

History and Impact of Gypsy Moth in North America and Comparison to Recent Outbreaks in Europe

Michael MCMANUS^{a*} – György CSÓKA^b

^aUSDA Forest Service, Hamden, Connecticut, USA

^b

Department of Forest Protection, Hungarian Forest Research Institute, Mátrafüred, Hungary

Abstract – The article summarizes information about the introduction, spread, population dynamics, and impacts of the gypsy moth in North America and elucidates comparisons with the importance of this forest pest in Europe. Additionally, the natural enemies (parasites, predators, and pathogens) that help regulate gypsy moth populations, are discussed at length. Gypsy moth outbreaks on both continents are associated with the presence, abundance and characteristics of oak forests. While oak forests in Europe are rather fragmented and their area has declined, oak forests in North America are both extensive and contiguous. Consequently there is an obvious disparity in the magnitude, impact, and synchrony of gypsy moth outbreaks in Europe and in North America. Even if the frequency and severity of outbreaks in Europe will increase in the future, the spread of outbreaks will be limited by the availability of suitable hosts and climatic factors. Conversely, gypsy moth will continue to spread to West and South in the United States and the area infested will increase significantly until it eventually occupies the natural distribution of oak species. Because of this prognosis, an emphasis has been placed on slowing the spread of the gypsy moth rather than treating defoliating populations.

Lymantria dispar L / outbreak frequency / spread / North America / Europe

Kivonat – A gyapjaslepke története és jelentősége Észak-Amerikában - összehasonlítás az utóbbi időszakok európai tömegszaporodásaival. A tanulmány összefoglalja a gyapjaslepke Észak-Amerikába történő behurcolásának, megtelepedésének, terjeszkedésének történetét. Elemzi a faj jelentőségét, összehasonlítva az európai helyzettel. A fentiekén túl ismerteti a gyapjaslepke természetes ellenségeit (ragadozók, parazitoidok, kórokozók). A gyapjaslepke tömegszaporodásai mindkét kontinensen a tölgyek jelenlétével, tömegességével, illetve a tölgyesek jellegzetességeivel vannak összefüggésben. Amíg Európában a tölgyesek területe jelentős mértékben fragmentálódott és csökken az utóbbi évszázadokban, Észak-Amerikában a tölgyesek még napjainkban is nagy kiterjedésűek és összefüggőek. Következésképpen a tömegszaporodások szinkronizáltsága, nagyságrendje és hatása eltérő Európában és Észak-Amerikában. Még ha az előrejelzéseknek megfelelően a klimatikus változások miatt a gyapjaslepke tömegszaporodásai gyakoribbá és nagyobb kiterjedésűvé válnak is a jövőben, az alkalmas tápnövények elterjedése, illetve más környezeti tényezők korlátozni fogják azokat. Ezzel ellentétben a gyapjaslepke Észak Amerikában folytatni fogja déli és nyugati irányú terjeszkedését, egészen addig, amíg a tölgyek természetes elterjedési területét le nem fedi. Ebből az előrejelzésből kiindulva a hangsúly a STS (Slow the spread = a terjeszkedés lassítása) programra helyeződött át, a tömegszaporodási stádiumban lévő populációk elleni védekezés helyett.

gyapjaslepke / tömegszaporodások gyakorisága / terjeszkedés / Észak-Amerika / Európa

* Corresponding author: mlmcmamus@fs.fed.us; 51 Mill Pond Road, Hamden Connecticut 06514 US

1 INTRODUCTION

The exploits of the gypsy moth (*Lymantria dispar* L.) in the United States are well known and have been well documented in the scientific literature and by the media over the past 100 years. Although substantial efforts and resources have been committed to eradicate, contain, or control this pest, it is now well established in the eastern U.S. and is gradually extending its range to the south and west. Although *L. dispar* populations have declined significantly since 1990 when about 3 million ha were defoliated, this defoliator remains the most important insect pest in the deciduous forests of the eastern United States. Unlike many forest pests that threaten commercial timber values, the gypsy moth devastates not only forests but also urban forest communities and affects people. During the outbreak phase when populations can increase 100-fold in successive years, larvae can pose a hazard to human health and disrupt the public's enjoyment of outdoor activities. The defoliation caused by outbreak populations reduces the vigour and general health of forest and shade trees and renders them susceptible to attack by secondary mortality-causing agents. The intensity of tree mortality, which usually peaks 2 to 5 years after an episode of defoliation, is highly variable and site specific. In urban residential areas, expenditures by the public for spraying pesticides to prevent defoliation by the gypsy moth can be astronomical.

In this article, we synthesize and summarize in general terms the history, dynamics, and current status of the gypsy moth and its management in the U.S. and discuss differences that exist between the behaviour of populations in the U.S. and Europe and their associated impacts.

2 HOSTS AND OUTBREAKS

In Europe, distribution of the gypsy moth corresponds approximately with two vegetation zones: temperate deciduous forests and Mediterranean scrub. The northern limit proceeds through southern Sweden and Finland and descends from about 60° to 50° lines of latitude through Europe and Russia. The southern limit begins in the west in northern Morocco, Algeria, and Tunisia and proceeds east to include all of the Mediterranean islands, on a line through Israel into Asia (CIE, 1981).

The hosts for the gypsy moth in Europe vary somewhat depending on how its distribution corresponds with the predominant vegetation in various geographical regions. Close to the northern limits of its range, i.e., Lithuania, species of birch (*Betula*) and alder (*Alnus*) are the primary hosts, whereas in Spain, Portugal, and Sardinia, cork oak (*Quercus suber*) is the dominant host and stands of this species have incurred frequent episodes of defoliation. In the rest of Europe, the distribution of the gypsy moth is associated with the presence of up to seven species of *Quercus*, especially *Q. petraea*, *Q. cerris*, and *Q. robur*; however *Q. petraea* is less preferred among the Central European oaks. In Central Europe, hornbeam (*Carpinus betulus*) is often intermixed in stands of oaks and is considered to be an equally preferred host along with species of *Populus*, *Alnus*, and *Salix* (Hirka 2005, Csóka 2007).

Black locust (*Robinia pseudoacacia*) stands in Hungary and Slovakia are occasionally defoliated by *L. dispar* larvae however this species is not considered to be an acceptable host in the U.S. Even conifers (mainly *Picea*) can be occasionally totally defoliated during outbreaks (Csóka 2007).

Although the gypsy moth was introduced into North America in 1869, it is still considered to be an "invasive species" because it continues to spread and extend its range to the south and west and has yet to occupy fully the extensive oak forests that are native to the eastern and central regions of the United States. Conversely, *L. dispar* is native to Eurasia – outbreaks were recorded in the 1600's in Spain, 1750's in Germany, 1840's in Hungary, and

in 1880 in France. In southern regions of France and in the Balkans, *Q. suber*, *Q. pubescens*, and *Q. ilex* serve as the primary hosts for *L. dispar*. An exception to the close association between oak species and *L. dispar* populations occurs in the Danube Delta of Romania which contains 27,000 ha of *Populus* and *Salix* stands, species which serve as excellent hosts for gypsy moth larvae.

Extensive studies conducted on hosts of the gypsy moth in the U.S. provide insight as to why this pest has been and continues to be one of the major forest health problems. According to Liebhold et al (1997), among the top 20 preferred tree species ranked by their total basal area are 13 species of *Quercus*, *Populus* spp. (*tremuloides*, *grandidentata*) paper birch (*Betula papyrifera*), and American basswood (*Tilia americana*). Fifty species of oak are represented in two-thirds of the forest cover types in Eastern North America and are the dominant species in over 77 million ha of hardwood forest (Stein et al. 2003). Most or all of these species are probably equally preferred by larvae but have not been evaluated as hosts. There are oak cover types unique to regions on the west coast of the U.S. that are equally susceptible to gypsy moth populations. During outbreaks, gypsy moth larvae will also readily feed on many species of conifers [*Pinus*, *Picea*, *Abies*, *Tsuga*, and *Larix*] especially when defoliation of preferred species is severe.

According to Bogenschutz et al (1989), outbreaks of the gypsy moth are not uncommon in Central Europe yet it is not considered to be a forest pest in Germany. In general, the damage caused by *L. dispar* in Europe is greater from west to east and from north to south (McNamara, 1995). Outbreaks have been most numerous and severe in the Balkan peninsula due to the abundance of oak species and climate—high temperatures and moisture deficits – that appears to be optimal for *L. dispar* development and survival. In Serbia, 16 outbreaks have been recorded between 1862-1998, the largest occurring in 1997 when 500,000 ha were infested (Marović et al. 1998). In Romania, treatments were applied on 600,000 ha of forest land in 1988 to control gypsy moth populations. Twenty-two outbreaks have been recorded in Hungary between 1843 and 2007 (Figure 1), with a maximum of 212 thousand hectares damaged in 2005 (Csóka – Hirka 2007).

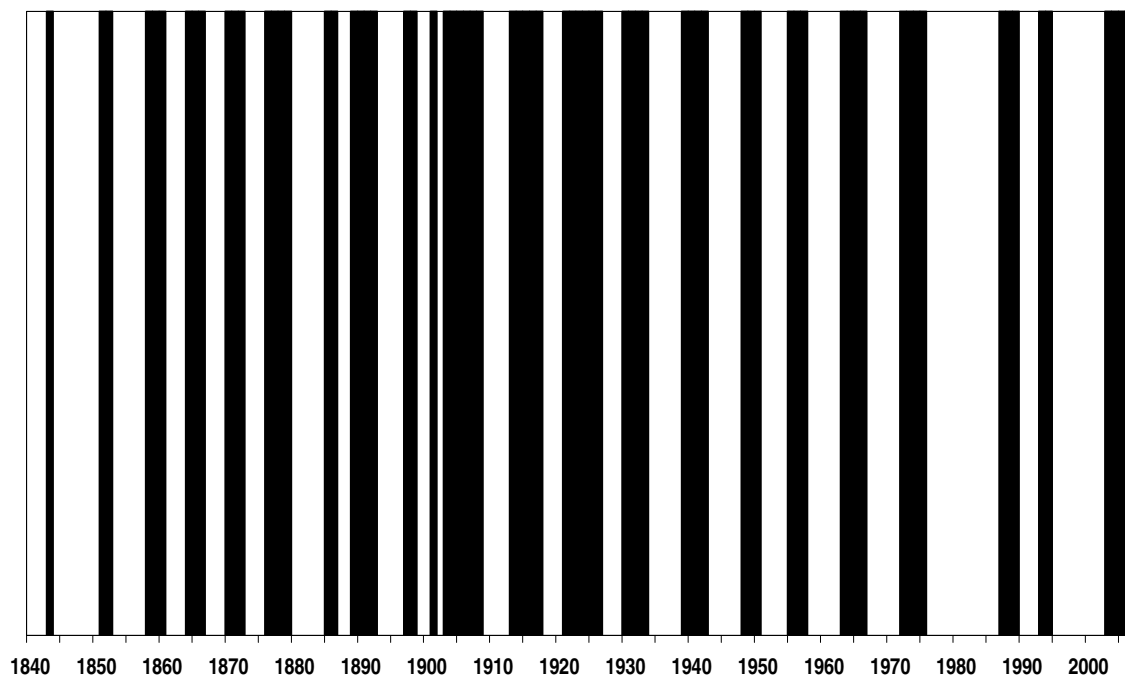


Figure 1. Outbreaks of gypsy moth in Hungary from 1840 to present (Csóka – Hirka 2007)

In North America, the history of outbreaks is associated with the spread of *L. dispar* into new areas dominated by preferred species followed by the rapid expansion of populations in the absence of the gypsy moth's complex of natural enemies. The extent of outbreaks, measured by the total forested area defoliated, has worsened dramatically as the area infested has increased. Annual defoliation exceeding 500,000 ha occurred in 20 years between 1970-1995, a period when the distribution of *L. dispar* populations expanded significantly to the south and west (Figure 2). Over 5.2 million ha were defoliated in 1981, 3 million ha in 1990. Outbreaks are most severe in oak-pine associations which occur on dry, sandy sites and on ridgetop stands characterized by poor, shallow soils, rock outcroppings, and preferred species such as chestnut oak (*Q. prinus*).

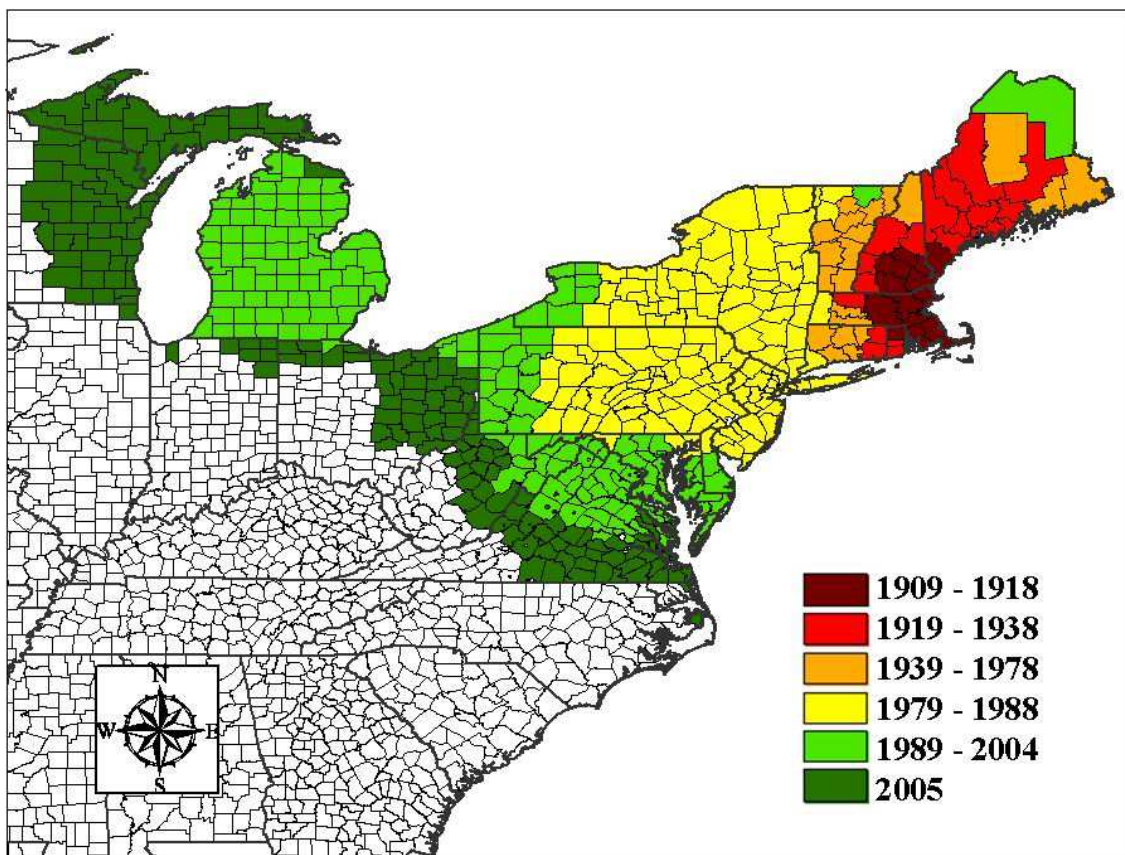


Figure 2. The spread of the gypsy moth in the U.S since it was introduced in 1869

3 ESTABLISHMENT AND SPREAD

In 1869, egg clusters of the gypsy moth were transported from France to Medford, Massachusetts by a French mathematician and astronomer, Etienne Leopold Trouvelot, who was conducting laboratory experiments to cross the gypsy moth with a native silkworm, *Antheraea polyphemus* (Cramer). Somehow, larvae of the gypsy moth escaped and established on vegetation in the immediate area. It was not until the summer of 1889, 20 years after its introduction, that the insect became so abundant and destructive on fruit and shade trees that it attracted public attention. The extensive defoliation and nuisance created by enormous numbers of larvae are vividly described in Forbush and Fernald (1896). Trouvelot's poor judgement provided North America with one of its worst pest problems (Liebhold et al. 1989).

In 1890, the State of Massachusetts appropriated funds to exterminate the pest which at that time infested an area of 2539 km² and encompassed 30 cities and towns. Control efforts were so successful that by 1899, little defoliation was detected and only a few moths were found. Therefore, further control was terminated; this was a poor decision because by 1905, gypsy moth populations had expanded rapidly, thousands of hectares of forests were defoliated, and the pest had spread to surrounding states. In 1906, the Federal Government appropriated money to prevent the spread of the insect because it was recognized that egg masses and other life stages were being carried on commodities along major roadways. This eventually led to the enactment of a Domestic Federal Quarantine against the insect in 1912 which is still in effect today.

Despite efforts by the federal and state governments, *L. dispar* continued to spread to the north and west at an estimated rate of 9.6 km/year. Several isolated infestations were found far removed from the infested regions; additionally, a new infestation covering over 1000 km² was found to the south in New Jersey. This introduction was traced to a shipment of blue spruce (*Picea*) trees that had been imported from the Netherlands.

Two extensive efforts were made between 1923 and 1958 to stop or at least slow the rate of spread of the gypsy moth to the west. Between 1923 and 1941, a Barrier Zone was established that encompassed 27,300 km² in a north-south line from Canada to New York City (Felt, 1942). All infestation that were detected within this Barrier Zone were eliminated using chemical and mechanical methods. This program was terminated in 1941 due to a shortage of federal funds and complicated further by the nation's involvement in World War II. The Barrier Zone is credited with effectively slowing the rate of spread of the gypsy moth prior to 1941. Gypsy moth populations expanded greatly during the early 1950's, at which time state and Federal officials conducted an in depth appraisal of the problem and considered re-establishing the Barrier Zone to prevent additional spread and reduce damage (Perry 1955). In 1956 the U.S. Congress made funds available to initiate an eradication program; 223,000 ha in three states were sprayed with DDT which had been used experimentally between 1944-48 in Pennsylvania, and another 1.2 million ha were sprayed in 1957. By 1958, less than 51 ha of defoliation were recorded anywhere within the generally infested area; however, the use of DDT was curtailed because of questions that surfaced about residues on food and feed crops and concern over its detrimental effects on beneficial organisms, fish and wildlife. At this time, any hopes for eradicating the gypsy moth or even stopping its spread were abandoned.

The areas of infestation and defoliation in the eastern U.S. increased substantially between 1959-1969 and reached a peak in 1971 when over 800,000 ha were defoliated. The U.S. Congress provided a special appropriation of several million dollars over a four-year period (1975-1978) to accelerate research and development on gypsy moth with emphasis placed on developing an integrated pest management (IPM) approach (McManus, 1978). After a massive outbreak occurred in 1979-1982 – four million ha of forest land was defoliated in 1981 – it became apparent that there was a need to develop and evaluate a more aggressive approach to manage gypsy moth populations before they reach high densities that cause defoliation. Two 5-year projects were initiated to evaluate the feasibility of managing gypsy moth populations at low densities employing a monitoring system that consisted of a 1-km fixed point grid of pheromone traps. The first program was deployed on 60,000 ha in the state of Maryland (1983-1987); because of the success of this effort, the second program was initiated on five million ha in the states of Virginia and West Virginia (Reardon, 1991).

The most recent outbreak in North America occurred from 1989 to 1993 and affected forested areas in 12 different states. Over 2.8 million ha were defoliated in 1990 and the worst defoliation occurred in several of the most recently infested states to the south and west of the New England region. In contrast, there has been insignificant defoliation by *L. dispar* since

that time, a fact which has been attributed to the occurrence and spread of the fungal pathogen, *Entomophaga maimaiga* sp. nov. This will be discussed in a forthcoming section.

Liebhold et al. (1992) analyzed the rate of spread of *L. dispar* in North America using historical records and concluded that there was a high rate of spread (9.45 km/year) between 1900-1915, a low rate of spread (2.82 km/year) between 1916-1965, and a very high rate of spread (20.78 km/year) from 1966-1990 (Figure 2). The extended period of time when spread was minimal can be attributed to the Federal Domestic Quarantine, which restricted the movement of life stages by regulated commerce, the enforcement of the Barrier Zone and broad use of mechanical and chemical controls. The dramatic increase in spread that occurred in the latter part of the last century was probably facilitated by the following: (1) the use of DDT was abandoned and the dependency on chemical pesticides in general was diminished; (2) newly infested states to the south and west contained contiguous, mature forests where 50-60% of the total basal area of forests was dominated by oak species.; (3) the outbreaks that occurred in the 1970's and from 1979-1982 enhanced the natural and artificial spread of the gypsy moth. It's been well documented that the inadvertent transport of egg masses and other life stages from infested to uninfested areas increases dramatically during outbreak periods (McFadden and McManus, 1991). This has been the primary mechanism for spread of the gypsy moth in North America.

4 DYNAMICS OF POPULATIONS

In North America, the gypsy moth is considered to be an eruptive species because the timing of outbreaks has been irregular and difficult to predict. An enormous amount of effort has been expended to understand better why gypsy moth populations fluctuate over several orders of magnitude in consecutive years. Much of this research has been summarized in several excellent reviews (Leonard 1974; Montgomery and Wallner 1988; Elkinton and Liebhold 1990; Liebhold et al. 2000). *L. dispar* populations can persist for several years at densities so low (latency) that it's difficult to detect life stages except for male moths. When populations are released (progradation), they expand rapidly into the outbreak phase (culmination) which may persist for 1-3 years. Campbell and Sloan (1978) suggested that gypsy moth populations in North America demonstrate bimodal stability in that density dependent processes maintain densities at both innocuous and outbreak levels for long periods of time, however more recent studies suggest that there is little evidence for strong regulation of low-density populations (Liebhold et al. 2000).

The defoliation record in North America indicates that episodes of defoliation were synchronous in the New England states in the early 1900's, and there are many examples in the 20th century – apart from the severe outbreak in 1979-81 – in which defoliation appeared to be synchronous regionally. This suggests some climatic release phenomenon, though analyses of historical climate data have not established a correlation between weather and gypsy moth outbreaks (Miller et al. 1989). Williams and Liebhold (1995) reported that North American gypsy moth populations exhibit little or no periodicity, however, it has since been suggested that disjunct populations can become synchronous due to regional stochasticity, most likely related to weather variability (Liebhold and Kamata 2000). Montgomery and Wallner (1988) reported that several studies in Europe indicate that some gypsy moth populations are cyclic, with high densities developing every 8-11 years, however there had been no quantitative evaluations of cyclic patterns at that time. However Johnson et al. (2005) analyzed gypsy moth defoliation records >30 years among 11 regions across three continents (North America, Europe, Asia) and concluded that most *L. dispar* populations around the world tend to oscillate at periodicities between 8-12 yrs. Oscillations were synchronized at

distances up to ca. 1,200 km within continents, however there was no evidence for synchrony of gypsy moth populations between continents. The authors concluded that while the precise identity of the mechanisms causing these oscillations is not certain, it's possible that they are a product of one or more trophic interactions that are similar between the U.S. and Europe.

5 NATURAL ENEMY COMPLEX

5.1 Parasitoids

A program to introduce parasitoids from Eurasia into *L. dispar* populations in the Eastern U.S. began in 1905 and continued intermittently for 70 years (Hoy 1976). Although over 40 species of parasitoids were introduced, only 10 species became established and only eight species are recovered consistently and are considered to be important in U.S. gypsy moth populations – two that attack eggs, five that attack larvae, and one that attacks pupae (Fuester – Ramaseshia 1989). With few exceptions, i.e. *Compsilura concinnata*, those species that were introduced early in the last century and became established are also the most important and abundant species that are reported in European studies. This program is considered to be one of the few massive projects in biological control history.

Hoy (1976) suggested that relatively few parasitoid species were established over the duration of the release program because often times the numbers of individuals released were small, there was an insufficient host population present at the time of release, or there was a lack of alternate or overwintering hosts necessary to sustain species such as *Glyptapanteles liparidis* and *G. porthetriae*. Unfortunately, one of the common established species, *C. concinnata*, is a generalist parasitoid that attacks more than 200 species of Lepidoptera. Conservation biologists claim that *C. concinnata* is responsible for the decline in populations of silk moths (Saturniidae) and many other species that are listed as sensitive or endangered (Boettner et al. 2000).

When the egg parasitoids *Ooencyrtus kuvanae* and *Anastatus disparis* were introduced into the U.S., the latter was thought to be the more important of the two, however just the opposite occurred. *O. kuvanae* has been the dominant parasitoid found throughout the distribution of *L. dispar* in North America (Brown 1984) and commonly parasitizes between 25 to 50% of eggs in most egg masses depending on egg mass size and dimension.

A tachinid species, *Aphantorhopsis* (= *Ceranthia*) *samorensis* (Villo) was released in the U.S. and repeatedly in Ontario, Canada between 1992 and 1996 however establishment was never confirmed (Nealis – Quednau 1996). This parasitoid is considered to be an important cause of mortality among *L. dispar* populations in France during periods of latency. Another tachinid, *Blepharipa schineri* was investigated thoroughly as a candidate for release however it was not pursued because of concern about its potential competitiveness with *Parasetigena silvestris* and *B. pratensis*.

According to Grijpma (1989), 165 species of parasitoids (109 Hymenoptera, 56 Diptera) have been recorded from gypsy moth populations throughout Europe, however only approximately 20 species are recovered consistently (Lipa 1996; Zubrik – Novotny 1992). There are many similarities among the parasitoid complexes in Europe and North America however there are a few notable differences. Whereas *O. kuvanae* is an important component of the parasitoid complex in the U.S., it is insignificant in *L. dispar* populations in Europe. Egg parasitism varies from 0 to 5% even though this species was introduced repeatedly into many European countries (Brown 1984). Two larval parasitoids, *G. liparidis* and *G. porthetriae* are among the most important species in Central Europe whereas neither species is established in North America. *Blepharipa pratensis* and *P. silvestris* are recognized as the most important species that attack *L. dispar* populations on both continents whereas

C. concinnata, which is common in the U.S., is insignificant in Europe. Hoch et al. (1999) stated that the guild of more specialized, oligophagous species are more important parasitoids of gypsy moth populations in central Europe, whereas typical generalists such as the polyphagous tachinids *C. concinnata* and *Exorista larvarum* are recorded only in low numbers. Despite the greater abundance of parasitoid species in Europe, the overall role of parasitism in the dynamics of gypsy moth populations probably is equivalent to that which has been recorded within the generally infested area of North America. Rates of parasitism and the occurrence of species within the parasite complex vary widely among sites and on the phase of the gradation under study. Liebhold et al. (2000) concluded that there is no definitive evidence of density-dependent regulation of gypsy moth populations by parasitoids.

5.2 Predators

Although predation is thought to have a substantial impact on gypsy moth populations, especially when populations are in latency, it is difficult to actually determine the importance of an individual predator or predator groups because predators by definition are generalist feeders. Shortly after the gypsy moth was recognized as a serious pest in the United States, naturalists emphasized the importance of birds as primary predators of gypsy moth larval stages (Forbush and Fernald 1896). Bess et al. (1947) were the first to suggest that small mammals (mice and shrews) were important predators of gypsy moth larvae in the litter of mesic forests. Campbell and Sloan (1977) found that predation of pupae by small mammals, especially *Peromyscus leucopus*, was important in maintaining low-density populations at innocuous levels. The survival of pupae at different densities and in selected microhabitats was estimated by Smith (1985), who developed a methodology for exposing gypsy moth pupae affixed to bait boards using beeswax. Several studies have been conducted in the past 10 years suggesting that year-to-year variation in the abundance of small mammal populations, specifically *P. leucopus*, is a major determinant of change in gypsy moth populations (Elkinton et al. 1996; Jones et al. 1998). These studies indicate that the level of predation is determined by small mammal abundance, which is in turn linked to the production of acorns (mast) that are a major source of food for overwintering predator populations. However Liebhold et al. (2000) concluded that because small mammals are generalist predators and gypsy moths are a less preferred food item, they do not appear to regulate populations in a density-dependent fashion. However he does suggest that failure of acorn production may precede gypsy moth outbreaks by 2-4 years and thus contribute to the release of populations from low densities.

The importance of small mammals as predators of gypsy moth populations in Europe was ignored until preliminary studies were conducted in the Ukraine in the 1980's to measure predation of lyophilized pupae placed within four microhabitats in oak forests (Smith et al. 1998). Sherman live traps were used to estimate the diversity and abundance of small mammals on the sites. The authors found that where estimated small-mammal densities were 750/ha, 98% of pupae were destroyed within 72 hours of their placement in the litter. Ten species of mammals were identified, though *Apodemus sylvaticus* and *Clethrionomys glareolus* were the most abundant. Prior to these studies, foresters in Russia perceived that small mammals were primarily pests that destroyed forest regeneration. Recent studies in Austria using the same methodologies demonstrated that between 67 to 92% of pupae placed at the base of trees and up to 100 cm high on tree boles were destroyed by *A. sylvaticus* and *A. flavicollis*. This suggests that species of *Apodemus* apparently are the ecological equivalent of *P. leucopus* in European forests (Gschwanter et al. 2000).

References to vertebrate predation in Eurasia are fairly common however all except Rothschild (1958) emphasize the importance of birds in maintaining *L. dispar* populations at low densities e.g. Turcek (1950). Furuta and Koizami (1975) suggested that avian predators

aggregate into plots with high densities of gypsy moth larvae and cause density-dependent mortality, however most studies have been directed at measuring predation by birds of gypsy moth egg masses. Reichart (1959) concluded that 25 to 90% of eggs in overwintering egg masses were destroyed by birds. Higashiura (1989) has shown that high levels of bird predation on gypsy moth egg masses occurred in Japan however he suggests that the eggs are unpalatable to birds and are fed upon only to avoid starvation during stressful periods.

The predation of gypsy moth egg masses by birds in North America has not been well documented and there are few if any examples where overwintering egg masses have been destroyed or disrupted. Forbush and Fernald (1896) listed 38 bird species observed eating larval stages of the gypsy moth, however most of these observations were made when *L. dispar* populations were at outbreak levels, a time when predation has no significant impact on host populations (Smith and Lautenschlager, 1978). It is concluded that birds are opportunistic feeders on *L. dispar* populations and that gypsy moth life stages are not a major component in the diet of the most common North American species.

The importance of invertebrate predators in the dynamics of gypsy moth populations in the U.S. has not been determined conclusively though it is recognized that *Calasoma sycophanta* and species of ants and spiders are known to prey on gypsy moths at various life stages. Smith and Lautenschlager (1978) suggested that some of the mortality attributed to vertebrates by other investigators may actually have been caused by ground beetles and ants. The same authors provide an excellent synthesis of what is known about predators of *L. dispar*. Although *C. sycophanta* is distributed throughout the range of *L. dispar* in Europe and North America, it is abundant only during periods of gypsy moth outbreaks and also feeds on many different species of Lepidoptera (Weseloh et al. 1995). Therefore it is doubtful that this predator is important as a regulator of gypsy moth populations.

5.3 Pathogens

In North America, most high density populations of *L. dispar* eventually collapse due primarily to the action of a nuclear polyhedrosis virus (NPV) which kills mainly late instar larvae especially under conditions where there is high competition among larvae for rapidly declining host foliage. The NPV has been the most important factor causing the collapse of outbreak populations since the gypsy moth was introduced into North America. Woods and Elkinton (1987) demonstrated that NPV mortality followed a bimodal pattern- an early peak of mortality in the early instars contaminates foliage which is consumed by late instar larvae resulting in high levels of mortality. The interactions among NPV, foliage chemistry, virulence and transmission are discussed in the review by Elkinton and Liebhold (1990). The significance of pathogens other than the NPV in the dynamics of gypsy moth populations in North America usually is incidental.

According to Weiser (1987), in addition to the NPV, several species of microsporidia, a granulosis virus (GV), a cytoplasmic polyhedrosis virus (CPV), and species of fungi and nematodes cause infections in Eurasian gypsy moth populations. However, normally only the NPV and microsporidia cause significant mortality. A CPV caused 42% larval mortality in Austria in 1973 and there are reports of microsporidia causing 70% mortality at various life stages in the Ukraine (Zelenskaya, 1980) and in Yugoslavia (Sidor 1979). At least four species of microsporidia have been isolated and identified from larval populations throughout the range of gypsy moth east to Siberia. These protozoans have not been recovered from populations in North America. Individual species are being considered for introduction into the United States as a classical biological control agent.

A dramatic change in the dynamics of gypsy moth populations in the Eastern U.S. occurred in 1989 when the fungus *Entomophaga maimaiga* was first detected among *L. dispar* populations in the state of Connecticut (Hajek et al. 1990). Shortly thereafter this fungal

pathogen caused a panzootic among gypsy moth populations in the eastern U.S. (Elkinton et al. 1991) and is considered to be the most significant addition to the gypsy moth natural enemy complex in North America. *E. maimaiga* has spread rapidly into the central U.S. and north through Ontario, Canada (Nealis et al. 1999) and has also been introduced intentionally within most states where the gypsy moth is established. Unlike the NPV, which is most pronounced in high-density populations, *E. maimaiga* acts as a density-independent mortality factor and resting spores can persist in forest soils for 10-11 years, thus providing a source of inoculum over time (Weselov – Andreadis, 1992). Epizootics of this fungus often decimate high density *L. dispar* populations in its native Japan but only under humid conditions (Soper et al. 1988). However weather does not appear to be a limiting factor in North America. Although *E. maimaiga* has not been recovered in European *L. dispar* populations, it was introduced at two localities in Bulgaria and has persisted at low levels for a period of five years and caused localized epizootics in 2005 (Pilarska et al. 2006).

6 IMPACTS

The impacts that occur over time after the gypsy moth invades a new area are varied and complex. Defoliation of forests and urban trees can have profound direct and indirect effects on individual trees, components of forest ecosystems, and people. No doubt, the initial severity of the gypsy moth problem and its continued status as a serious pest in the U.S. can be attributed to the fact that it was introduced into the region of the U.S. that was dominated by hardwood forests consisting of mixed oak stands where the basal area of oak species exceeded 60%. The categories of impact that have been studied include timber (mortality and growth loss), recreation, residential, water quality, species displacement, regeneration, and wildlife to mention only a few. The literature on these subjects is very extensive and consequently we have chosen to summarize the effects of *L. dispar* defoliation on trees and forest stands. More comprehensive information on socioeconomic impacts is provided by Leuschner et al. (1996).

It was recognized during the early part of the 20th century that the initial outbreaks in the New England region (Massachusetts and surrounding states) caused extensive defoliation and tree mortality. Between 1911 and 1931, extensive records of defoliation and tree condition were collected in over 122 plots. This database was analyzed in later years and published as a monograph (Campbell and Sloan 1977) which is considered to be the definitive description of forest stand responses to the gypsy moth. As the gypsy moth spread to the south and west, data were collected by individual states mainly on levels of defoliation and tree mortality. On some dry sites where the basal area of oak was high (65-80%), mortality of oaks after 2-3 years of successive heavy defoliation exceeded 90%. Davidson et al. (1999) provide the most inclusive summary of trends in defoliation and mortality in the affected states as the gypsy moth infestation spread. Their general conclusions were as follows:

- Certain tree species (oaks) are defoliated at higher rates than other species, and frequently suffer greater mortality than less susceptible species.
- As the intensity (amount of foliage removed) and duration (number of consecutive episodes) of defoliation increases, the amount of tree mortality increases.
- Tree mortality tends to increase rapidly after 2-3 years of consecutive defoliations or if additional stressors such as drought occur.

Maximum tree mortality usually occurs 3-5 years after an episode of defoliation and is usually caused by secondary agents such as *Armillaria mellea* and *Agilus bilineatus* which readily attack the severely weakened trees.

There is little consensus in the European literature as to the impact of gypsy moth defoliation among the countries of Central and Eastern Europe. Several references state that maximum oak mortality following gypsy moth defoliation is 25 to 30%, though there is insufficient information on levels of defoliation and subsequent tree mortality. There have been several severe outbreaks in the former Yugoslavia, the most recent occurring between 1995-1999 (Mihajlovic et al 1998). It was reported that at the culmination phase, 500,000 ha of forests, orchards, and parks were attacked and it was estimated that losses in volume increment could have been 23-50%. Another example of significant oak mortality following *L. dispar* defoliation occurred in the state of Hesse after the outbreak of 1993-94 (Gossenauer-Marohn 1995). Tree mortality was exacerbated by a period of drought and by a significant lowering of the water table in forested areas in the Rhine-Main-Valley.

There is also a difference in the complex of mortality-causing agents in Europe. Species of *Armillaria* are found throughout the region, but they are not considered as important as is *A. mellea* in causing oak mortality in North America. Rather, tree mortality is frequently attributed to other pathogens in the genera *Ophiostoma*, *Ceratocystis*, *Phytophthora*, and *Diplodia* that can be transmitted by secondary insect species such as the oak bark beetle, *Scolytus intricatus* Ratz. And in Germany, three species of *Agrilus* – *A. biguttatus*, *A. angustulus* and *Coraebus bifasciatus* – are considered the major cause of oak mortality. Buprestids, mainly *Agrilus biguttatus* is known in Hungary to cause significant oak mortality 1-2 years after gypsy moth damage, but sometimes after severe drought – independent of the gypsy moth damage (Csóka – Kovács 1999, Hirka 2005, 2006, Csóka – Hirka 2007).

Studies in Europe have focused more on the overall decline of oak in forests in response to multiple stressors than on the effects of individual stress agents such as the gypsy moth (Fuhrer 1998, Csóka et al. 1999).

7 MANAGEMENT ACTIVITIES

Efforts to control or manage *L. dispar* populations in the U.S. began in 1896 and have continued without interruption until today. Initially the primary goal was to eradicate the pest, however at that point in time, entomologists and politicians underestimated the severity of the threat, nor did they possess the technology to detect low density populations or to control them with pesticides. When eradication failed, a Federal Domestic Quarantine was implemented (1912) and extended efforts were made to establish Barrier Zones to prevent further spread. Although these tactics succeeded in slowing the rate of spread of the gypsy moth, they failed to prevent the accidental introduction of life stages beyond the infested region and from additional introductions from abroad.

When the use of DDT was prohibited in 1958, it was finally recognized and accepted that eradicating or preventing the spread of the gypsy moth in the U.S. was no longer an attainable goal. Since that time, decisions to suppress (spray) potentially damaging populations are made by the responsible land manager on federal lands and by the responsible state official on state and private lands, based on the assessment of the density of gypsy moth populations per unit area. Participation in suppression projects is voluntary and is conducted through a Federal Cooperative Forestry Assistance Act. The Federal Government provides ca 50% of the cost of spraying on state and private lands. Most projects are conducted on high-use recreational lands, residential areas, and on environmentally sensitive habitats.

After the demise of DDT, the chemical pesticides Orthene®, Dylox®, and Carbaryl® were used against the gypsy moth with limited success. Dimilin® (diflubenzuron) was registered for use against *L. dispar* in 1976, and by 1982, Dimilin and Btk (*Bacillus thuringiensis kurstaki*) were being used almost exclusively. The use of Btk increased greatly

after the 1980's due to the discovery of more potent strains, improved formulations, and better application technology. By 1995, Btk products Foray® and Dipel ®) were used on over 70% of the area treated aerially to suppress gypsy moth populations in North America and have essentially displaced the use of chemical pesticides. In addition to these very structured and regulated control programs, there is a vast amount of spraying and physical efforts being directed against the gypsy moth by homeowners and woodlot owners especially during outbreak years.

Two USDA agencies – the Forest Service (FS) and Animal and Plant Health Inspection Service (APHIS) – have been assigned the responsibility for protecting the forests and trees of the U.S. from the adverse effects of the gypsy moth. To this end, a new national program was initiated in 1995 that embraced the following strategies: *suppression*, to reduce high density populations of gypsy moth larvae in the generally infested area and prevent or minimize heavy defoliation; *eradication*, to eliminate isolated infestations of gypsy moth that are detected and to prevent their establishment in new areas; and *Slow The Spread (STS)*, to reduce the rate of spread of the gypsy moth from the generally infested area into uninfested areas.

The need for this new approach was magnified by several recent events; (1) introduction of the Asian biotype of the gypsy moth into ports on both the east and west coasts; (2) a continued increase in the number of isolated gypsy moth infestations that have been detected outside of the generally infested area due to inadvertent introductions; and (3) a desire by the public to reduce the use of broad-spectrum chemical pesticides in favor of environmentally acceptable alternatives.

Although eradication and suppression have been components of the USDA's gypsy moth program since early in the last century, the strategy to slow the spread of the insect is new. This concept had been discussed at length for many years (McFadden and McManus 1991), and a demonstration project to evaluate this strategy was implemented in 1993 in a four-state area that encompassed more than 3 million ha. Renewed interest in reducing the rate of spread of the gypsy moth to the south and west was precipitated by the dramatic increase in the area that was generally infested between 1989 and 1994 (2.1 million ha), and by documentation that the insect was spreading at a rate of about 21 km per year (Liebhold et al. 1992).

Further justification was provided by an economic analysis of the benefits that would be realized by initiating a program to slow the spread of the gypsy moth (Leuschner et al. 1996). This analysis estimates potential program benefits over 25 years ranging from \$774.8 to \$3,801.5 million, (present value) under different scenarios whereby the rate of spread is reduced by 4 to 20 km per year. About 83 percent of the potential benefits are associated with residential impacts and costs associated with projected management activities.

The STS program focuses on populations in the transition zone that are not targeted for traditional eradication and suppression efforts (Sharov et al. 2002). In this zone, small populations are recently established, still at very low densities, and are discontinuous from one another. Because it is almost impossible to find life stages at these low densities, grids of pheromone traps are deployed to trap male moths and thereby delimit isolated populations. Thus the basic premise of STS is to locate and apply site-specific treatments to these isolated populations to prevent them growing together (coalescing) and thus contributing to the expansion of the population front (Liebhold et al. 1992). Results to date suggest that STS has reduced the rate of spread by ca 50% even though most of the cost is dedicated to monitoring populations and relatively small areas are being treated with environmentally acceptable tactics such as pheromone disruption, Btk, and Gypchek (Mayo et al. 2003).

8 CONCLUSIONS

During the last century, when gypsy moth populations were expanding their range to the south and west of New England and massive outbreaks occurred in newly infested forest lands, several biocontrol specialists suggested that the gypsy moth problem was more severe in the U.S. than it is in Europe because the pest's natural enemy complex in Europe was more diverse and better able to regulate populations. In fact, there are many more species of parasitoids that have been recovered from gypsy moth populations in Europe based on reports in the literature. However, with possibly a few exceptions (*G. liparidis*), the species of most importance in Europe have been established in North America and are also the most important.

Likewise, there have been entomopathogens recovered from *L. dispar* populations in Europe; however, the NPV is unquestionably the major pathogen that causes collapse of high-density populations throughout the geographic range of the gypsy moth. Species of microsporidia, which do not occur in North American populations, are common in European populations and at times cause significant levels of mortality among larvae. Conversely, *E. maimaiga*, which does not occur in Europe (except for the recent introduction in Bulgaria), is a significant cause of mortality among *L. dispar* populations in Japan and North America. Predators are not considered to be important in regulating gypsy moth populations on any continent because they usually are generalist (opportunistic) feeders that are mainly active during outbreaks when host densities are high. Therefore, it is the consensus of most gypsy moth researchers that despite the occurrence of a more diverse natural enemy fauna in Europe, their impact on the dynamics of gypsy moth populations is similar to that measured in North America.

In comparing the frequency of outbreaks between continents, Johnson et al. (2005) tested for synchrony among gypsy moth populations in 11 regions across three continents (North America, Europe, and Asia) and concluded that most populations tend to oscillate at periodicities between 8 and 12 years. However, analyses also suggest that in North America, there is evidence of a 5-year periodicity on more xeric sites, specifically oak-pine forest types that have a high basal area of oak species. Marovic et al. (1998) also reported that outbreaks in certain lowland forests in Serbia also occur every 4-5 years; however, information was not provided on the composition of these forests. Similarly high frequency of outbreaks is recorded in warmer and dryer regions of southeastern part of Hungary in *Quercus robur* stands (Leskó et al. 1994, Hirka 2006, 2007, Leskó et al. 2007).

The obvious disparity between gypsy moth outbreaks in Europe and North America is in their magnitude and impact. The area defoliated (ha) during outbreaks in Europe is much less than that which occurs within the generally infested region of North America. This can be attributed more to the reduced area of oak forests in Europe and their fragmentation into smaller parcels. For example, of the estimated 15 million ha of forest land in France, approximately 11% are classified as oak forest types (Table 1). In Croatia, where pedunculate oak forests used to occupy >70% of some forest regions, only 24% of the forested lands consist of oak.

Conversely, oak forests in North America are both extensive and contiguous. There are more hectares of oak type forest in each of the five U.S. states listed in Table 1 than in six of seven European countries in which *L. dispar* is still considered to be a forest pest and where control activities are deployed. The prognosis for the gypsy moth and its associated impacts in the U. S. is not encouraging. Based on an analysis conducted by Liebhold et al. (1997), there are 19 states currently not infested by *L. dispar* that contain >1 million ha of forests that are classified as susceptible to gypsy moth defoliation and damage. This suggests that the costs

associated with managing this pest will continue to accelerate and that there is a strong justification for slowing the spread of this pest into currently uninfested states.

Table 1. Forest statistics for selected countries/states affected by the gypsy moth

Location	Forest land (million ha)	Distribution % broadleaf/conifer	Oak forests (million ha)	Percentage of oak (%)
EUROPE				
Germany	10.7	29/71	1.1	10
France	15.0	64/36	1.7	11
Austria	3.9	31/69	0.7	2
Slovakia	2.0	58/42	0.3	12
Hungary	1.8	86/14	0.6	33
Croatia	2.5	86/14	0.6	24
Romania	6.3	69/31	0.8	18
USA				
Pennsylvania	6.9	94/6	3.4	49
West Virginia	4.9	91/9	3.8	78
Michigan	7.7	76/24	1.5	40
Wisconsin	6.0	80/20	2.4	40
Missouri	5.7	80/20	4.2	74

The situation in Europe is more stable in that *L. dispar* has been established in many of the same forested regions for over a century, and with few exceptions, the area of oak forests and associated preferred species has declined significantly. One exception is Hungary, which experienced its highest level of defoliation (212 thousand hectares) in 2005. During the last outbreak in Hungary, even montane beech forests occurring at higher altitudes were damaged. Most of these forests have never suffered gypsy moth damage previously (Hirka 2006). Although Hungary has only 1.8 million ha of forest land, ca. 33% of the forest is classified as “oak type”. It is likely that outbreaks will continue to occur every 8-10 years in most European countries and that the Balkan countries will continue to experience outbreaks of a greater magnitude.

REFERENCES

- BESS, H.A. – SPURR, S.H. – LITTLEFIELD, E.W. (1947): Forest site conditions and the gypsy moth. Harvard Forest Bulletin 22. 56 pp.
- BOETTNER, G. H. – ELKINTON, J.S. – BOETTNER, C.J. (2000): Effects of a biological control introduction on three nontarget native species of Saturniid moths. Conservation Biology 14: 178-1806.
- BOGENSCHUTZ, H. – MAIER, K. – TREBITZKY, C. (1989): Gypsy moth outbreaks in southwest Germany, 1984-1986. In: Wallner, W.E. – McManus, K.A. (tech. cords.) Proceedings, Lymantriidae: a comparison of features of New and Old World tussock moths. U.S. Department of Agriculture Forest Service, Northeastern Forest Experiment Station General Technical Report NE-123. 89-100.
- BROWN, M. W. (1984): Literature review of *Ooencyrtus kuvanae* (Hymenoptera: Encyrtidae), an egg parasite of *Lymantria dispar* (Lepidoptera: Lymantriidae). Entomophaga 29: 249-265.

- CAMPBELL, R. W. – SLOAN, R.J. (1977): Forest stand response to defoliation by the gypsy moth. Forest Science Monograph 19. 34 pp.
- CAMPBELL, R. W. – SLOAN, R.T. (1978): Numerical bimodality among North American gypsy moth populations. Environmental Entomology 7: 641-646.
- COMMONWEALTH INSTITUTE OF ENTOMOLOGY (1981): Distribution maps of pests, Series A, Map No. 26 (Revised). *Lymantria dispar* (L.). CAB International, Wallerford, United Kingdom.
- CSÓKA, GY. – HIRKA, A. (2007): A gyapjaslepke kártételt követő kárláncolatok ["Damage chains" following the gypsy moth damage]. In: Csóka, Gy. – Varga, Sz. (eds.) 2007: Gyapjaslepke (Gypsy moth), Agroinform, Budapest (in press) (Hungarian with English summary)
- CSÓKA, GY. – HIRKA, A. (2007): A gyapjaslepke jelentősége [Importance of gypsy moth]. In: Csóka, Gy. – Varga, Sz. (eds.) (2007): Gyapjaslepke [Gypsy moth], Agroinform, Budapest (in press) (Hungarian with English summary)
- CSÓKA, GY. – KOVÁCS, T. (1999): Xilofág rovarok – Xylophagous insects. Agroinform, Budapest, 1999. (Bilingual – Hungarian and English)
- CSÓKA, GY. – TÓTH, J. – KOLTAY, A. (1999): Trends of sessile oak decline in North-Eastern Hungary. In: Forster, B. – Knizek, M. – Grodzki, W. (eds.): Methodology of Forest Insects Disease Survey in Central Europe. Proceedings of the Second Workshop of the IUFRO WP 7.03.10. 48-53.
- DAVIDSON, C. B. – GOTTSCHALK, K.W. – JOHNSON, J.E. (1999): Tree mortality following defoliation by the European gypsy moth (*Lymantria dispar* L.) in the United States. A review. Forest Science 45: 77-84.
- ELKINTON, J. S., HEALY, W.M. – BUONACCORSI, J.P. – BOETTNER, G.H. – HAZZARD, A. – LIEBHOLD, A.M. – SMITH, H.R. (1996): Interactions among gypsy moth, white-footed mice, and acorns. Ecology 77:2332-2342.
- ELKINTON, J. S. – HAJEK, A. – BOETTNER, G. – SIMONS, E. (1991): Distribution and apparent spread of *Entomophaga maimaiga* (Zygomycetes: Entomophthorales) in gypsy moth (Lepidoptera: Lymantriidae) populations in North America. Environmental Entomology 20: 1601-1605.
- FELT, E. P. (1942): The gypsy moth threat in the United States. Eastern Plant Board Circular No. 1.
- FORBUSH, E. H., – FERNALD, C.H. (1896): The Gypsy Moth. Wright and Potter Printing Co., Boston, MA. 495 pp.
- FUESTER, R. W. – RAMASESHIAH, G. (1989): A comparison of the parasite complexes attacking two closely related Lymantriids, pp. 501-556. In: Wallner, W.E. – McManus, K.A. (tech. cords.): Proceedings, Lymantriidae: a comparison of features of New and Old World tussock moths. U.S. Department of Agriculture Forest Service, Northeastern Forest Experiment Station General Technical Report NE-123. 554 pp.
- FUHRER, E. (1998): Oak decline in Central Europe: a synopsis of hypotheses. In: McManus, M.L. – Liebhold, A.M. (eds.): Proceedings, population dynamics, impacts, and integrated management of forest defoliating insects; 1996 August 18-23; Banska Stiavnica, Slovak Republic. U. S. Department of Agriculture Forest Service, Northeastern Forest Experiment Station General Technical Report NE-247. 7-24.
- GRIJPMAN, P. (1989): Overview of research of Lymantriids in eastern and western Europe. In W.E. Wallner, W.E. – McManus, K.A. (tech. cords.): Proceedings, Lymantriidae: a comparison of features of New and Old World tussock moths. U.S. Department of Agriculture Forest Service, Northeastern Forest Experiment Station General Technical Report NE-123. 21-49.
- GSCHWANTNER, T. – HOCH, G. – SCHOPF, A. (2002): Impact of predators on artificially augmented populations of *Lymantria dispar* L. pupae (Lep.: Lymantriidae). Journal of Applied Entomology 126: 66-73.
- HAJEK, A. – HUMBER, R. – ELKINTON, J. – MAY, B. – WALSH, S. – SILVER, J. (1990): Allozyme and restriction fragment length polymorphism analyses confirm *Entomophaga maimaiga* responsible for 1989 epizootics in North American gypsy moth populations. Proceedings, National Academy of Sciences. USA. 87: 6979-6982
- HIGASHIURA, Y. (1989): Survival of eggs in the gypsy moth, *Lymantria dispar*. I. Predation by birds. Journal of Animal Ecology 58: 403-412.
- HIRKA, A. 2005: A 2004. évi biotikus és abiotikus erdőgazdasági károk, valamint a 2005-ben várható károsítások [Biotic and abiotic damage in the Hungarian forests in 2004, and the damage forecast for 2005]. Hungarian Forest Research Institute, Budapest, pp. 126. (Hungarian with English summary)

- HIRKA, A. 2006: A 2005. évi biotikus és abiotikus erdőgazdasági károk, valamint a 2006-ban várható károsítások [Biotic and abiotic damage in the Hungarian forests in 2005, and the damage forecast for 2006]. Hungarian Forest Research Institute, Budapest, pp. 124. (Hungarian with English summary)
- HIRKA, A. 2007: A 2006. évi biotikus és abiotikus erdőgazdasági károk, valamint a 2007-ben várható károsítások [Biotic and abiotic damage in the Hungarian forests in 2006, and the damage forecast for 2007]. Hungarian Forest Research Institute, Budapest, pp. 128. (Hungarian with English summary)
- HOCH, G. – GSCHWANTNER, T. – SCHOPF, A. (1999): The gypsy moth and its natural enemies at different population densities in the oak forests of eastern Austria. IOBC Bulletin 22: 121-128.
- HOY, M. A. (1976): Establishment of gypsy moth parasitoids in North America: an evaluation of possible reasons for establishment or non-establishment. In: Anderson, J.F. – Kaya, H.K. (eds), Perspectives in Forest Entomology. Academic Press, New York. Chapter 15: 215-232.
- JOHNSON, D. M. – LIEBHOLD, A.M. – BJORNSTAD, O.N. – MCMANUS, M.L. (2005): Circumpolar variation in periodicity and synchrony among gypsy moth populations. Journal of Animal Ecology 74: 882-892.
- JONES, G. G. – OSTFELD, R.S. – RICHARD, M.P. – SCHAUBER, E.M. – WOLFF, J.O. (1998). Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. Science 279:1023-1026.
- LEONARD, D. E. (1974): Recent developments in ecology and control of gypsy moth. Annual Review of Entomology 19: 192-229.
- LESKÓ, K. – HIRKA, A. – CSÓKA, GY. 2007: A gyapjaslepke populációdinamikája Magyarországon [Population dynamics of gypsy moth in Hungary]. In: Csóka, Gy. – Varga, Sz. (eds.) 2007: Gyapjaslepke [Gypsy moth], Agroinform, Budapest (in press) (Hungarian with English summary)
- LESKÓ, K. – SZENTKIRÁLYI, F. – KÁDÁR, F. 1994: Gyapjaslepke (*Lymantria dispar* L.) populációk fluktuációs mintázatai 1963-1993. közötti időszakban Magyarországon. [Fluctuation patterns of gypsy moth populations between 1963 and 1993 in Hungary]. Erdészeti Kutatások. 84. 163-176 (Hungarian with English summary)
- LEUSCHNER, W. A. – YOUNG, J.A. – WALDON, S.A. – RAVILI, F.W. (1996): Potential benefits of slowing the gypsy moth's spread. Southern Journal of Applied Forestry 20: 65-73.
- LIEBHOLD, A. – N. KAMATA, N. (2000): Are population cycles and spatial synchrony characteristic of forest insect populations? Population Ecology 42:205-209.
- LIEBHOLD, A. M. – J. HALVERSON, J. – ELMES, F. (1992): Quantitative analysis of the rate of spread of gypsy moth in North America. Journal of Biogeography 19:513-520.
- LIEBHOLD, A. M. – GOTTSCHALK, K.W. – LUZADER, E.R. – MASON, D. – BUSH, A.R. – TWARDUS, D.B. (1997): Gypsy moth in the United States: an atlas. U. S. Department of Agriculture Forest Service, Northeastern Forest Experiment Station General Technical Report NE-233. 33 pp.
- LIEBHOLD, A. M. – V. MASTRO, V. – SCHAEFER, P.W. (1989): Learning from the legacy of Leopold Trouvelot. Bulletin of the Entomological Society of America 35: 20-21.
- LIEBHOLD, A. – ELKINTON, J. – WILLIAMS, D. – MUZIKA, R-M. (2000): What causes outbreaks of the gypsy moth in North America? Population Ecology 42:257-266.
- LIPA, J. (1996): Present status of noxious Lymantriidae in Europe and Poland, pp 13-31. In: Proceedings, International Conference, Integrated management of forest Lymantriidae; 1996 March 27-29; Warsaw-Sekocin, Poland. Warsaw, Forest Research Institute.
- MAROVIĆ, R. – MAROVIĆ, M. – JANČIĆ, G. – LAZAREV, V. (1998): Gypsy moth outbreaks in Serbia, pp. 1-6. In: The Gypsy Moth Outbreaks in Serbia. Acta entomologica Serbie (Special Issue). Belgrade, Serbia.
- MAYO, J.H. – STRAKA, T.J. – LEONARD, D.S. (2003): The cost of slowing the spread of the gypsy moth (Lepidoptera: Lymantriidae). Journal of Economic Entomology 96:1448-1454.
- MCFADDEN, M. W. – MCMANUS, M.L. (1991): An insect out of control? The potential for spread and establishment of the gypsy moth in new forest areas in the United States. In: Baranchikov, Y.N. – Mattson, W.J. – Hain, F.P. – Payne, T.L. (eds.): Forest Insect Guild; patterns of interaction with host trees. U.S. Department of Agriculture Forest Service, Northeastern Forest Experiment Station General Technical Report NE-153. 172-184.
- MCMANUS, M. L. (1978): Expanded gypsy moth research and development program. Journal of Forestry 76: 144-149.

- MCNAMARA, D. G. (1996): EPPO's perspective on the gypsy moth in Europe. In: Proceedings, 1995 Annual Gypsy Moth Review; 1995 November 5-8; Traverse City, MI. Michigan Department of Agriculture, Lansing. 60-65.
- MIHAJLOVIĆ, L. J. – GRBIĆ, C. – D VANDIĆ D. (1998): The latest outbreaks of gypsy moth, *Lymantria dispar* L., in the region of Serbia in the period 1995-1998. In: The gypsy moth outbreaks in Serbia. Acta entomologica Serbie (Special Issue). Belgrade, Serbia. 80-88.
- MILLER, D. R. – MO, T.K. – W. E. WALLNER, W.E. (1989): Influence of climate on gypsy moth defoliation in southern New England. Environmental Entomology 18:646-650.
- MONTGOMERY, M. E. – W. E. WALLNER, W.E. (1988): The gypsy moth: a westward migrant. In: Berryman, A.E. (ed.): Dynamics of Forest Insect Populations. Plenum Publishing Corp. 353-373.
- NEALIS, V. G. – QUEDNAU, F.W. (1996): Canadian field releases and overwinter survival of *Ceranthia samarensis* (Villeneuve) (Diptera: Tachinidae) for biological control of the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae). Proceedings, Entomological Society of Ontario 127: 11-20.
- NEALIS, V. G. – RODEN, P.M. – ORTIZ, D.A. (1999): Natural mortality of the gypsy moth along a gradient of infestation. Canadian Entomologist 131:507-519.
- PERRY, C. C. (1955): Gypsy moth appraisal program and proposed plan to prevent spread of the moths. U.S. Department of Agriculture Forest Service, Washington, D.C. Technical Bulletin No. 1124.
- PILARSKA, D. – MCMANUS, M.L. – P. PILARSKI, P. – GEORGIEV, G. – MIRCHEV, P. – LINDE, A. (2006): Monitoring the establishment and prevalence of the fungal entomopathogen *Entomophaga maimaiga* in two *Lymantria dispar* L. populations in Bulgaria. Journal of Pest Science 79: 63-67.
- REARDON, R. (1991): Appalachian gypsy moth integrated pest management project. Forest Ecology and Management 39: 107-112.
- REICHART, G. (1959): Birds destroying eggs of *Lymantria dispar* L. Aquila 77: 315-317.
- ROTHSCHILD, G. 1958: Exterminatin by rodents of the gypsy moth in the area of mass reproduction. (Translated from Russian). Byull. Mosk. O-VA. Ispyt. Prir. Otd. Briol. 63: 129-130.
- SHAROV, A. A. – LEONARD, D.S. – LIEBHOLD, A.M. – ROBERTS, E.A. – DICKERSON, E.A. (2002): Slow the Spread: a national program to contain the gypsy moth. Journal of Forestry 100: 30-35.
- SIDOR, C. (1979): The role of insect pathogenic microorganisms in the protection of environment. Mikrobiologija 16: 173-186.
- SMITH, H. R. (1985): Wildlife and the gypsy moth. Wildlife Society Bulletin 13: 166-174.
- SMITH, H. R. – LAUTENSCHLAGER, R.A. (1978): Predators of the gypsy moth. U.S. Department of Agriculture Handbook 534. 72 pp.
- SMITH, H. – ELKINTON, J. – WALLNER, W. – LUNCHENKO, G. – BARANCHIKOV, Y. (1998): Comparison of the potential role of small mammal predators of forest pest insects in the U. S. and former Soviet Union: a study of ecological equivalents. In: Euro-American Mammal Congress, Santiago de Compostela, Spain. (abstract) 294-295.
- SOPER, R, M. – SHIMAZU, M. – HUMBER, R.A. – RAMOS, M.E. – HAJEK, A. (1988): Isolation and characterization of *Entomophaga maimaiga* sp. nov., a fungal pathogen of gypsy moth, *Lymantria dispar* from Japan. Journal of Invertebrate Pathology 51: 229-241.
- STEIN, J. – BINION, D. – ACCIAVATTI R. (2003): Field guide to native oak species of eastern North America. U.S. Department of Agriculture Forest Service FHTET-2003-01, 161p.
- TURCEK, R. J. (1950): The bird population in some deciduous forests during an outbreak. Bulletin of the Institute of Forest Research of the Czech Republic 3: 108-131.
- U.S. DEPARTMENT OF AGRICULTURE (1995): Gypsy moth management in the United States: a cooperative approach. Final environmental impact statement. Volumes 1-5. Washington, D.C.: U.S. Department of Agriculture.
- WEISER, J. (1987): Patterns over place and time. In: James R. Fuxa and Yoshinori Tanada, eds. Epizootiology of insect diseases. John Wiley and Sons, New York, 215-244.
- WESELOH, R. – ANDREADIS, T. (1992): Mechanisms of transmission of the gypsy moth (Lepidoptera: Lymantriidae) fungus *Entomophaga maimaiga* (Entomophthorales: Entomophthoraceae) and effects of site condition on its prevalence. Environmental Entomology 21: 901-906.
- WESELOH, R. – BERNON, G. – BUTLER, L. – FUESTER, R. – MCCULLOUGH, F. STEHR, F. (1995): Releases of *Calasoma sycophanta* (Coleoptera: Carabidae) near the edge of gypsy moth (Lepidoptera: Lymantriidae) distribution. Environmental Entomology 24: 1713-1717.

- WILLIAMS, D. W. – LIEBHOLD, A.M. (1995): Influence of weather on the synchrony of gypsy moth (Lepidoptera: Lymantriidae) outbreaks in New England. *Environmental Entomology* 24: 987-995.
- WOODS, S. A. – ELKINTON, J.S. (1987): Bimodal patterns of mortality from nuclear polyhedrosis virus in gypsy moth (*Lymantria dispar*) populations. *Journal of Invertebrate Pathology* 50: 151-157.
- ZELINSKAYA, L. M. (1980): Role of microsporidia in the abundance dynamics of the gypsy moth *Porthetria dispar*, in forest plantings along the lower Dnieper River (Ukrainian Republic, USSR). *Vestn. Zool.* 1: 57-62.
- ZUBRIK, M. – J. NOVOTNY, J. (1996): The complex of gypsy moth (*Lymantria dispar* L.) parasitoids in Slovakia and other Central European countries. In: S.L.C. Fosbroke and K. W. Gottschalk, eds. *Proceeding, U. S. Department of Agriculture interagency research forum 1996; 1996 January 16-19; Annapolis, MD. U.S. Department of Agriculture Forest Service, Northeastern Forest Experiment Station General Technical Report NE-230. Radnor, PA.* 83-88.