to 95 percent mortality of the caterpillar population, which leaves numbers that can only minimally damage subsequent year tree health. In this way, the virus, with its specificity to *L. dispar,* acts as an effective management technique once introduced into an infested landscape. A recent advance in this area has lead to the commercial production of Gypshek, which is a NPV product registered with the Environmental Protection Agency that can be used for ground and aerial application. However, due to its high production cost, many commercial groups have little interest in the development and marketing of Gypshek (Thorpe et al. 1998).

Chemical Control Agents

Chemical agents are another technique used to control populations of *L. dispar*. These pesticides can be stomach and/or contact poisons to the invasive species. One particular pesticide is Orthene (with various other trade names), which is registered for aerial and ground application. With the active ingredient acephate, it is also toxic to bees and some *L. dispar* parasites (McManus et al. 1999).

Sevin is a second chemical agent with the active ingredient carbaryl. It is used with aerial and ground application, and was once the most widely used chemical in control programs (McManus et al. 1999). Other Environmental Protection Agency registered pesticides that are rarely used include methoxychlor, phosmet, trichlorfon, malathion, and synthetic pyrethroids (McManus et al. 1999).

Difluenzuron (trade name Dimilin) is a new type of pesticide that interferes with the larvae's normal molting process. It has no effect on adult insects, but can affect other crustaceans and immature insects that experience molting stages (McManus et al. 1999). The timing of application of this and other pesticides is not as critical as it is with biological control methods. However, chemical pesticides often affect other non-target species and may even be hazardous to human health, making them a less desirable management technique.

Natural predators

Natural predation is often an overlooked opportunity for control of *L. dispar*. There are a number of natural predators of *L. dispar* that have been found to help keep population numbers low and stable for many years. However, the predators are all opportunistic feeders, meaning that they only feed on *L. dispar* if other preferred food sources are scarce. Twenty mammal species feed on the exotic caterpillar, along with some reptiles, fish, spiders, and amphibians with the major vertebrate predator being *Peromyscus leucopus* (white-footed mouse) (Reardon and Fuester 1999). A few of the many natural insect enemies include *Ooencyrtus kuvanae* (wasp), *Cotesia melanoscela* (wasp), *Compsilura concinnata* (fly), *Exorista larvarum* (fly), *Brachymeria intermedia* (wasp) and several species of the Coleoptera family, such as *Calosoma sycophanta* (carabid beetle) (Reardon and Fuester 1999, McManus et al. 1999).

Besides vertebrates and insects, over 38 bird species have been seen to prey on *L. dispar*. Such species include *Picoides pubescens* (Downy Woodpecker), *Cyanocitta cristata* (Blue Jay), *Quiscalus quiscula* (Common Grackle), *Dendroica spp*. (warblers), and *Parus spp.* (chickadees) (McManus et al. 1999, Forbush and Fernald 1896).

Laboratory-Reared Populations

Laboratory rearing of *L. dispar* populations has been ongoing for many years. With laboratory-reared populations, it is possible to genetically modify the species to perform in ways to enhance its management. One such technique has been the sterile insect technique, described by Ridgway and Inscoe (1992). This autocidal technique rears sterilized insects for population suppression. It is successful if the sterile insects interact with the non-sterile, target population, thereby decreasing the number of successful fertile matings that occur.

Lab research has also focused on regulating sex pheromone production, regulating sperm release, characterization of regulating enzymes, understanding blood proteins and egg development, and characterization and isolation of hormones (Kelly 1992). The future holds much opportunity for more research on laboratory rearing, especially in coincidence with a few of the biological control methods introduced above.

Silviculture

Silviculture is a method utilized to manage *L. dispar* populations by manipulating forest stands to reduce preferred host species. By doing so, the stand will be less susceptible to defoliation. The appropriate silvicultural treatment is dependent on the anticipated amount of defoliation, the characteristics of the host stand, and the economic viability of the stand (McManus et al. 1999).

McManus et al. (1999) describes various subsets of the silviculture method of management. By "predefoliation thinning," a stand that is an anticipated host is selectively thinned to reduce preferred species, as well as encourage residual tree growth and seed production. "Presalvage thinning" is used if a preferred host species covers more than 50 percent of the infected area. In this silviculture method, trees that are weakened prior to outbreak are selectively removed. Treatment during an outbreak is usually not recommended with silviculture methods since thinning can cause a shock effect on the forest stand.

Though not a specific silviculture method, harvesting *L. dispar* killed oak timber is a potential economic tradeoff to the forest destruction. Niskala and Kucera (1988) found that *Quercus spp.* harvested within a year after their death can be sold for timber use and wood products. With each year that the dead trees remain standing, they are more susceptible to fungus and insect attacks.

The longer they are left unharvested, the more loss of economic value with a rapid decrease in the number of products they may be used for. If recently killed timber is harvested, though, it may be used as high quality lumber, veneer, railroad ties, pulpwood, and other products.

Discussion of Techniques

There is a considerable amount of research taking place regarding *L. dispar,* its monitoring and management. There is even research on application technology of various insecticides and biological control agents (Bullard 1992). This research has not only evaluated the agent used but also how it is applied. Examples of this include cross wind application versus with wind applications, improving the evenness of effective swaths, and the control of pesticidal drift (Bullard 1992).

Research is also evaluating the effectiveness of management strategies utilized thus far to control the spread of *L. dispar*. Sharov (1998) studied how the Slow-the-Spread (STS) pilot project, initiated by the USDA Forest Service in 1993, worked in diminishing the spread of the exotic species into North Carolina, Virginia, West Virginia, and Michigan. The study found that the rate of population spread declined after 1990 when suppression of isolated outbreaks began. Sharov (1998) also discovered that *L. dispar* populations in Virginia and West Virginia declined due to *E. maimaiga*, with the rates of spread becoming negative.

Thorpe et al. (1998) evaluated the impact of ground-based applications of Gypchek versus Btk treatment. They found that no dose of Gypchek was as effective in reducing *L. dispar* larval populations as Btk. McCullough and Bauer (2000) also support Btk as an effective, easily used management technique for the exotic species.

Blumenthal and Wilt (1998) believe that the health of northeastern hardwood forests is dependent on NPV and *E. maimaiga*. However, Weseloh (1998) believes that if *E. maigaima* is to be effective at all, large populations of resting spores need to be present in coincidence with adequate moisture. If these situations are satisfied, *E. maigaima* will remain an effective natural biological control agent of *L. dispar*.

It appears that Bt, NPV, and *E. maimaiga* are all potentially viable and useful natural control agents. Stand specific factors should be evaluated prior to chosing a technique, whether it is one of the three biological methods described, a chemical method, or a silvicultural technique. Other factors should also be considered when assessing the application of various biological control agents, as well as chemical agents. These factors include the stability of the agent, its ease of handling, residual activity, deposit efficiency, and cost.

Chemical methods are second to biological control methods due to their lack of specificity to the target species *L. dispar*. They also pose health hazards to humans and should not be used on infestations within close proximity to human establishment. It certain circumstances, however, it may be necessary to use a chemical agent in combination with a biological control agent to get desired reductions on *L. dispar* population numbers.

Natural predation is an environmentally safe technique but is not always as effective as some of the biological control methods. This is primarily due to the opportunistic nature of the predators. It is also dependent on their presence, health, and viability within the host stand landscape. Predators can be introduced into landscapes to aid in the control of *L. dispar* if the ecosystem is host to their biological needs. Natural predation is most successful if used in conjuction with other techniques.

Effects of *L. dispar* on Forest Restoration

For the restoration ecologist, population outbreaks may result in a need for restoration of decimated natural forests as well as damage or eliminate previously restored broadleaved forests. The initial condition of a forest stand killed by *L. dispar* and in need of restoration is usually described as a site with little to no living woody vegetation. The key, then, to the timing of this type of restoration requires a clear understanding of the moth's life cycle. A possible timeline for forest restoration efforts would be to use natural control agents, such as Btk or *E. maimaiga*, or chemical control agents on the forest affected by *L. dispar*. This attempt would be to kill any present life form of the species. Treatment is most effective if applied soon after egg hatch, since younger caterpillars are more susceptible than older ones.

The application of control agents should then be followed by a period of monitoring *L. dispar*'s return or survival. One possible monitoring technique described above is the use of female pheromones as bait to trap male species. Two other techniques, the "five minute walk" and the "fixed radius plots," are best to use after egg deposition. These techniques are both common ways to count the number of egg masses in a stand. These two monitoring techniques are best if used throughout planting in late fall, and again in early spring before egg hatch, to identify surviving populations that should be immediately eradicated.

Site preparation can be performed after the application of control agents and throughout the monitoring period. Site preparation should not be too extensive if the restoration is of a stand damaged by previous *L. dispar* defoliation. The soil is often primed with increased nutrients, due to dead timber decomposition, along with increased soil moisture, due to decreased interception and transpiration losses. If no significant nutrient leaching, soil erosion, or invasion by woody exotics has occurred over the period of forest mortality, most sites will be primed and ready for planting or seeding. The understory should also be evaluated. If the period since mortality is within the same growing season, the understory may not be altered extensively. However, if it has been a year or more since tree mortality, the understory may be significantly more dominant and may require selective clearing and management to prep the site for the survival of newly planted woody species.

Considering that egg hatch, in the early spring, coincides with leaf bud of most hardwood trees, planting of saplings should not take place at this time. The ultimate window for planting seems most appropriate in the fall, after eradication efforts have subsided and monitoring has found no surviving or newly introduced populations. A number of options are then available to the restoration ecologist in regards to the type of planting to be done on site.

If restoration of eastern broadleaved forests is to be successful and perpetual, careful monitoring for the presence of *L. dispar* in its various life stages must take place throughout the entire growing season. Any discovered life form must be eliminated from the restoration site, as well as the surrounding peripheral landscape. Computer modeling may also be employed to aid in the speculation of population outbreaks. But most importantly, collaborative management and monitoring of *L. dispar* should take place across the North American continent to control and hopefully diminish existing populations of the species and in turn preserve the integrity of deciduous forests.

Conclusion

Population outbreaks will be a reoccurring factor with *Lymantria dispar* since complete eradication of this exotic species is rather unlikely. Management of populations in various stages of life seems most appropriate in preventing severe defoliation of eastern North American broadleaved forests. Largescale application of Btk, and other biological control means, seems to have the greatest amount of success at this point and should be continually reassessed in light of emerging techniques. Management techniques, however, are most successful if coupled with public education about the transport of the species in its various life forms.

To the restoration ecologist, *L. dispar* poses an indefinite threat to the integrity of eastern broadleaved forests. With careful coordination of the restoration effort with the species' life cycle, as well as appropriate management and monitoring techniques, it may be possible to restore a deciduous forest stand damaged by *L. dispar*. However, with its capacity to destroy large forest stands, its evasiveness to complete eradication, and its highly successful mode of artificial dispersal, *Lymantria dispar* will continue to be a prevalent problem to the health, balance, and survival of eastern broadleaved forests in North America.

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