

Review

A study of natural enemies and pathogenic agents of gypsy moth

*Seyid Hamid¹, Saadi Tarzi² and Leila Bobak Ferdowsi²

¹Department of Forestry, Faculty of Agriculture and Natural Resources, University of Kurdistan, Sanandaj-Iran

²Department of Forestry, Faculty of Agricultural Sciences University of Guilan, Rasht, Guilan, Iran.

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The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera, Lymantriidae), is a forest pest native to Europe and parts of Asia. It was accidentally introduced from Europe into Massachusetts in 1869. The gypsy moth is a highly polyphagous folivore species that feeds on over 300 species of woody plants. Among its most preferred hosts are oaks and aspens. The research was conducted with the purpose of gathering natural enemies and pathogenic agents of gypsy moth. Natural enemies refer to the predators, parasitoids and pathogens that affect pest insects such as the gypsy moth. These natural enemies are important in helping to control gypsy moth outbreaks and in keeping populations low in the years between outbreaks. A diverse group of birds, mammals, amphibians, and insect predators feed on gypsy moth eggs, caterpillars and pupae. Mice are important predators of gypsy moth caterpillars and pupae.

Keywords: Gypsy moth, *Lymantria dispar*, natural enemies.

INTRODUCTION

The gypsy moth *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) was accidentally introduced to North America from Europe by a renowned scientist, Etienne Leopold Trouvelot, near Boston, Massachusetts in 1869 (Dixon and Flotz, 1985). He wanted to study silkworms, but ended up releasing one of the most devastating forest pests ever seen in North America (Gerardi and Grimm, 1979). It is known as a polyphagous herbivore in Europe and was also accidentally introduced and established through much of northeastern USA (Doane and McManus, 1981). The gypsy moth is a highly polyphagous folivore species that feeds on over 300 species of woody plants (Leonard, 1981). Among its most preferred hosts are oaks and aspens (Stoyenoff et al., 1994). Some trees are resistant to the gypsy moth including honey locust, black locust, silver maple, green ash, dogwood, sycamore, horse chestnut, firs, and tulip trees (Herms, 2003). The gypsy moth passes through four stages: egg, larva, pupa, and adult (moth stage) (McManus et al., 1989). Only the larvae damage trees

and shrubs. Gypsy moth egg masses are laid on branches and trunks of trees, but egg masses may be found in any sheltered location (Kavosi, 2008). Egg masses are buff colored when first laid but may bleach out over the winter months when exposed to direct sunlight and weathering. The hatching of gypsy moth eggs coincides with budding of most hardwood trees. The female deposits her eggs in an egg mass in June and July. Larvae usually emerge in early April they climb to the outer branches or top of trees which coincides with bud break (Hajizadeh, 2011). Larvae are dispersed in two ways. Natural dispersal occurs when newly hatched larvae hanging from host trees on silken threads are carried by the wind for a distance of about 1 mile. Larvae can be carried for longer distances. Artificial dispersal occurs when people transport gypsy moth eggs thousands of miles from infested areas on cars and recreational vehicles, firewood, household goods, and other personal possessions (McManus et al., 1989). After dispersing and feeding on various plants, the larvae go through five or six stages and complete their development in late June or early July after they attach themselves to a surface with strands of silk. They transform into pupae at this location (McManus et al.,

*Corresponding author email: seyid_hamid@gmail.com.

1989). In 1889, Massachusetts initiated the first gypsy moth eradication program. It was so successful at controlling the gypsy moth population in the state that lawmakers terminated the program in 1900. This was realized to be a mistake when, by 1910, the gypsy moth population quickly recovered in Massachusetts and spread to the neighboring states of Maine, New Hampshire, and Rhode Island. More than 81 million acres of forests have been defoliated by the gypsy moth since 1924, and more than 12 million acres have been aerially sprayed to control its populations since 1970 (USDA, 1995). Natural enemies refer to the predators, parasitoids and pathogens that affect pest insects such as the gypsy moth (McCullough et al., 1999). These natural enemies are important in helping to control gypsy moth outbreaks and in keeping populations low in the years between outbreaks. A diverse group of birds, mammals, amphibians, and insect predators feed on gypsy moth eggs, caterpillars and pupae. Mice are important predators of gypsy moth caterpillars and pupae (McCullough et al., 1999). Some of natural enemies that affect gypsy moth are native to North America. Others were deliberately introduced from Europe, Asia, India, and northern Africa, where gypsy moth is native (Mott and McCullough, 2001). The gypsy moth has been the target of several extensive biological control programs since its introduction into North America in the 19th century (Kenis and Vaamonde, 1998). More than 60 species of natural enemies, parasitoids, predators and pathogens were introduced from 1906 to present but most failed to establish, for various reasons (Hoy, 1976). Only 11 parasitoids, two predators and two pathogens became established, and among these some became major natural enemies of the gypsy moth in North America (Doane and McManus 1981; Schaefer et al., 1989). The impact of these exotic natural enemies on gypsy moth populations in north America is hard to assess because of the difficulty of determining what would be the situation had these natural enemies not been introduced (Hajek et al., 1993). Several authors claim that exotic natural enemies play an important role in regulating gypsy moth populations both at sparse densities and in outbreak situations (Clausen 1978; Berryman, 1991). Nevertheless, the impact of these exotic natural enemies cannot be considered as totally satisfactory. Indeed, the gypsy moth is still the major pest of broadleaved forests in eastern North America and its distribution is expanding further west and south, despite the expensive eradication programs carried out at the edge of its present distribution (Kenis and Vaamonde, 1998). The research has therefore conducted with the purpose of gathering natural enemies and pathogenic agents of gypsy moth.

Predators

Many larger animals use gypsy moths and other insects

as food sources. Like most predators, some are particular about what life stage they will eat and others are simply opportunistic. Some mammalian predators of the gypsy moth include white-footed mice, shrews, chipmunks, voles and squirrels. Shrews, which are often mistaken for mice, are voracious insect feeders that consume their own weight in prey each day. Nuthatches, chickadees, towhees, vireos, northern orioles, catbirds, robins and blue jays can keep sparse gypsy moth populations in check. Large numbers of gypsy moths will attract starlings, grackles, red-winged blackbirds and crows, which flock together and need a food source for the entire group. Spiders, ants and daddy longlegs take care of most gypsy moth larvae and pupae that are near the ground. Ground beetle larvae and adults feed readily on gypsy moth larvae and pupae. These beetles will climb trees to find gypsy moth larvae and are very active. Normally, however, they usually work in the background, quickly and efficiently consuming their prey (McCullough et al., 1999 and Hickman, 2005).

Entomopathogens

The microbial insecticide known as *Bt.* or B.t.k (*Bacillus thuringiensis* var. *kurstaki*) is often used to protect tree foliage in residential areas during gypsy moth outbreaks. Unlike conventional insecticides, B.t.k. will not harm vertebrate or insect predators (McCullough et al., 1999, Moody, 1988). When populations are high, aerial application of *Bt* is the most widely-used strategy for preventing defoliation. *Bt* formulations used for gypsy moth suppression affect only Lepidoptera larvae, and are harmless to other animals, including bees and other insects, birds, pets, and humans. *Bt* can be very effective at preventing defoliation when applications are timed accurately (Smitley and Davis, 1993). Applications should be made when the majority of larvae are second instars, as young larvae are more susceptible to *Bt*, and coverage is better when aerial applications are made before leaves fully expand and the spray can still penetrate the canopy. There is some concern that *Bt* sprays can prolong outbreaks by interfering with natural enemies. However, this does not seem to be the case. Research has shown that aerial applications of *Bt* have little overall impact on the effectiveness of gypsy moth parasites, predators, or pathogens (Andreadis and Weseloh, 1990). On the other hand, *Bt* sprays also seem to have little effect on the inherent population dynamics of gypsy moth, the populations of which tend to increase or decrease independent of whether they had been sprayed with *Bt* in previous years (Smitley and Davis, 1993). About 100 bacteria are reported as pathogenic agents of insects (Doane, 1970), among which, only following four bacteria are introduced as controllers of insects: *B. thuringiensis* (*Bt*), *B. papillae*, *B. lentimorbus*, and *B. spaericus* (Yendol et al., 1990). These species have

spores and are more resistant against unfavorable environmental agents rather than others. Among these four bacilli, only *Bt* has developed successfully being widely produced and presented in several countries as a commercial insecticide being used for crops of trees and farms and recently as a controller of larvae of butter flies in stored crops (Elkinton and Liebhold, 1990). This suggests that goals and expectations of gypsy moth suppression programs should focus on protecting trees from defoliation during gypsy moth outbreaks, rather than long-term reduction of gypsy populations (Herms, 2003).

Birds

Many birds do not like to feed on large, hairy gypsy moth caterpillars, but other species seem to relish them. Yellow-billed and black-billed cuckoos, blue jays, orioles and rufous-sided towhees are among the species that feed on gypsy moth caterpillars. Some birds, such as the black-capped chickadee, will also feed on egg masses and can sometimes cause substantial egg mortality (McCullough et al., 1999).

Mammals

Shrews, mice, voles and other small mammals often feed on gypsy moth caterpillars and pupae that they encounter on the ground and around the bases of trees. Mice seem to prefer the large female pupae to the smaller male pupae. This selective feeding can have a greater impact on the overall gypsy moth population than random feeding. Chipmunks, skunks and raccoons also feed on gypsy moth larvae and pupae, and squirrels feed on pupae (McCullough et al., 1999).

Insect predators

Some insects are also important predators of gypsy moth. For example the calosoma beetle (*Calosoma sycophanta*) is a "specialist" that it feeds almost entirely on gypsy moth. Several native insects are also good predators and attack gypsy moth, as well as other plant-feeding insects. Ants can also be important predators of young caterpillars. Many other insect predators and spiders are opportunistic feeders and will consume gypsy moth larvae or pupae when they are available (McCullough et al., 1999).

Parasitoids

The term "Parasitoids" refers to certain species of wasps and flies that have a very specialized life cycle. Parasitoids lay their eggs inside, on or near the body of a

host insect, such as gypsy moth caterpillar. The larval stages of most parasitoids resemble maggots. Parasitoids larvae live by feeding on tissues in the body of the host insect, killing it in the process. Once the parasitoid has completed its development, it emerges from the host insect. Several parasitoids are important natural enemies of gypsy moth. Parasitoids attacking hosts at low density are likely to be polyphagous. Indeed, when similar host exposure experiments are made in North America, the main parasitoid reared is the polyphagous tachinid *Compsilura concinnata* (Gould et al., 1990). However, there are good indications that *C. samarensis* is not polyphagous. First, the only one other host record besides the gypsy moth is the lymantriid *Orgyia recens* Hbn (Mihalyi, 1986). Second, extensive collections of macrolepidopteran larvae at sites where *C. samarensis* was reared in high numbers from exposed gypsy moth larvae did not give rise to any *C. samarensis*. Finally, to test the ability of *C. samarensis* to develop in other hosts, artificial inoculations of *C. samarensis* maggots found by dissection of mature females were made on larvae of several macrolepidopteran species. This method was successful on the gypsy moth (Quednau, 1993) while on the other hosts, the maggots usually penetrated into the larvae but failed to develop further. *Ceranthia samarensis* is presently reared in Canada to augment the number of females available for release (Quednau, 1993) and field cage releases started in 1991 in Ontario. Such investigations on parasitism in low density populations should not be restricted to Western Europe. Similar studies could be done in other regions where the gypsy moth usually remains at endemic levels, particularly in Asia. A few examples are described here:

(i) *Ooencyrtus kuvanae*

One of the most important parasitoids of the egg of gypsy moth is *Ooencyrtus kuvanae* (Howard) (Hym: Encyrtidae), which currently spread throughout the Holarctic region. It was first transferred from Japan to America in 1908, then released having multiplied to 10,000 adult insect in the regions where the compression of gypsy moth was high (Brown, 1984). Research conducted in Bulgaria confirmed that *O.kuvanae* have one or two generations in spring and five in summer; only one parasitoids grows in each egg of the pest, and in exchange for per 20 host eggs, one parasitoid must be considered in release. *O. kuvanae*, close species to *O. masii* has been more biologically studied because it is used in a biological control against *L. dispar*. This little wasp is a specialist that parasitizes the eggs of gypsy moth. It was introduced into the United States for biological control of gypsy moth many years ago and is now well established in most of the region infested by gypsy moth. The tiny, dark adult wasps can often be

observed if you look closely at gypsy moth egg masses. You may also see the small, round holes in the egg mass where the adult wasps emerged. Because the wasp is small, it can usually attack only the eggs in the upper layer of a gypsy moth egg mass. In many years, it is able to kill 20 to 30% of the eggs in an egg mass. Although *Ooencyrtus* wasps are rarely available from commercial suppliers, you can help to protect populations that are established in your area. For example, if you intend to scrape off and destroy egg masses as part of your gypsy moth management program, it is best to wait until winter (McCullough et al., 1999).

(ii) *Cotesia melanoscelous*

Parasitoid fields of Tachinidae family enjoy more abundance and efficiency rather than Sarcophagidae family. 10 species have been reported from Tachinidae family to act as parasitoids of larvae and pupae of gypsy moth, among which, the main ones are: *Compsilura concinnata*, *Parasitigena silvestris*, *Exorista larvarum*, *Sturmia scutellata* in republic of Czech, *P. silvestris* and *S. scutellata* are known as the main parasitoid fields of Pupae of gypsy moth. The efficiency of predatory of hunter beetles called *Carabus nemoralis*, *Calosma sycophanta*, L., and *Pterostichus pensylvanicus* is subject to study (Leonard, 1974). This is another specialized wasp that was introduced specifically for biological control of gypsy moth. The first generation of the wasp will attack very young gypsy moth caterpillars and is often successful in subduing the young host caterpillar. A second generation of the wasp can attack larger gypsy moth caterpillars, those that are about halfway through their development. This parasitoid pupates in a small, oblong yellowish cocoon. These cocoons are frequently observed near a dead gypsy moth caterpillar or attached to the bark of an infested tree. In some cases, this parasitoid can be an important source of mortality. However, the small wasps sometimes have difficulty attacking larger gypsy moth caterpillars, and the wasp has its own natural enemies that may limit its effectiveness. Avoiding applications of broad-spectrum chemical insecticides in early and midsummer will help protect this species (McCullough et al., 1999).

(iii) *Compsilura coccinnata*

This fly attacks gypsy moth caterpillars, as well as the caterpillars of more than 100 other moth and butterfly species. It was introduced for gypsy moth control many years ago and is well established throughout much of the northeastern and north central United States. It has three generations a year, although only one of these generations attacks gypsy moth caterpillars. After feeding in the body of a gypsy moth caterpillar, this parasitoid

pupates in a reddish brown pauperism often seen on or near the body of the dead caterpillar. This parasitoid may be important in helping to keep gypsy moth populations in check and prolonging in the period between outbreaks (Moody, 1988; McCullough et al., 1999).

Pathogens

Gypsy moth and other insects are affected by a variety of organisms that cause disease, including fungi, bacteria, viruses and protozoan. Two diseases are especially important in controlling gypsy moth outbreaks (McCullough et al., 1999 and Hickman, 2005).

NPV- The virus disease

The gypsy moth nuclear polyhedrosis virus (commonly known as NPV) builds rapidly in dense populations, which usually causes outbreaks to collapse within two or three years. The virus can also be formulated as an insecticide that is specific to gypsy moth. However, since the virus can be produced only from live caterpillars, supplies are extremely limited, and application of the NPV spray is generally limited to environmentally sensitive habitats, such as those containing endangered butterflies and moths. Nucleopolyhedrosis virus (NPV) has the most dramatic effect on gypsy moth infestations, causing entire gypsy moth outbreaks to hang as liquefied bags in the trees. These bodies are dark, flaccid, feel gooey and are seen in the hundreds, if not thousands. This virus will eliminate most outbreaks. *Entomophaga maimaiga*, fungi, is found in most established gypsy moth populations. It appears similar to NPV but effects both small and large infestations of gypsy moths (McCullough et al., 1999; Hickman, 2005).

Entomophaga maimaiga

The fungal pathogen *Entomophaga maimaiga* also significantly impacts gypsy moth populations, even when populations are low. The fungus, which infects the caterpillar stage, can be disseminated to new gypsy moth infestations by dispersing resting spores. However, it spreads easily when environmental conditions are favorable, and quickly becomes established on its own. The effectiveness of *Entomophaga* is not predictable, being highly dependent on the occurrence of rainfall events at critical moments during the spring. Although *Entomophaga* can cause gypsy moth populations to decline dramatically in wet years, outbreaks still occur where *Entomophaga* is established, especially during dry springs (McCullough et al., 1999). Efficiency of pathogenic fungi including *Entomophaga maimaiga* and *Paecilomyces farinosus* which have been separated from

surface skin of larvae and egg mass of gypsy moth, have been assessed (Dunbar et al., 1972). Most research about natural enemies of gypsy moth is in connection with parasitoids (Weseloh, 1972).

CONCLUSION

Gypsy moth population growth rates depend on numerous factors, including the composition of tree species in a forest stand, the density of predators, and climate. Campbell and Sloan (1978) suggested that predation by small mammals is also density-dependent in low-density gypsy moth populations. However, experiments by (Elkinton et al., 1989) did not support that hypothesis. In areas infested by gypsy moth for many years, there is little or no relationship between male moth counts and subsequent defoliation at the same location (Carter et al., 1992 and Liebhold et al., 1995). Natural enemies play an important role in gypsy moth control during normal years of light infestations. Scientists are actively looking for parasites and predators of the gypsy moth, principally in Europe and Asia. Over ten foreign biological control agents (parasitoids, predators and disease organisms specific to gypsy moths) have been introduced for control purposes. Natural enemies include wasps, flies, ground beetles, and ants. Spiders eat small caterpillars. Birds such as chickadees, bluejays, nuthatches, towhees, and robins are control agents as several woodland mammals like whitefooted mice, shrews, chipmunks, and squirrels. Gypsy moths have several diseases, caused by bacteria, fungi, or a virus. The NPV virus disease is the most destructive to this pest. When conditions are right, it will nearly eliminate gypsy moths in an area for a few years. The disease occurs, and works best in control after a long period of rain or during very humid weather when the caterpillars are feeding. In 1989, outbreaks of the gypsy moth in seven northeastern U.S. states suddenly collapsed due to the fungal pathogen *Entomophaga maimaiga*. In 1992, *E. maimaiga* epizootics covered most of the distribution range of the gypsy moth in North America (Hajek et al., 1993). This pathogen was first introduced from Japan to North America in 1910 and 1911 but was not recovered in the field until 1989. It is not yet clear whether the strain which recently decimated the gypsy moth populations comes from this early introduction, in which case its sudden virulence might have resulted from natural selection, or from a new, accidental introduction (Hajek et al., 1993). However, regardless of the origin of this introduction, this example shows that there is still potential for classical biological control of the gypsy moth in North America. The most promising direction appears to be a continuation of the introduction of the parasitoids *Blepharipa schineri* and *Ceranthia samarensis*, studies on egg predators, investigations of low density parasitoids in poorly studied regions, and investigation of

the existence of more efficient biotypes of natural enemies already established in North America, particularly the parasitoids *Parasetigena silvestris* and *Cotesia melanoscelus*.

REFERENCES

- Andreadis TG, Weseloh RM (1990). Discovery of entomophaga maimaiga in North American gypsy moth, *Lymantria dispar*. Proc. Natl. Acad. Sci. USA 87: 2461–2465.
- Berryman AA (1991). The gypsy moth in North America: a case of successful biological control. J. Tree. 6:110-111.
- Brown MW (1984). Literature review of *Ooencyrtus kuvanae* (Hymenoptera: Encyrtidae), an egg parasite of *Lymantria dispar* (Lepidoptera: Lymantriidae). Entomophaga. 29: 249 – 265.
- Campbell RW, Sloan RJ (1978). Numerical bimodality among North American gypsy moth populations. Environ. Entomol. 7: 641-646.
- Carter MR, Ravlin FW, McManus ML (1992). Effect of defoliation on gypsy moth defoliation on gypsy moth phenology and capture of male moth in pheromone-baited traps. Environ. Entomol. 21:1308 -1318.
- Clausen CP (1978). Introduced Parasites and Predators of Arthropod Pests and weeds: A World Review. Agric. Handb. 480. Washington, DC: U.S. Dept. Agric., For. Serv.
- Dixon WN, Foltz JL (1985). The gypsy moth *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae). Entomology Circular. No. 270.
- Doane CC (1970). Field application of a Streptococcus causing brachyosis in larvae of *portheiria dispar*. J. Invertebr. Pathol. 17: 303 – 307.
- Doane CC, McManus ML (1981). The Gypsy Moth: research towards integrated pest management. USDA For. Serv. Tech. Bull. No. 1585, 757 p.
- Dunbar DM, Weseloh RM, Walton GS (1972). A fungus observed on egg clusters of the gypsy moth, *Porthetria dispar* (Lepidoptera: Lymantriidae). Ann. Entomol. Soc. Am. 65: 1419 – 1421.
- Elkinton JS, Gould AM, Liebhold AM, Smith HR, Wallner WE (1989). Is gypsy moth population in North America regulated at low density? Pp. 233-249. In Wallner WE, McManus KA. The Lymantriidae: a comparison of features of new and old world tussock moths. U. S. For. Serv. Gen. Tech. Rep. NE- 123.
- Elkinton JS, Liebhold AM (1990). Population dynamics of gypsy moth in North America. Annu. Rev. Entomol. 35: 571 – 596.
- Gerardi MH, Grimm JK (1979). The history, biology, damage and control of the gypsy moth *Porthetria dispar* (L.). Associated Univ. Presses, Inc., Cranbury, NJ. 233p.
- Gould JR, Elkinton JS, Wallner WE (1990). Density dependent suppression of experimentally created gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations by natural enemies. J. Anim. Ecol. 59: 213-233.
- Hajek AE, Humber RA, Elkinton JS (1993). Mysterious origin of *Entomophaga maimaiga* in North America. Amer. Entomol. 41: 31-42.
- Hajizadeh G (2011) the comparison of integrated and pheromone control on the intensity and spatial distribution of *Lymantria dispar* (L.), M.Sc. Thesis, Gorgan of Agricultural Sciences & Natural Resources, University Press. 104.
- Herms DA (2003). Assessing management options for gypsy moth. Insect control. Pp 14 -18.
- Hickman R (2005). Battling gypsy moth. Illinois parks and recreation web extra.
- Hoy MA (1976). Establishment of gypsy moth parasitoids in North America: an evaluation of possible reasons for establishment or non-establishment. In Anderson JF, Kaya HK (eds.) Perspectives in Forest Entomology. Academic, New York: 215-232.
- Kavosi MR (2008). Study of distribution gypsy moth, *Lymantria dispar* (L.) in the North forests, The First Symposium of Climate Change and Dendrochronology, Sari University. p10.
- Kenis M, Vaamonde CL (1998). Classical biological control of the gypsy moth, *Lymantria dispar* (L.), in North America: Prospects and new strategies. Pages 213-221 in McManus ML, Liebhold AM (1998). Proceedings: Population dynamics, impacts, and integrated

- management of forest defoliating insects. USDA Forest Service General Technical Report NE-247.
- Leonard DE (1974). Recent developments in ecology and control of the gypsy moth. *Annu. Rev. Entomol.* 59: 197 – 227.
- Leonard DE (1981) Bioecology of the gypsy moth p. 9-29. In: Doane, C.C., and McManus ML (ed.) the gypsy moth research toward integrated pest management. U. S. Dept. Agric. For. Serv. Tech. Bull. 1584: 1-757.
- Liebholt AM, Macdonald WL, Bergdahl D, Mastro VC (1995). Invasion by Exotic Forest Pests: A Threat to Forest Ecosystems. *Forest Science Monographs* 30. 49 p.
- McCullough DG, Raffa KA, Williamson RC (1999). Natural Enemies of Gypsy Moth: The Goodguys! *Extension Bulletin E-2700*. 4p.
- McManus M, Schneeberger N, Reardon R, Mason G (1989). Gypsy moth. *Forest Insect and Disease Leaflet* 162. Washington, DC: US Dept. Of Agriculture, Forest Service. 13 pp.
- Milhayi F (1986). Diptera II Furkeszlegyek- Aszkalegyek Tachinidae-Rhiniphoridae. *Fauna Hungariae* 161, Vol. XV, Pt. 14-15, 425 p.
- Moody BH (1988). Forest insect and disease conditions in Canada. *Forest insect and disease survey forestry Canada*.
- Quednau FW (1993). Reproductive biology and laboratory rearing of *Ceranthia samarensis* (Villeneuve) (Diptera: Tachinidae), a parasitoid of the gypsy moth, *Lymantria dispar* (L.). *Canad. Entomol.* 125: 749-759.
- Schaefer RW, Fuester RJ, Chianese LD, Rhoads B, Tichenor Jr (1989). Introduction and North America establishment of *Coccygomimus disparis* (Hymenoptera: Ichneumonidae), a polyphagous pupal parasite of Lepidoptera, including gypsy moth. *Environ. Entomol.* 18: 1117-1125.
- Smitley DR, Davis TW (1993). Aerial application of *Bacillus thuringiensis* for suppression of gypsy moth (Lepidoptera: Lymantriidae) in Populus-Quercus forests. *Economic Entomology* 86: 1178-1184.
- Stoyenoff JL, Witter JA, Montgomery MA (1994). Nutritional indices in the gypsy moth under field conditions and host switching situations. *Oecologia* (1994) 97:158-170.
- USDA (1995). Gypsy moth management in the United States: A cooperative approach. Final Environmental Impact Statement. Washington, DC.
- Weseloh RM (1972). Influence of gypsy moth egg mass dimensions and microhabitat distribution on parasitization by *Ooencyrtus kuvanae* (Hymenoptera: Encyrtidae). *Ann. Ent. Soc. Am.* 65: 64 – 69.
- Yendol WG, Bryant JY, McManus ML (1990). Penetration of oak canopies by a commercial preparation of *Bacillus thuringiensis* applied by air. *J. Econ. Entomol.* 83: 1732 – 1739.