

Host-plant Relationships and Comparative Ecology of Conifer-feeding Budworms (*Choristoneura* spp.)

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Abstract

North American budworms are eruptive insect species that form intimate ecological relationships with their host trees. Population data for the eastern spruce budworm and jack pine budworm implicate natural enemies as primary determinants of population collapses. Yet the dynamics of these two species display markedly different temporal and spatial characteristics. One possible explanation for these differences is variation in the strength of the density-dependent relationship between the budworms and their host trees via the effects of defoliation on the adequacy of the host tree. The proposed density-dependent relationship operates through the concept of risk of dispersal. In the jack pine budworm, previous defoliation reduces subsequent production of pollen cones by the host tree. These pollen cones are critical to survival of early stages of the jack pine budworm so that defoliation has an immediate negative feedback on survival of future generations of budworm. In contrast, the eastern spruce budworm is less reliant on pollen cones for early-season survival because of their capability of mining old needles. However, defoliation over several years creates non-host gaps in the forest and may also increase early-season mortality resulting from dispersal of small larvae. Thus host-plant relationships may be density-dependent sources of mortality in these life systems via their effect on the risk of mortality resulting from dispersal. Variation in the strength of this density-dependent interaction contributes to differences in the dynamical behavior of the different budworm species.

The eastern spruce budworm, *Choristoneura fumiferana* (Clemens), and the jack pine budworm, *C. pinus pinus* Freeman, are eruptive species that periodically cause severe defoliation of their respective host trees throughout northern conifer forests east of the Rocky Mountains in North America. These species share a near-identical geographic range, life cycle and seasonal ecology. Eggs are laid in masses on the needles of the host trees in mid-summer. Eclosion occurs within two weeks. Neonates do not feed but settle in sheltered niches on the tree where they pass the winter. Larvae emerge in early spring, typically before the current-year buds have flushed. This precocious emergence forces the budworms to feed temporarily on alternative food sources. Both species readily utilize pollen cones (male strobili) of the host tree which typically develop in advance of vegetative shoots. Eastern spruce budworm may also mine old needles (McGugan 1954). Jack pine budworm, however, appears unable to mine the needles of its host (Nealis 1995). In all cases, extensive movement may be associated with this foraging and budworms are frequently observed ballooning on silken threads between trees at this time of year (Sanders 1991). As current-year buds expand and flush, budworms web together the needles, feed for the remainder of their larval period with relatively little further movement, and pupate near these feeding sites. During these later feeding and pupal stages budworms are attacked by a variety of natural enemies (Sanders 1991, Nealis 1991, 1995).

Most losses to budworm populations occur during the early larval stages before they establish feeding sites. This paper examines the ecological relationship between the host-plant and mortality of budworms early in the season. The hypothesis presented is that defoliation of the host plant by high population densities of budworms increases the risk of mortality to subsequent budworm generations by increasing the likelihood of early-season dispersal and/or the relative rate of mortality that results from this dispersal, i.e. by increasing the risk of dispersal. Thus, early-season dispersal losses can be viewed as a lagged, density-dependent mortality factor in the budworm system. Variation in the strength of the host-plant relationship and dispersal losses result in differences in the observed dynamics of these budworms.

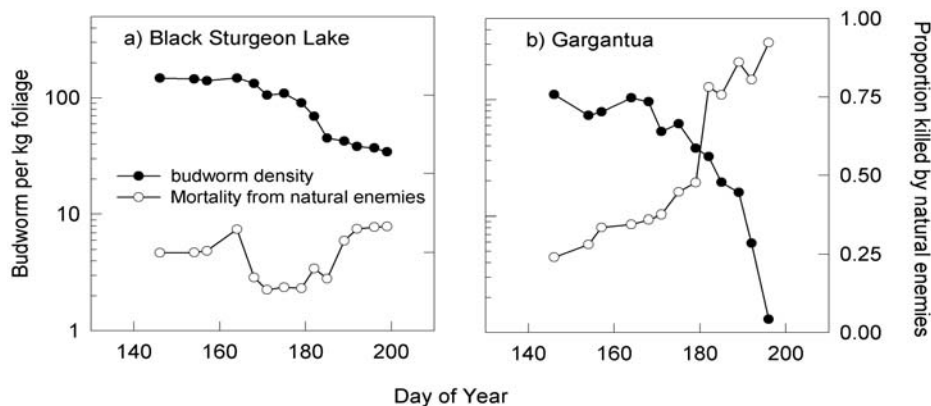


Figure 1.—Changes in density of eastern spruce budworm (solid circles) and mortality resulting from natural enemies (open circles) in a) a continuing outbreak at Black Sturgeon Lake; and b) a collapsing outbreak at Gargantua, Ontario, Canada in 1985.

Population Dynamics

Royama (1984) concluded that the primary fluctuation in populations of the eastern spruce budworm, the 35-year regular oscillation in density, is caused by lagged, density-dependent mortality occurring in the late-larval and pupal stages. The most probable agents responsible for this mortality are generalist predators, parasitoids, and possibly pathogens. This interpretation is consistent with theoretical models which view cyclic population behavior as the result of lagged, numerical responses of predators to changes in prey density (Royama 1992). Further support for this view comes from the apparent lack of the effect of major host-trees, balsam fir (*Abies balsamea*) and spruces (*Picea* spp.), on the primary fluctuation in eastern spruce budworm populations. When budworm kills all of the trees in a stand, populations necessarily collapse. But populations also collapse in forests where mortality of host trees is not complete (Royama 1984, Nealis and Régnière 2003). Experimental work by Lawrence et al. (1997) showed that plant quality does play an important role in the ecological relationship between the budworm and its host tree but it is a seasonal dynamic interaction not clearly related to temporal patterns in the density of eastern spruce budworm populations.

Overall, then, eastern spruce budworm population dynamics are viewed as “top-down” with regulation of populations imposed by “higher” trophic levels. Examples that illustrate these density and mortality patterns from outbreaks in northern Ontario, Canada, in 1985 are provided in Fig. 1. Continuing outbreaks such as Black Sturgeon Lake have little mortality caused by natural enemies and their densities do not change greatly over the generation (Fig. 1a) whereas collapsing populations such as observed at Gargantua display dramatic reductions in density associated with a sharp increase in mortality from natural enemies at the end of the feeding period (Fig. 1b). A similar pattern of increased parasitism in the late-larval stages during collapses of outbreaks of the jack pine budworm was documented by Nealis (1991). Further, the same species of generalist natural enemies in the same rank order of relative abundance were implicated in both the eastern spruce budworm and jack pine budworm systems (Nealis 1991, 1995).

Despite their similar life cycle and ecology, the population dynamics of the eastern spruce budworm and jack pine budworm differ in an important aspect. Whereas eastern spruce budworm populations display long-term cyclicity with outbreaks synchronized over hundreds of thousands of ha (Royama 1984), jack pine budworm outbreaks are short-lived and more sporadic (McCullough 2000). Where cyclical behavior in jack pine budworm populations has been detected, it is associated more with abiotic conditions such as fire history, weather, and soils than with natural enemies (Volney and McCullough 1994, McCullough 2000). Moreover, outbreaks of the jack pine budworm show no particular synchrony with eastern spruce budworm outbreaks despite the fact that both species share an identical guild of natural enemies and geographic sympatry.

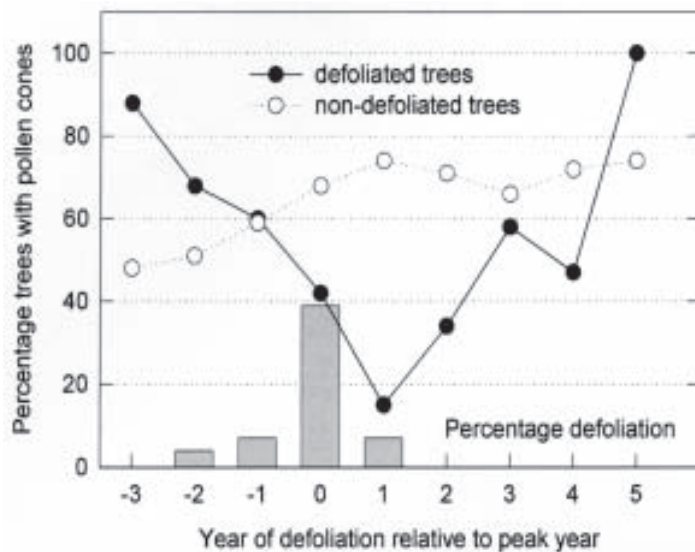


Figure 2.—Percentage of jack pine trees producing pollen cones in non-defoliated stands (open circles) and in stands defoliated by the jack pine budworm (closed circles). Histogram illustrates mean percentage defoliation in defoliated stands standardized by year of peak defoliation (i.e. year of peak defoliation = 0). Data derived from 180 sample plots in Ontario, Canada. Modified from Nealis et al. (2003).

An explanation for the the short-term nature of jack pine budworm outbreaks relative to those of the eastern spruce budworm may lie in the obligatory relationship between the jack pine budworm and the pollen cones of its host tree, jack pine (*Pinus banksiana*). The preference of early-stage jack pine budworm to feed on pollen cones of its host tree was first recognized by Graham (1935). Jack pine is a prolific producer of pollen cones under most forest conditions and outbreaks of jack pine budworm often follow periods of particularly heavy pollen cone production in open stands of mature trees (McCullough 2000, Nealis et al. 2003). Nealis and Lomic (1994) demonstrated that survival of early-instar jack pine budworm is related directly to the local abundance of pollen cones in a stand; when pollen cones are sparse, mortality increases because budworms disperse from host trees and often fail to find a suitable feeding site.

Defoliation by high-density populations of the jack pine budworm, however, causes a dramatic reduction in the propensity of the host tree to produce pollen cones the following year. Comparison of pollen cone production of several thousand trees in a series of defoliated and non-defoliated sites in Ontario, Canada, over a 7-year time series revealed that the probability of a jack pine tree producing pollen cones was reduced by 85% in the year immediately following peak defoliation (Fig. 2). Thus as high-density populations of jack pine budworm cause severe defoliation, they reduce the availability of the necessary resource for future generations. The greater the severity of the defoliation, the greater the reduction in future propensity to produce pollen cones (Nealis et al. 2003). This sets up a negative feedback with a lag in the system analogous to a predator/prey cycle except in this case the jack pine budworm is the predator and the pollen cones serve as the prey.

The feedback between the effects of defoliation and subsequent survival is less evident in the eastern spruce budworm system. First, although eastern spruce budworm is similar to jack pine budworm in that it feeds preferentially on the pollen cones of its host (Blais 1952), it is far less reliant on these structures since early stage larvae also readily mine old needles (McGugan 1954) and are adapted to maximizing the nutritional value of this suboptimal food source (Trier and Mattson 1997).

There is, nonetheless, evidence of a density-related effect in the host-plant relationship that may influence dynamics of the eastern spruce budworm. Figure 3 illustrates a time series of log survival of early-stage eastern spruce budworm (log density of budworms in their first feeding site minus the log density of eggs) from Black Sturgeon Lake, Ontario, Canada. The outbreak lasted 15 years and thus provides us with an unusually long time series. Here, we see something quite different from the pattern described by Royama (1984); survival in these early stages decreases steadily throughout the time series. This trend is very gradual at first and would have been less convincing, or perhaps not

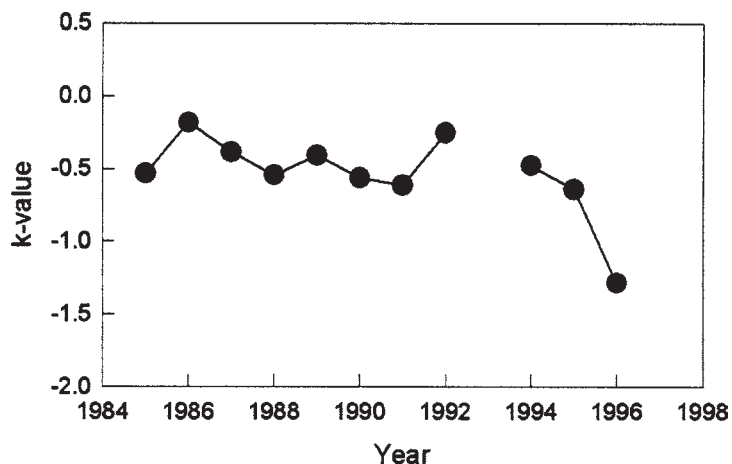


Figure 3.—Annual log difference (k-value) between density of eastern spruce budworm at the egg and early-larval stages throughout a prolonged outbreak at Black Sturgeon Lake, Ontario, Canada. An accurate estimate of egg density in 1993 is not available.

even apparent in the shorter time series that was available to Royama (1984). Note the abrupt downturn in rate of survival after approximately 10 years of defoliation in Fig. 3.

An hypothesis to explain this trend is that increasing early-season losses in the eastern spruce budworm are also the result of previous defoliation in the stand as was the case with the jack pine budworm. In the eastern spruce budworm however, the effect of defoliation becomes a factor only after repeated annual defoliation causes whole-tree mortality of host species with consequent development of canopy gaps (Kneeshaw and Bergeron 1998). Even if the rate of dispersal does not change, mortality resulting from this dispersal would increase because of the lower likelihood of dispersing larvae landing on a suitable host plant. A relative increase in the loss of early-stage budworm has been reported when stands are thinned for management purposes (Jennings et al. 1983). In the case of Black Sturgeon Lake (Fig. 3), significant tree mortality began around 1990 and accelerated throughout the remainder of the outbreak (Nealis and Régnière 2003). Population regulation thus occurs at a larger spatial scale with the eastern spruce budworm because it is through large-scale changes in stand composition that dispersal losses are mediated, rather than through small-scale changes in tree characteristics as occurs with the jack pine budworm.

Comparative dynamics

The interpretation of dynamics presented here is based on the concept of risk of dispersal. Risk of dispersal is the product of the propensity of an early-stage larva to disperse or forage for a feeding site and the likelihood of that movement resulting in mortality. It is density-dependent variation in the risk of dispersal, variation that is both intrinsic to the specific insect-tree interaction as well as within a system over time, that is key to this interpretation.

Most mortality in the life cycles of both eastern spruce and jack pine budworm occurs before the insects establish feeding sites. Because these species emerge in the spring before current-year foliage of their hosts is available, losses associated with foraging in an inadequate environment are common. Both budworm species benefit from the presence of pollen cones as these structures are available early in the season and therefore enhance survival of early larval stages. For jack pine budworm, the importance of these pollen cones is critical since feeding on previous-season foliage is not an option and the risk of mortality from dispersing in a relatively open forest situation is high. Thus, the depression of pollen cone production resulting from previous defoliation is a strong, density-dependent effect that increases the propensity of jack pine budworm to move and thereby increases its risk of dispersal. This results in a tight, fast-acting feedback between defoliation, or jack pine budworm density, and survival in subsequent generations. Outbreaks are short-lived and tree mortality is confined to suppressed and intermediate tree classes (McCullough 2000). Retention of susceptible, dominant trees in the stand and recovery of pollen cone production to pre-defoliation levels within a few years (Nealis et al. 2003) results in the potential for recurrence of outbreaks within a relatively short time-frame.

Defoliation by the eastern spruce budworm also reduces pollen cone production in balsam fir (Ghent 1958). The effect of this reduction in availability of pollen cones on eastern spruce budworm populations, however, is not apparent because of the capability of the budworm to mine needles as an alternative food source (McGugan 1954). Moreover, defoliation actually induces production of epicormic shoots in balsam fir and white spruce (Nealis and Régnière 2003) further buffering the negative effects of defoliation on survival of subsequent budworm generations. Consequently the negative feedback between herbivory-induced changes to the tree condition and survival of eastern spruce budworm is very weak; in fact, it simply functions on a longer time scale. Unlike jack pine budworm, where tree mortality tends to be restricted to suppressed trees, persistent defoliation by the eastern spruce budworm usually results in at least some mortality of dominant trees and the development of gaps within the stand (Kneeshaw and Bergeron 1998, Nealis and Régnière 2003). Thus, even if the propensity for early-stage eastern spruce budworm to disperse does not change greatly over the course of an outbreak, the likelihood of mortality resulting from that dispersal will certainly increase as more of the landbase becomes occupied by non-hosts (Jennings et al. 1983). Either way, the risk of dispersal increases slowly over time.

Conclusion

Theoretical population dynamics models tell us that when lagged, density-dependent processes operate within a persistent system, cyclical population behaviour can be expected (Royama 1992). If conifer-feeding budworm systems all have lagged, density-dependent host-plant relationships, are these sufficient to explain the eruptive nature of their populations? Are natural enemies merely following, not driving, population cycles?

A definitive answer to these questions will require a more comprehensive modelling of population dynamics. This modelling will rely on obtaining better estimates of parameters relating the host-plant interactions to changes in population densities and with sufficient estimates of the influence of natural enemies. A useful working model should reconcile the existing weight of both theoretical and empirical evidence associating population cycles with the action of natural enemies and the emergence of new data and hypotheses gained from the comparative approach provided in this paper.

If the collapse of budworm populations is caused ultimately by a *per capita* increase in the rate of mortality due to natural enemies and these same natural enemies are ubiquitous in forests inhabited by both eastern spruce and jack pine budworms, then it is necessary to add another element that explains why these different budworm species exhibit different dynamics in terms of the frequency and duration of outbreaks. The evidence of the comparative approach is that differences in the strength of the feedback between defoliation and changes in the host-tree that render the host less suitable for early-stage budworm may be that missing element. This aspect of the insect-host relationship requires more explicit inclusion in general models of budworm population dynamics. Structurally, inclusion of the insect-host relationship would result in a model with at least two density-dependent processes affecting budworm density at two distinct stages in the life cycle. The first, the insect-plant feedback outlined here, varies systematically between systems as outlined in this paper. The second density-dependent process, the impact of natural enemies, is stochastic in that many other intractable factors, such as the relative abundance of alternative hosts for generalist natural enemies, influence the numerical response of these natural enemies. The important concept here is that the likelihood of natural enemies impacting significantly generation survival of the budworm is conditioned by what happens earlier in the life stage; i.e. by the first density-dependent process. This is because an increase in apparent mortality from generalist natural enemies can be brought about by either a numerical increase in those natural enemies, or by a decrease in the abundance of budworms entering the susceptible stages.

The need to include more explicitly the insect-host interactions in budworm population dynamics has been recognized before, especially for the western spruce budworm and the jack pine budworm (Campbell 1993). Process-oriented research, however, has focused on possible changes in the quality

of foliage following defoliation. One technical problem that exists is that it is not clear what constitutes meaningful measures of quality or how these may be applied to interpretation of population patterns. In contrast, measurement of quantitative or topographical changes in the host-tree at either the individual or stand level is straightforward. Combining these with sufficient measures of budworm density at the critical stages (egg mass and early-feeding stages) should prove revealing.

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