6.6 Ecology and Biological Control of Outbreak Populations of Winter Moth in the Northeastern United States

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The winter moth, *Operophtera brumata* L. (Geometridae: Lepidoptera), a leaf-feeding inchworm native to Europe, invaded the northeastern USA about 20 years ago and has caused widespread defoliation of many deciduous trees ever since (Elkinton et al., 2010, 2015). The winter moth has continued to spread west and south across Massachusetts and Rhode Island (Elkinton et al., 2014). In 2012, outbreaks occurred for the first time in southeast Connecticut and coastal Maine (Elkinton et al., 2015).

Beginning in 2004, we have collected yearly life table data on winter moth from red oak, *Quercus rubra* L. (Fagaceae) and red maple, *Acer rubrum* L. (Sapindaceae), two of the dominant deciduous trees in our forests, at 12 sites that have been heavily infested in eastern Massachusetts. Analyses of those data show that winter moths fluctuate with a biannual cycle of high and low densities. Mortality is strongly density dependent in the larval stage, but not consistently density dependent in the pupal stage. Overwintering mortality is also density dependent. Research by Pepi et al. (2016) showed that mortality in the larval stage and the overwintering stage were both dominated by density-dependent larval dispersal. Other forms of larval mortality, such as by pathogens or predators, were insignificant. Overcompensating density dependence in this stage explains the biannual cycle of density evident in our data and in previously published data from Nova Scotia (Embree, 1965).

Prior to the current winter moth invasion in the northeastern United States, there had been three previous invasions to North America: Nova Scotia in the 1930s, Oregon in the 1950s and to British Columbia in the 1970s. All three prior invasions have been suppressed by the introduction of parasitoids from Europe, in particular the tachinid fly *Cyzenis albicans* (Fallén) (Diptera: Tachinidae), and low-density populations of winter moth now persist indefinitely in these regions, similar to those in most of Europe (Roland and Embree, 1995). We have introduced many thousand *C. albicans* distributed across 43 sites in eastern Massachusetts, Rhode Island, Connecticut and Maine (Fig. 6.6.1), and it has established at 21 of those sites. As reported from Nova Scotia in the 1950s (Embree, 1965), it typically takes 3 to 5 years before recovery of *C. albicans* at release sites. Since there is only one generation per year of both the fly and the winter moth, it takes several years for the 1500-2000 flies released at a site to catch up with the millions of winter moths that exist at that site. We have now recovered the fly at all 17 of the sites where it was released prior...
to 2012 (Fig. 6.6.1). At several of those sites, establishment of *C. albicans* was documented for the first time in 2016. We expect it will soon be established at all, or most, of the 43 release sites.

![Cyzenis albicans release and recovery locations in the northeastern USA.](image)

Prior to 2015, *C. albicans* for release in the northeastern United States were obtained from Vancouver Island, British Columbia, where it had been established in the 1970s. Starting in 2015, however, we switched our collection efforts to Wellesley, Massachusetts, where high levels of parasitism were documented, comparable to what we encountered in British Columbia. Furthermore, the flies we collect in Wellesley are presumably better adapted to northeastern climatic conditions. Late-instar winter moth larvae are collected at sites where parasitism by *C. albicans* is high and the larvae are reared to the pupal stage. *Cyzenis albicans* pupates inside the winter moth pupae. The fly puparia are kept over the winter and adult flies released the following spring.

Each year 100-500 late-instar winter moth larvae are collected from each of the now 43 previous release sites. Larvae are reared to the pupal stage and dissected in mid-summer to document establishment of *C. albicans* and to measure percent parasitism. Parasitism at a release site in Wellesley, Massachusetts has fluctuated between 15 and 40% over the past 5 years. In 2017, both defoliation and the densities of winter moth pupae remained low at that site. Levels of parasitism at several of our older release sites had increased markedly in 2016 compared to previous years and now exceed 25%, which is the level at which effects on winter moth density in Wellesley were observed over the past five years. Furthermore, winter moth densities across many sites declined dramatically in 2016-2017. These data suggest we are on the verge of converting winter moth into a non-pest in the areas where *C. albicans* is established.

Roland (1988, 1990) and Roland and Embree (1995) published an intriguing analysis of the successful biological control of winter moth in Canada by *C. albicans*. Roland claimed that the reduction in winter moth density was caused mainly by pupal mortality due to predators and not the direct effect of *C. albicans* parasitism. This pattern was true both in Nova Scotia and on Vancouver Island. He proposed that the impact of *C. albicans*
parasitism was enhanced by the action of soil predators in the form of predatory beetles. For example, he hypothesized that these generalist predators are able to regulate winter moth densities only when C. albicans has reduced those densities to a manageable level. Our preliminary data from the release site in Wellesley supports this idea. Winter moth densities at this site have declined by 95% over the past five years, whereas parasitism by C. albicans has varied between 15% and 48% over the same time interval. That means that parasitism alone cannot account for this large drop in density.

Predation experiments (Broadley, unpublished data) involving deployment of winter moth pupae at this and other sites will determine if Roland’s ideas are correct. High levels of predation by invertebrate and vertebrate predators have been documented at these sites. This work is described on this system in a follow-up talk (This volume, 7.1) at this symposium. The research of Broadley and Roland illustrates why it is important to understand the impact of C. albicans in the context of all the other causes of mortality occurring in the winter moth system. What the prognosis is for winter moth densities in the northeastern United States remains to be seen, but it is vital that we try to quantify and explain the other factors influencing winter moth densities, in addition to C. albicans. We are hopeful that the introduction of C. albicans, in conjunction with these other native sources of mortality, will convert winter moth into a non-pest, much as it apparently did in the three previous introductions to North America.

References


