

Genetic and ecological controls of post-diapause development in *Choristoneura*

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RESUME

The conifer-feeding members of the genus *Choristoneura* in North America are among the most destructive forest pests and are capable of defoliating in excess of 100 million hectares in any one year. Although they appear to be adapted to a single host species, the budworms are often capable of exploiting several coniferous hosts. The synchrony between host bud development and spring emergence of these insects is critical to the success of larvae in colonizing the host. The genetic control of early spring development in the insect guarantees that populations retain a wide array of phenotypes. This trait is inherited with low heritability and is therefore not easily changed by selection. This strategy ensures that a segment of the insect population will persist in environments where bud break varies widely from year to year. Natural hybrids of *C. occidentalis* and *C. retiniana* suggest that reproductive isolation among the several conifer feeding *Choristoneura* species is not always effective. This permits the acquisition of additional variation in spring emergence rates in mixed populations when their host species form mixed stands either from natural or anthropogenic disturbance. The variation and adaptive capabilities encountered in these populations will frustrate attempts to select resistant host stock that depend on the asynchrony of bud development and insect emergence.

INTRODUCTION

Conifer-feeding members of the genus *Choristoneura* are among the most damaging defoliators in North America. The three species that are normal problems for forest managers are the spruce budworm, *C. fumiferana* (Clerk) feeding on spruces (*Picea* spp.) and firs (*Abies* spp.); the western spruce budworm, *C. occidentalis* Free., feeding principally on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) but also on spruces and firs; and the jack pine budworm, *C. pinus* Free., feeding on jack pine (*Pinus banksiana* Lamb.). An additional species, the Modoc budworm, *C. retiniana* (Wlsh.), that feeds on white fir *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., seldom causes extensive damage (Furniss and Carolin 1977). A review of the taxonomic relationships among these, and other conifer feeding species may be found in Powell (1995) and their distributions are given by Harvey (1985, 1996). Collectively, these species may defoliate over 10 million hectares of forest in a single year and individual outbreaks may last for several years (Cerezke and Volney 1995). Their impacts on forest biomass production are dramatic (Maclean, 1985) and the resulting failure to fix carbon in these northern forests during these outbreaks is thought to have a significant effect on the global carbon cycle (Kurtz *et al.*, 1995). Despite their economic importance little is known about the genetic structure of *Choristoneura* populations, particularly with respect to life history traits.

The relationship among the various named conifer-feeding *Choristoneura* entities and between the insect groups and their hosts remains enigmatic (Powell and De Benedictis, 1995) because interpreting phenetic relationships, pheromone based evidence and molecular-genetic information all suggest different evolutionary relationships. Not the least of these problems is the extreme degree of similarity among populations and variations within populations (De Benedictis, 1995). Furthermore, natural hybrids between putative species suggest that isolating mechanisms are not always effective (Volney *et al.* 1984). Stehr (1967) suggested that the key to determining species relationships among *Choristoneura* was the host associations and the mechanisms by which these insects are adapted to their hosts. In addition this understanding would assist in evaluating the genetic improvement

strategies for the host populations. The purpose of this paper is to review the post-diapause development of *Choristoneura* populations with the view to understanding the ecological constraints they face in colonizing their hosts.

POST-DIAPAUSE DEVELOPMENT IN *CHORISTONEURA*

The essential features of budworm life cycles are common within the group. McGugan (1954) described the life cycle of *C. fumiferana* which can be used as a model for the group. Egg masses are laid on host foliage in mid-summer. These eggs hatch within two weeks, first instars disperse, find suitable hibernation sites and spin a hibernaculum, often on host branches. The larvae do not feed but molt to the second instar within the hibernaculum where they over-winter. By spring, diapause development is complete and, after the accumulation of sufficient heat units, larvae emerge to initiate feeding. They might mine buds at this stage if buds are sufficiently developed. More often they mine old needles until bud development permits the colonizing of the current year's developing foliage. There are usually six instars with pupation occurring on the host tree. Moths emerge in early July, mate and lay eggs. Dispersal may occur in the spring as larvae before they mine buds, again as large larvae but most importantly as adults where passive dispersal in weather fronts may carry moths several hundred kilometres in a single night (Dobesberger *et al.* 1983).

There are several variations to this pattern. The jack pine budworm seems unable to mine needles and is dependent on microsporangiate strobili for early instar survival (Nealis and Lomic, 1994). *C. bienis* Free., which occurs at high elevation in the Canadian Rocky Mountains, requires two years to complete development (Harvey, 1967). Although these are extreme variations, some members of all species probably display these traits.

The median time to complete post-diapause development in several species was found to vary very little within species from western North America and among the different rearing studies of spruce budworm (Volney, 1985). This indicates that, for these species groupings, temporal factors do not serve to isolate populations as

they all complete development at the same time. The variance in total development time was found to be smaller than expected from a simple accumulation of variances in times of the different stages of post-diapause development in *C. occidentalis* and *C. retiniana* (Volney and Liebhold 1985). In analyzing this phenomenon, it was found that there was a negative correlation between successive development rates among individuals (*ibid.*). This system of controls in development almost guarantees that seasonal isolating mechanisms among sympatric western *Choristoneura* species populations would be ineffective because it reduces the variances in times of adult emergence. An analysis of post-diapause development in *C. occidentalis* and *C. retiniana* revealed that there are no genetic differences among the species or their hybrids in the time to complete larval feeding (Volney and Liebhold 1985) as would be expected if adult emergence was to be synchronized.

It was surprising, therefore, to find that field studies of *C. fumiferana* total post-diapause development in western Canada was remarkably different from that reported for development in eastern Canada (Volney and Cerezke, 1992). A study of variation in total post-diapause development conducted in controlled temperature environments failed to show any genetic differences in this trait over 15° latitude within the range of white spruce (*Picea glauca* (Moench) Voss) in western Canada (Weber 1994). This suggests that the differences between populations might be controlled by ecological factors affecting survival at critical junctures in the life cycle of the insect.

Volney and Liebhold 1985 found marked differences among *C. occidentalis* and *C. retiniana* populations in their post-diapause pre-emergence development. The "green" morphs, diagnostic of *C. retiniana*, emerge sooner than the "brown" morphs, diagnostic of *C. occidentalis*, and their hybrids emerge at times that are intermediate to those of the parental types. Although there is considerable overlap in the emergence times, the order of emergence is the same as that of bud-break in the respective host species (Douglas-fir for *C. occidentalis* and white fir for *C. retiniana*). The variation in emergence times permit each insect population to colonize the principal host of the other species. This trait is mainly responsible for synchronizing

budworm development with that of its host and is thus thought to be the ecological relationship that determines success of the various populations.

The genetic control of post-diapause pre-emergence times could only be examined in the "green" morphs because it is impossible to distinguish larvae of hybrids from those of "true" *C. occidentalis*. In comparing this trait among *C. retiniana* populations, we found very low heritabilities where there was little evidence of genetic exchange with *C. occidentalis* (Volney *et al.* 1983). This is the pattern that would be expected in a life history trait that was closely associated with success of the population (Falconer, 1960). Where hybridization has occurred heritabilities are quite high, approaching 1.0, which suggests that selection can be very effective in rapidly correcting the genetic composition of inappropriately adapted populations. It is this pre-emergence development that is critical to spring survival in *Choristoneura* but the insects face a dilemma: they must synchronize their development with host phenology but, whereas their emergence depends on air temperatures, they respond to cues that are not identical to those that initiate bud development for bud break varies with soil and air temperatures. The insects apparently have solved this problem with a genetic system that conserves variation in spring emergence times. The permeable mating system among the putative insect species, adapted to particular hosts, also permits them to overcome any erosion of this variation as well.

HOST ASSOCIATIONS

Stehr (1967), in discussing the significance of hosts in determining the range of the different conifer-feeding *Choristoneura* species, suggested that the ecotone between forest regions would present problems in interpreting the relationships between species. Although Stehr (1967) recognized that *Choristoneura* species feeding on pine were ecologically isolated from those feeding on abietoid species, he offered no description for the relationship between sympatric species feeding on different abietoid species except to conclude that the evolutionary history of the group might be discerned from the geological and climatological history of North American forest communities. Speculation on the impact of this history on the

Holocene distribution of the various *Choristoneura* entities was provided by Volney (1985) and a longer evolutionary history was developed by Powell and DeBenedictis (1995). Their phylogeography depends in large part on the history of the principal host of present-day species. That Volney *et al.* (1984) would discover natural hybrids of *retiniana* and *occidentalis* suggest that the reproductive barriers between species that cross the abietoid/pine barrier of the hypothetical cladogram (Powell and DeBenedictis, 1995) have been permeable for a long time. This would suggest that the host has had a far stronger influence on isolating populations than the mating systems that have evolved to date. I speculate here that the success of each species is primarily related to the synchrony between its host phenology and the post-diapause development.

The evidence associating *C. occidentalis* and *C. fumiferana* emergence and survival with synchrony of host shoot development was reviewed by Shepherd (1985) who indicated that insect development in the field, if properly synchronized with host bud flush, will result in elevated survival. This occurs in *C. occidentalis* when the insects emerge early to mine needles, then mine buds and so complete most of their early instar development protected in feeding tunnels adjacent to the shoots' rachis. If insects emerge late, the late instars will be forced to complete feeding exposed on fully elongated shoots. This population would incur substantially more mortality than a cohort that was properly synchronized with its host. Experimental studies by Lawrence *et al.* (1997) suggest that the phenological window for spruce budworm on white spruce may begin as much as four weeks prior to budbreak and is terminated at the end of shoot elongation. It appears that the early emergence of larvae is critical in synchronizing the population to take advantage of the swelling buds early in spring.

Several *Choristoneura* species feeding on abietoid hosts have evolved needle mining habits. The adaptive significance of this was elegantly demonstrated by Trier and Mattson (1997) for the spruce budworm. In mining needles the second instars can sustain themselves and develop to third instars by avoiding the less nutritious structures, such as the resin ducts and cuticle, of needles. By completing an early instar in needles the insects shift their development relative to that of the host so that

development is completed on the most succulent and nutritious tissues (Lawrence *et al.* 1997). By contrast *C. pinus*, which feeds on pine, is unable to mine needles. (Perhaps the spacing of resin ducts in pine needles are sufficiently close together so that larvae are unable to avoid them). Pine feeders depend, instead, on mining reproductive buds prior to mining vegetative buds to survive in the spring (Nealis and Lomic 1994.)

CONCLUSIONS

To successfully colonize its host in spring *Choristoneura* larvae face the problem of anticipating bud-break by emerging several weeks before the event. They overcome this time of adversity by either mining needles or reproductive buds. The precise cues that trigger emergence are little understood. Certainly temperature drives the process but whether there are host cues that act in concert with the thermal environment to regulate emergence is unknown. Nevertheless, the insect population seems to overcome the uncertainty of budbreak by retaining phenotypes that spread their emergence over several weeks. Our current understanding would suggest that the host acts a phenological filter: early emerging individuals are unable to survive long enough to mine swelling vegetative buds whereas late emerging individuals must attempt to complete development on fully elongated shoots that are of lower nutritional value. It appears that the heritability of the time of emergence is low so that severe selection over several years would be necessary to change the median date of emergence. Further resisting this change is the mechanism by which the insects complete development and mate over a short time span. This ensures that late and early emerging individuals have the opportunity to contribute to the next generation. However, the adaptive association between insect species and its host can be rapidly eroded where sympatric host distributions permit the insect species to hybridize. Hybridization provides the opportunity for populations to rapidly acquire traits that permit them to colonize hosts with different phenological schedules, however.

Lawrence *et al.* (1997) reviewed the application of these results to selecting trees and provenances resistant to budworm attack. These include planting provenances in which bud-break is delayed or accelerated relative to insect emergence so that insect survival is reduced. The use of anti-feedants to induce asynchrony in the onset of feeding and suitable host phenology has also been suggested. Variation in the insect population and their ability to track host development would militate against the effectiveness of these strategies. A more promising approach may be to find and propagate host phenotypes that appear to be resistant to budworm attack. The variability in insect population densities and damage to trees within and among natural stand is substantial. The significance of this observation has not been exploited in attempting to develop resistant stock.

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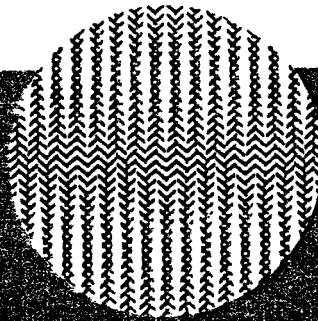
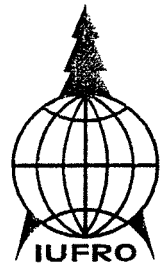
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