SUMMARY OF LIFE HISTORY AND HOSTS OF THE SPRUCE BUDWORMS

Robert L. Talerico

Research Coordinator, CANUSA-East, USDA Forest Service, Northeastern Forest Experiment Station, 370 Reed Road, Broomall, PA 19008

My purpose is to provide background information on the spruce budworms and point out some insect-host interaction relationships that have been noted by others. These and other interactions will be discussed in more detail in the papers that follow.

There are several budworms that feed on forest trees. For our discussions, we will be interested only in the spruce budworm (*Choristoneura fumiferana* Clemens) and the western spruce budworm (*C. occidentalis* Freeman). Other budworms that may be referred to are the 2-year budworm (*C. biennis* Freeman), jack pine budworm (*C. pinus* Freeman) and Modoc budworm (*C. viridis* Freeman). These are all native insects of coniferous forests in North America.

The spruce budworm and western spruce budworm are responsible for significant defoliation in North America. For example in 1982, nearly 24 million hectares or 60 million acres of fir and spruce were visibly defoliated by these insects. There was significant tree mortality at all locations, especially in the East.

I shall briefly review the life history of both budworms to provide a common ground.

Until recently, these species and several near relatives were considered to be strains of *C. fumiferana*. As a result, much early information concerning the western species was published under the name of the spruce budworm. These two budworms have similar life cycles and habits, but differ in geographic range and hosts. I'll use the spruce budworm as an example and note any differences for the western spruce budworm.

Life Cycle and Habits

The spruce budworm has a 1-year life cycle. The rate of development of each stage depends upon climatic factors that vary with geographic regions; thus the following calendar times are only approximate. In the Northeastern United States and Canada, moths lay their eggs in July. In the West, eggs are laid in July and August. Female budworms lay about 150 eggs in masses of about 20 eggs per mass. Ocasionally, egg masses with up to 60 eggs are found. The eggs are light green and are laid in shingle-like fashion, generally on the undersides of needles. Occasionally they appear on the top surface of the needle or overlapping upper and lower surfaces, and at times even on the bark. Egg masses are generally most abundant on shoots in the outer perimeter of the tree crown.

The eggs hatch in about 10 days to 2 weeks. Budworm larvae require six developmental stages or instars from hatching to pupation. Hatching and emergence of first-instar caterpillars are usually complete by mid-August, when one of the two major dispersal periods occurs. Small larvae react photo-positively to light and move upward toward the branch tips. During this activity, some larvae may spin down on silken threads and be carried away by air currents. Such movement or dispersion spreads the larvae over a wide area, but also results in the death of many larvae. Budworm larvae remaining on host foliage do not feed but instead spin cocoon-like shelters (hibernacula) within which they soon molt to the second instar. The budworms overwinter in this stage, preferably on old flower scars on bark scales, or where lichen grows on branches.

In April or May of the following year, second-instar budworms emerge from their hibernacula. Again in response to light, the larvae move toward the branch tips, and the second major airborne redistribution occurs. Again, some larvae drop on silken threads and are blown about by air currents. When these larvae land on suitable host foliage, they begin to feed. Larvae become established in needles of 1-year-old foliage or mine directly into the expanding vegetative buds. Larvae will preferentially eat the more nutritious staminate flowers of balsam fir (*Abies balsamea* (L.) Mill.), when available. Typically, only one balsam fir needle is mined by each larva and the larva molts to the third instar either within the confines of the needle mine or soon after it leaves the needle. By late May or early June, third-instar budworms begin feeding on the newly opened vegetative buds. Larvae feeding on staminate flowers remain in place until the food supply is exhausted; then they move to the new, expanding foliage.

Late-instar (L_4-L_6) budworms are found from early June to early July. A full-grown sixth instar ranges from 0.75 to 1 inch (2 to 2.5 cm) in length. The body is dark brown with yellowish spots along the back. The head capsule and collar are dark brown or black. The sixth-instar budworm consumes a greater percentage of foliage than any other instar. At sparse population levels, larvae feed only on young needles of current shoots. Sixth-instar budworms normally web two or more shoots together, forming a feeding shelter. When populations reach outbreak levels and all new foliage is consumed, the larvae are forced to feed on old foliage. This phenomenon, called back-feeding, can result in noticeably smaller pupae and smaller egg masses, presumedly because older foliage is less nutritious. As foliage is depleted, larval movement increases, and many larvae drop from the defoliated trees to feed on understory host seedlings and young trees.

Pupation occurs within the feeding shelters or other protected locations. A newly formed pupa ranges from 0.5 to 0.75 inches (1.3 to 2 cm) in length and is green when first formed, but becomes yellow. With age the pupa darkens to a dark gray or dark brown. In the East, pupation occurs in late June and lasts from 8 to 12 days. Elevation and aspect, of course, affect these times in the West. In the West, pupae may be found from mid-July to early August.

Moths are present in the field from late June to mid-August. The spruce budworm is usually grayish with dark brown markings and has a wing span of about 0.75 inches (2.0 cm). Color pattern varies: some moths have a more brownish or reddish tinge with the gray markings. The western budworm is slightly larger and has a conspicuous white dot on the outer margin of each forewing. Adults live about 2 weeks, during which time they do not eat. The male locates the female for mating when she releases a sex pheromone. Once mated, females generally do not fly until they have laid at least part of their egg complement. After laying most of their eggs, though, females are active fliers. Given proper weather conditions, both male and female moths may be transported great distances by winds and storm fronts. Such long-range dispersal affects population trends and brings the budworm to new areas.

Hosts

The spruce budworm inhabits the northern coniferous forest of the eastern half of North America. Larvae feed on a number of conifers, but balsam fir, white spruce (Picea glauca (Moench) (Voss), and red spruce (P. rubens Sarg.) are the major hosts in eastern North America. Black spruce (P. mariana (Mill.) (B.S.P.) is occasionally attacked, as are eastern hemlock (Tsuga canadensis (L.) Carr.), tamarack (Larix laricina (Du Roi) K. Koch), and white pine (Pinus strobus L.).

The forest types of eastern North America differ from west to east. In the Lake States region, balsam fir, white spruce, and black spruce are the major sources of food. These conifers occur in patches that average 15 to 25 acres (6 to 10 ha) and are separated by hardwood or mixed-wood stands. Where hemlock is a common associate, it can be defoliated and more easily killed. In Maine and the Canadian Maritime Provinces, the patchy pattern gives way to extensive areas of softwoods. In this region red spruce becomes a major component of the forest, replacing the white spruce component.

The western spruce budworm is isolated from its eastern sibling species by the mid western prairie that divides the continent. The western spruce budworm causes the greatest economic damage in stands of Douglas-fir (Pseudotsuga Menziesii (Mirb.) Franco), grand fir (Abies grandis (Doug. ex D. Don) (Linde), white fir (A. concolor (Gord. & Glend.) Lendl. ex Hildebr.), subalpine fir (A. lasiocarpa (Hook.) Nutt., blue spruce (Picea pungens Engelm.), Engleman spruce (P. englemanni Parry ex Engelm.) and white spruce (P. glauca (Moench) Voss.) Occasional hosts are corkbark fir (A. lasiocarpa var arizonica (Merriam) Lemm.), Pacific silver fir (A. amabilis Dougl. ex Forbes), Western larch (Larix occidentalis Nutt.), lodgepole pine (Pinus contonta var. latifolia Engelm.), ponderosa pine (P. ponderosa Dougl. ex Laws.), and western white pine (P. monticola Dougl. ex D. Don).

Balsam fir is the most vulnerable host, followed in order by white spruce, red spruce, and black spruce. It takes several years of defoliation to kill a tree. Fir will die after 4 to 7 years of repeated severe defoliations. White and red spruce can withstand at least an additional year or two of complete defoliation before dying. Generally, black spruce is not killed by budworm feeding except in the most severe outbreaks.

Severe defoliation by both budworms results in decreased tree growth, tree deformity, top killing, and finally death of trees, often over extensive areas. In fact, feeding habits can vary with the tree host and region. Both budworms may begin to feed on staminate flowers and conlets and complete their development on new foliage. In the northern Rocky Mountains, large larvae often feed on cones and seeds of western larch and Douglas-fir, then pupate in the cones.

Host-Insect Interactions

The relationship between the insect and its host tree is mediated by a number of physical and chemical factors. Some of these function in an all-or-none fashion, and their presence, even in small quantities, can render the plant completely unacceptable to some insects while having little effect on others. This so-called qualitative type of defense is exemplified by toxins such as alkaloids, terpenes and cyanide. Other factors function in a more quantitative manner and the degree of host suitability is inversely proportional to the level of the defensive factor in the host. Tannins, terpenes, and foliage toughness are examples of quantitative defenses. The distinction between these two classes of plant defense is arbitrary and not absolute. A given factor can function as a toxin to one insect and a quantitative defense to another. Generally, factors that make certain tree species immune from attack are likely qualitative, whereas factors that influence the susceptibility of a given tree species under different conditions, such as on different soil types, are likely quantitative. A close examination of the various interactions between the budworms and their primary hosts may provide important clues about the processes that make trees susceptible or resistant to damage by defoliation. Various characteristics of the tree or insect can be used to measure or quantify these interrelationships. Many of our speakers will be talking about such tree or insect characteristics as: growth rate, either radial or terminal, or development rate of the insect stages; phenology of tree development--whether it be synchronous or asynchronous with the insect; organic and inorganic compounds within the tree and their influence on the insect; available moisture for the tree and insect; fecundity of the insect; specialized sensors or organs in the insect for detecting special information in the environment or to cope with toxic plant substances. This latter category is relatively new and is just beginning to receive special attention.

The combination of these tree or insect characteristics has evolved into a complex system for the coexistence of the tree and insect. An examination of the historical record of the spruce-fir forest and recorded outbreaks of the spruce budworms reveals that when this complex biological system is left alone, both tree and insect species continue to exist in spite of vast mortality in populations of each. However, our perceived economic needs will not permit this natural progression.

Budworm outbreaks generally begin when there is an abundant supply of food; population crashes, on the other hand, usually occur only when the food supply is depleted. Various observations and studies have demonstrated that 3 to 4 years of severe defoliation result in a small complement of foliage with a suspected reduction in foliage quality, and therefore correspondingly smaller insects. These insects seem to function normally but their fecundity is clearly reduced (Miller 1963).

Variation in foliar nutrient content has been reported for various host species over time and by location (Shaw and Little 1972, Czapowskyj 1979). This variability is believed to play some role in the population dynamics of the budworm (Miller 1963). At least one research report has been able to provide evidence of a connection between foliage quality and insect development. Shaw, et al. (1978) were able to show that the addition of fertilizer to young balsam fir resulted in larger spruce budworms and higher survival. But attempts to demonstrate a relationship between insect survival or mature insect size and natural variations in foliar components have not been successful (Harvey 1981).

At the inception of a spruce budworm outbreak, a frequent observation is that individual host trees react differently to defoliation. This suggests that there are some differences in susceptibility (McDonald 1981). Unfortunately, as the budworm population increases these differences seem to disappear. This early evidence seems to suggest that a long-term program to develop resistant trees for planting would not be effective. However, these data are not vigorous or substantial. Hence, there still is reasonable expectation of finding and developing less susceptible cultivars of fir and spruce.

All primary host trees seem to be acceptable food sources, although there are some substantial differences between them in their capacity to grow budworms. Intuitive evidence seems to imply that foliage quality has some subtle influence on the population dynamics of the spruce budworms. Foliage quality differences likely provide some type of fine tuning or feedback information to this complex forest-insect system that might, for instance, induce budworms to disperse.

I believe the participants at this workshop will present research results to show that there are some quantifiable relationships between foliage quality and the budworms' population dynamics. Up to this point, work on foliage quality appears to have been conducted independently by entomologists and physiologists. The participants in this workshop represent these disciplines plus genetics, chemistry, forestry, and modeling. Some people believe that the best way to develop an understanding of the workings of host-insect interactions is through an interdisciplinary team approach. I hope this workshop will at least foster useful dialogue between these disciplines.

Literature Cited

Czapowskyj, M. M. Foliar nutrient concentrations in balsam fir as affected by soil drainage and methods of slash disposal. Res. Note NE-278. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station; 1979. 4 p.

Harvey, G. T. Food quality and quantity. In: Review of the spruce budworms outbreak in Newfoundland - its control and forest management implications. Information Report N-X-205. St. John's Nfld: Environment Canada, Canadian Forestry Service, Newfoundland Forest Research Centre; 1981: 110-112.

McDonald, G. I. Differential defoliation of a neighboring Douglas-fir trees by western spruce budworm. Res. Note INT-306. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1981. 10 p.

Miller, C. A. The analysis of fecundity proportion in the unsprayed area. In: The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. 75-87; 1963.

Shaw, G. G.; Little, C. H. A. Effect of high urea fertilization of balsam fir trees on spruce budworm development. In: Insect and mite nutrition. Amsterdam, Holland: North-Holland Publ.; 1972: 589-597.

Shaw, G. G.; Little, C. H. A.; Durzan, D. J. Effect of fertilization of balsam fir trees on spruce budworm and development. Can. J. For. Res. 8:364-374; 1978.