

A Theory on the Effects of Diverse Host-Climatic Environments in British Columbia on the Dynamics of Western Spruce Budworm

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The genus *Choristoneura* is diverse and adaptable. Speciation is occurring rapidly in western North America in response to diverse habitats and hosts. Outbreaks of *C. occidentalis* occur in many plant communities over a range of precipitation levels but the last outbreak in British Columbia was restricted to an elevational belt within the Cascade Mountains. It is suggested that only in those stands where developmental temperatures permit overwintering larval emergence to be synchronized with bud swelling can larvae survive in large numbers. Early emergents cannot establish in new buds, and late emergents, when in the last instars, are exposed to an extended period of high mortality after budflush. Also, after budflush, food quality may decrease considerably. Through moth dispersal, western budworm maintains a broad heterogenetic base and a long emergence period to accommodate synchronization with the buds in stands which fall within favorable climatic elevational belts of the mountains. On an occasional year, at all elevations, limits are exceeded and asynchronization results in high mortality. Larval dispersal enables the budworm to search out buds in the stand which are best synchronized and have the highest food quality to maximize survival. If crop trees can be selected which exceed the limits of synchronization or food acceptability, it may be possible to improve the long-term outlook for reduced damage.

Le genre *Choristoneura* est diversifié et adaptable. En Amérique du Nord, les espèces se différencient rapidement, en réaction à la diversité des habitats et des hôtes. Les infestations de *C. occidentalis* touchent de nombreuses communautés végétales réparties selon la gamme de pluviosités, mais la dernière infestation en Colombie-Britannique s'est cantonnée à une hauteur précise dans la chaîne des Cascades. Il semblerait que ce n'est que dans les peuplements où les températures de développement permettent la synchronisation de l'émergence des larves qui ont hiverné et du bourgeonnement, que les larves survivent en grand nombre. Si celles-ci sortent trop tôt, elles ne peuvent se fixer dans les nouveaux bourgeons, tandis que si elles sortent tard, elles sont exposées, aux derniers stades larvaires, à une période prolongée de forte mortalité après le débourrement. En outre, après le débourrement, la qualité de la nourriture peut considérablement diminuer. Grâce à la dispersion des imagos, la tordeuse occidentale s'assure une base hétérogène large et une longue période d'émergence qui permet de la synchroniser avec le bourgeonnement dans les peuplements montagnards aux altitudes et au climat favorables. En certaines années, à toutes les altitudes, les limites sont dépassées et le décalage chronologique provoque de fortes mortalités. La dispersion des larves permet à la tordeuse de rechercher, dans le peuplement, les bourgeons dont l'évolution est le plus synchronisée à ses besoins et qui constituent la nourriture de la plus haute qualité, afin de maximiser sa survie. Si on pouvait sélectionner des arbres de peuplement final qui excèdent les limites de la synchronisation ou de l'acceptabilité trophique, on pourrait réduire les dommages à long terme.

Diversification of *Choristoneura*

The "conifer-feeding budworms" in western North America are a large complex of partially isolated, partially interbreeding, and partially speciated populations living in *Pseudotsuga*, *Abies*, *Picea* and *Pinus* forests from Alaska to southern California (Powell 1980). This state of speciation and distribution probably reflects the influence of glaciation and the reoccupation of the deglaciated land by forests and their associated insects. Almost all of British Columbia was denuded by ice and the land surface was remoulded (Matthews 1979). Wet and temperate Pacific air masses moved across high mountain ranges alternately dropping large volumes of precipitation on the windward slopes and absorbing moisture from the lee sides. Temperatures ranged from deep arctic lows in winter to desert-like highs in the summer (Danks 1979). This diverse geography and climate could only be reoccupied by organisms with a high degree of diversification. The budworm has succeeded because it is flexible and adaptable, feeds on many hosts, flourishes in various climates, and has an aggressive capability to spread and occupy new forests.

The adaptability of the genus *Choristoneura* is evident in the complex of closely related species and their diverse geographical distributions (Harvey 1985). *Choristoneura occidentalis* Freeman occupies the central position, on its host Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) which, after deglaciation, probably spread northward from Washington through the warmer sites of southern British Columbia. A closely related species, *C. biennis* Freeman, was able to adopt a two-year life cycle, through selection for a second diapause, and occupy the cooler subalpine fir and Engelmann spruce forests (*Abies lasiocarpa* (Hook) Nutt. and *Picea engelmannii* Parry) of the high mountains (Shepherd 1961). *Choristoneura orae* Freeman may be a remnant of preglacial times which survived the glacial period in the Alaskan-Yukon refugia (Scudder 1979), because it is adapted to the cool Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) rain forests of the north coast. *C. fumiferana* is a resident of the *Picea* - *Abies* boreal forest which extends across Canada and into northern British Columbia, Yukon, and Alaska. The distribution of all these budworm species may meet and sometimes overlap in central British Columbia. The lack of distinctive morphological characteristics among these species makes identification difficult in this region.

In Oregon and California there are also overlapping populations of *C. occidentalis*, *C. carnana* (Barnes and Busck), and *C. retiniana* (Walsingham), which are hard to distinguish (Volney 1985). It is interesting that *C. retiniana*, which occurs south of the glacial limits, has a similar pheromone to *C. orae* of Alaska and northwest British Columbia (Daterman et al. 1984; Gray et al.

1984). Pine forests in California and Oregon occur in mountainous areas separated by wide dry valleys, which provide a degree of isolation. Three or four subspecies of *C. lambertiana* (Busck) are found in these areas and are hard to distinguish (Powell 1980). Western North America seems to be the center of speciation of the genus where the wide range of available habitats has offered *Choristoneura* the opportunity to diversify onto many hosts growing in a variety of climates. The species which causes most damage in western North America is *C. occidentalis*.

The remainder of this paper deals with the geographical relationships of *C. occidentalis* in British Columbia, the importance of synchronization of larval emergence with host bud swelling, the strategies the tree uses in responding to the budworm, and the strategies the budworm uses to survive and succeed in a variable environment. No attempt is made to review other theories on the dynamics of the budworm, but only how synchrony, foliage quality, and dispersal may affect budworm population ecology. For more complete coverage of other theories see Blais (1985), McKnight (1971), Royama (1984), and Wellington et al. (1950). Throughout this discussion, outbreaks are defined as populations of budworm numerous enough to cause defoliation that can be noticed and mapped from the air.

Geographical Relationships

The geographical pattern of budworm outbreaks in British Columbia varies from that of other defoliators. Many defoliators in British Columbia rise to outbreak levels for only short periods in any one stand. Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough)), forest tent caterpillar (*Malacosoma disstria* Hubner), western hemlock looper (*Lambdina fuscicornis lugubrosa* (Hulst)), and many other geometrids quickly increase, defoliate trees for one to four years, and then drop to low levels again (Shepherd 1977). Western spruce budworm is the exception. Population fluctuations are irregular and unpredictable. Outbreaks can collapse after one or two years or can last for several years in a particular stand (Harris et al. 1985; Johnson and Denton 1975). Numbers of budworm often increase to outbreak levels, decrease, and recover to outbreak levels again. Populations in any one valley are often synchronous. Within that valley trends upward or downward are similar, regardless of the population density of budworm in a particular stand. Meanwhile, populations within another valley, 300 km (186 mi.) away, may again be synchronized, but the trends can be different between the two valleys. The only factor I know that can regulate populations either directly or indirectly at that geographic scale is climate.

Some insect species require specific environmental conditions before they can reach outbreak levels which

occur only in certain sites (Andrewartha and Birch 1954; Shepherd 1977). Those conditions may also be reflected in the plant communities present. Therefore, there is often a close association between the distribution of specific plant communities and the distribution of outbreaks of some insect species. This association appears to be more pronounced in the more extreme conditions of the host's range. The black-headed budworm (*Acleris gloverana* Walsingham), for instance, has outbreaks in the wettest hemlock community of Vancouver Island (Shepherd 1977). The outbreaks do not extend into the adjacent dry hemlock or Douglas-fir communities. In contrast, outbreaks of Douglas-fir tussock moth are restricted to the hottest and driest communities within the range of Douglas-fir, and outbreaks of two-year cycle spruce budworm in the Canadian Rockies occur only in a specific plant community of the high altitude, cool, alpine fir/Engelmann spruce forests (Shepherd 1959). Again, the western spruce budworm is an exception. Outbreaks are not restricted to one or two communities, but occur from the moist forests of the mixed coastal-interior forests to the dry interior forests, covering a range of communities which vary considerably in amount of precipitation received (Shepherd 1977).

Outbreaks are restricted, however, by elevation. They appear as a belt in the mid-slope areas of the mountains, with populations decreasing above and below those elevations. Wulf and Cates (in press) also report that defoliation in Idaho and Montana is more common at mid to upper elevations and covers a range of habitat types. Preliminary investigations in British Columbia indicated that host distribution was not related to this elevation effect nor was moth dispersal, as moths readily moved into and laid eggs in stands above and below the defoliated belt. The effect had to be realized through differential survival. The actual elevation of maximum defoliation varies from year to year and place to place so that the location of the zone most favorable for budworm varies considerably and is not associated with a particular plant community or stand condition. Elevation belts of other insect or disease conditions in mountainous situations have been related to specific temperatures (Stark 1958, 1959; Shepherd 1977; MacHattie 1963; Henson 1952; Baltensweiler 1984) and I suggest that the distribution of outbreaks of the western spruce budworm is also related to temperature.

Large-scale patterns of outbreaks in British Columbia indicate the center of budworm defoliation has moved gradually to the northeast over succeeding years, following the prevailing wind flow pattern (Figure 1). In July, during the flight period, there is strong daytime heating of the air in the principal valleys of the Fraser and Thompson rivers resulting in uplifting and strong replacement winds flowing inland from the cool Pacific Ocean. The large mountains of the Cascade Range force the winds to funnel up the valleys with the

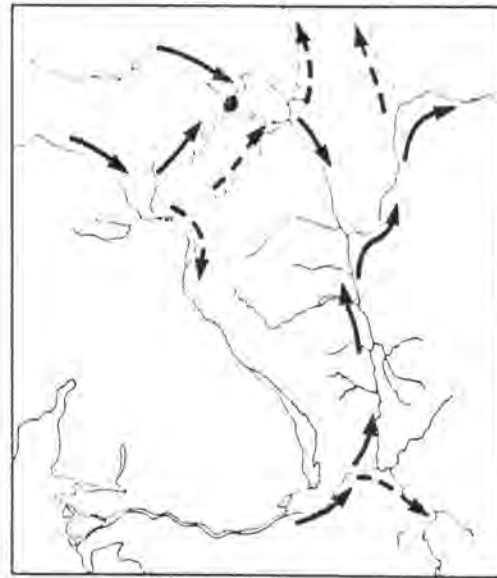


Figure 1. Direction of prevailing diurnal winds in S.W. British Columbia during the moth flight period. Mission Pass designated by a spot.

strongest winds occurring in late afternoon and continuing well after sunset. As the sun sets, radiation cooling begins on the shaded slopes and a thin layer of cool air begins sliding downslope. The time of turn-around in wind direction varies with the direction of slope exposure. Winds on the east and north-facing slopes reverse their direction earlier than on west or south-facing slopes. The daytime pattern of wind flow persists longer after dark in the main valleys than in the smaller side valleys. These winds are quite consistent under clear skies but if cloudiness blocks heating or pressure gradients reverse, the winds will slow or change direction so that year to year changes in frequency do occur, but in most years the prevailing direction is toward the northeast (personal communication, R. Silversides, Canadian Forestry Service, Victoria, British Columbia).

Male and female (*C. occidentalis*) moths begin flying at dusk and carry on for 2 or 3 hours after sunset, depending on temperature (Shepherd 1979). This occurs during the period of wind turn-around and direction of moth drift varies with each situation. In most years, though, dispersing females are transported in the same direction, seeding-in downwind stands. The effect of the immigrants on the indigenous insect densities is probably most marked in the preoutbreak low-density period when a relatively low number of immigrant moths can double or triple the population density. This sustained accumulation over a number of years probably hastens the outbreak.

There is an interesting example of a zone of wind convergence in British Columbia where two large budworm-spawning valleys come together at Mission

Pass above Seton Lake near Lillooet (Figure 1). There have been four outbreaks in British Columbia east of the Cascade Mountains since 1909. These upper slopes above Seton Lake have been defoliated in every outbreak and are often the first to become so (Harris et al. 1985).

Moth dispersal is an adaptation which allows the insect to spread its risks over many stands and survive wherever favorable situations occur. The environment varies in both time and space and the distribution of outbreaks coincides with the distribution of sites where conditions favorable for increase occur most often. In British Columbia, the location of these conditions is at mid-slope, resulting in elevation belts of defoliation.

Strong dispersal has another advantage for which I have coined the term "nomadic" strategy of survival. This strategy is more obvious with an insect like forest tent caterpillar where mortality factors like disease, parasitism, starvation through overpopulation and, perhaps, induced host resistance rapidly overtake the population (Hodson 1941). Only by dispersing to new stands at every generation can the population escape heavy depredation. This nomadic strategy may also play a role, at least in part, with budworm.

Synchronization with the Host

The time of larval emergence and dispersal relative to bud development is critical. Larvae go through two dispersal periods before feeding — one in August just after egg-hatch and another in spring just after emergence from overwintering. Behavior of *C. occidentalis* is similar to *C. fumiferana* at this stage. *C. fumiferana* larvae stream off the trees on silk threads carried by the wind until the silk touches and sticks to an object (Batzer 1968). Unless there are strong vertical air currents, the surrounding trees are the usual recipients and screen out the larvae. Larval dispersal redistributes larvae over the surfaces of the crowns which results in reduced competition and maximum occupation of all buds that are in a suitable stage of development.

The larvae prefer to penetrate swollen buds and live in an ideal natural greenhouse where it is warm, well protected, and where there is an abundance of freshly-growing food (Wellington 1948). If the larvae hatch too early, they cannot penetrate the tough bud scales and are forced to feed on mature needles (McGugan 1954). In Douglas-fir, the production of flower buds is quite sporadic and is unlikely to influence long-term population trends. There also appears to be a territorial behavior in *C. occidentalis*, restricting occupancy to one budworm per bud (McDonald 1979). Redistribution continues until the larvae are quite large (Beckwith and Burnell 1982). Populations are thus reduced to the carrying capacity of the host and losses due to competition would be expected to be directly related to

population density above the bud complement of the trees (Thomson 1979). The effect may be a great loss of young larvae but the process tends to ensure maximum population survival.

Weekly observations of bud and insect development in 100 marked buds at each of many sites located at different elevations in southern British Columbia indicated that population trends during the larval period can be divided into three phases, depending upon the development of the host buds (Figure 2): 1) a needle-mining phase which occurs before larvae can penetrate the hard overwintering buds, 2) a protected phase where larvae live inside developing buds, and 3) an exposed phase after buds flush and larvae have lost their protection. Techniques to establish these developmental phases are given in Shepherd (1983). During needle mining, larvae emerge from overwintering diapause, are unable to penetrate the tight buds, and are forced to mine old needles which suffer rapid abscission (McGugan 1954); many larvae are lost as they search for suitable buds (Figure 2). In contrast, larvae that emerge after buds have swollen mine directly into the buds and few larvae are lost. During this protected phase, large increases in larval density may occur as larvae continue to emerge from diapause and mine buds. Maximum larval density in buds usually occurs just before flush, although, in cases of poor synchronization, the maximum number can occur during needle mining. As soon as the buds flush, the larvae lose their protection and survival drops rapidly. Birds and ants are primary predators of *C. occidentalis* larvae and pupae in the open shoots (Campbell and Torgersen 1983). Predators are often compensatory, i.e., as bird predation decreases, ant predation increases, and vice versa. However, from the budworm point of view, the type of predator is immaterial; more important is the length of time of exposure to predation. The daily loss rate is almost constant during this period (Campbell and Srivastava 1984) and percent survival plotted over days of exposure results in an exponential curve (Figure 3).

Contrasting synchronization between bud development and larval emergence occurred in my study sites between 1979 and 1980 (Figure 2). In 1979, bud development was advanced enough for emerging larvae to penetrate the buds directly and survival was good in the younger instars. However, the buds flushed early and the exposed period before pupation was lengthy. Survival declined and was close to zero by the pupal stage. In 1980, larvae emerged before the buds were swollen, and loss was high while the larvae mined old needles. Larvae which emerged late successfully occupied the newly swollen buds. Bud flush was late relative to insect development resulting in a short exposure period and good survival of late instars. The resultant survival of the 1980 population was much greater than that of the 1979 population.

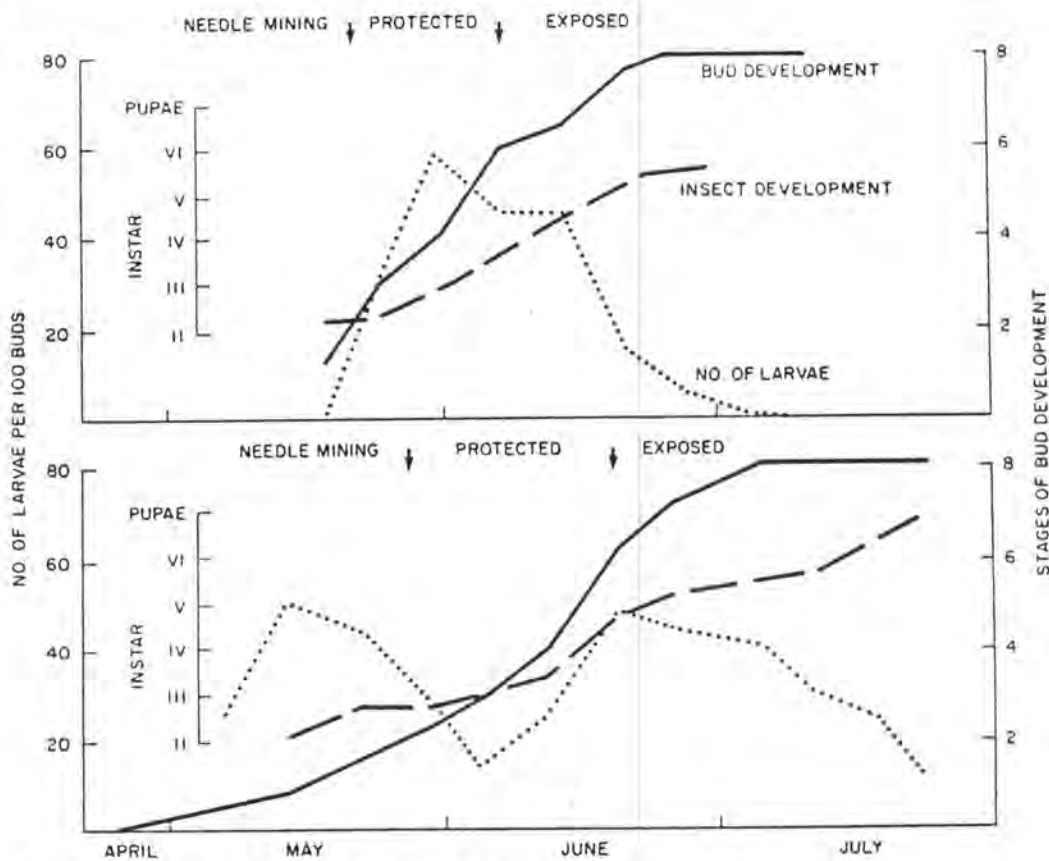


Figure 2. Comparison in population trends between two years with different synchronization of bud and budworm developments. The three phases in population trends during the larval period are indicated.

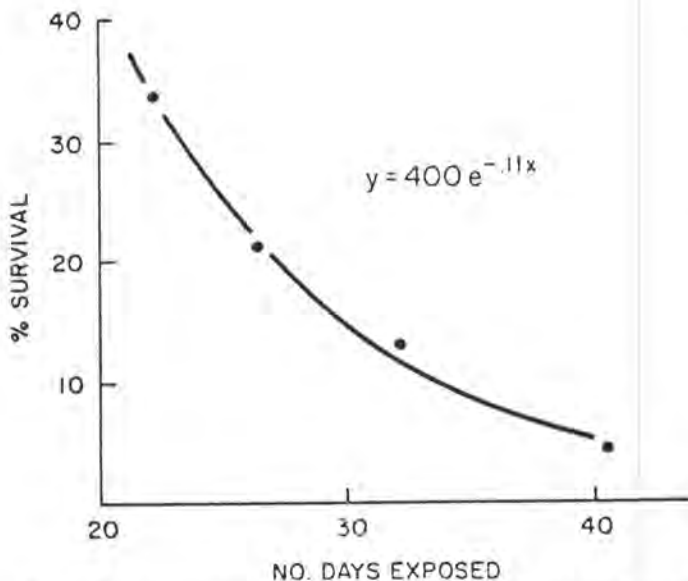


Figure 3. Relationship between the length of the exposure period between budflush and pupation and percent survival between maximum budworm density and pupation.

Maximum survival would be expected to result from good synchronization between bud swelling and larval emergence; a long period between bud swelling and budflush and a short period between budflush and moth emergence. The weather that would result in this development pattern would be, presumably, an average spring with no prolonged warm spells in March or April, ensuring good synchronization between bud swelling and larval emergence. After larvae enter the buds, cool temperatures which slow down bud development would be the most favorable, but, after budflush, hot dry weather would speed larval development and decrease exposure time. Beckwith and Kemp (1984) have compared shoot growth of grand fir and Douglas-fir for different crown levels as related to degree-days. Their models adequately predict shoot growth from temperature, indicating that bud developmental stages can be predicted, given adequate temperature records. The study by Thomson et al. (1983) on the effects of elevation on budworm development also provides a useful predictive model.

The synchronization between budflush and larval emergence depends upon developmental temperatures which vary considerably with elevation and between years (Hermann, in press). In an experiment where overwintering larvae were set out at different elevations, larvae at the valley bottom emerged long before buds were ready to be mined, and were lost, whereas at higher elevations, emergence and bud swelling coincided (R.F. Shepherd, unpublished data). Occasionally years occur when spring temperatures are unfavorable for good synchronization at all elevations and populations drop drastically. In contrast, there are also years when populations greatly increase. Ives (1974), Thomson et al. (1984), and Wellington et al. (1950) have all related weather patterns or extremes in temperatures to occurrences or collapses of eastern or western budworm outbreaks.

In New Brunswick, emergence of *C. fumiferana* usually occurs before bud swelling on black spruce (*Picea mariana* (Mill.) B.S.P.), and this tree species is being planted to minimize budworm damage, although the degree of asynchrony may vary year by year depending on weather. In Newfoundland, with different spring temperatures and a different provenance of black spruce (but with the same genetic stock of budworm as in New Brunswick [Dobesberger et al. 1983]), the high level of black spruce damage may be related to a much closer synchronization between bud swelling and larval emergence.

There is also great variability in defoliation by *C. occidentalis* among trees within stands (McDonald 1981). Many trees which are exposed to the same attack, density, and weather conditions support different population densities. This may be related to phenology. Insect survival would probably be lower on early- or late-flushing trees.

Blais (1957), Eidt and Cameron (1971), Eidt and MacGillivray (1972), and Wulf and Cates (in press) recognized the importance of synchronization of budflush with larval emergence of *C. fumiferana*. They showed how differences in dates of flushing between different host species and between individual balsam fir trees, manipulated experimentally by cold treatment, influenced rates of larval establishment. Greenbank (1956) also recognized that synchronization could be important and suggested that during increasing trends leading to an outbreak, larval development was probably more advanced relative to bud development, thus decreasing the time of exposure.

It appears that *Choristoneura* populations are able to maintain flexibility by having a wide emergence period which allows cohorts to be available whenever buds are susceptible to mining. However, after those cohorts are established, their course is fixed and they are vulnerable to reactions and vacillations of the host and to the weather.

Tree Strategies

It is necessary to understand the interaction between the host tree and the budworm and the response of the tree to attack if we wish to reduce budworm impact through enlightened forest management. Trees are a dynamic part of the interaction and their variability and response must be considered.

Some slow-growing, and long-lived trees contain relatively high amounts of chemicals, such as tannins which are deterrents to insect feeding. Production of these chemicals may provide adequate protection but at a high metabolic cost (Feeny 1975). An alternative for plants is to be short lived, fast growing, highly reproductive and widely dispersive so they can avoid attack. A third possible strategy would be for the tree to be fast growing but, if attacked, to quickly respond by producing allelochemicals. The latter is the most efficient strategy but it does encounter high risks, especially with conifers where only the actively growing tissues, such as new foliage, are capable of responding.

A close correlation in timing between the flush of oaks and the early feeding stages of winter moth (*Operophtera brumata* (L.)), and oak leaf roller (*Tortrix viridana* L.), has already been noted by Feeny (1975) and Schütte (1960). The tannin content of oak leaves increased from a low level in April to 2.4 percent in September while the presence of as little as 1 percent caused a significant reduction in larval growth and pupal weight of winter moth. Thus, insects that hatched before flush starved to death and those that hatched well after flush suffered because they were forced to feed on older foliage with higher tannin contents. As a result, trees within an oak forest which were not synchronized with egg hatch suffered less damage than those closely synchronized.

It is also possible that damage in one year may induce changes in allelochemicals in the new foliage in subsequent years (Schultz and Baldwin 1982). Haukioja and Niemela (1977) found pupation was delayed when geometrid larvae (*Oporinia autumnata* Bkh.) were fed leaves collected from birch trees from which adjacent leaves had been mechanically torn two days earlier. Also there was still a detectable delay when larvae were fed with new undamaged leaves taken from a plant which suffered leaf damage two years previously. A foliage reaction such as this would be expected to vary considerably between trees and could result in large differences in subsequent infestation rates.

Trees vary considerably in the quality and quantity of terpenes produced and this may be one of the reasons for the differences in population densities noticed among trees in any stand (Hermann, in press; Wulf and Cates, in press). In addition to the production of secondary chemicals, reactions by the host could include a reduction in needle size, nutritional levels, or

physical food quality, as occurs with reaction to feeding by the larch bud moth (*Zeiraphera diniana* Gn.), (Baltensweiler 1984), or an increase in secondary bud production to overcome the effects of defoliation. The latter is obvious with some *Pseudotsuga* attacked by budworm. As Daskotch et al. (1981) pointed out, much work on nutritional content of foliage has shown that it does not vary much among species or individuals and it is generally adequate. Attention has now shifted to the secondary chemicals which are produced in the foliage. These vary considerably among species and individuals and often act as deterrents to attack by insects. Production of these secondary chemicals may change in response to insect damage or host stress situations.

The concentration of feeding deterrents in foliage varies considerably during the time of shoot development and the feeding period of the larvae. As an example of the type of interaction that may be involved, note the fluctuations in quality and quantity of terpenes in foliage (von Rudloff 1972, 1975; Hunt and von Rudloff 1974) Von Rudloff and Granat (1982), von Rudloff and Rehfeldt (1980), and von Rudloff (1972) have shown, for a number of conifers including *Picea* and *Abies*, that the relative terpene contents are quite stable in foliage older than 6 months, but there are considerable fluctuations within the buds and shoots just before and after flush. For example, in the first week of May, before white spruce flushes, the buds contain mainly α -pinene, limonene, myrcene, and β -pinene. By the end of May, the percentage of α - and β -pinene in young leaves has decreased to a minimum. Thereafter, the percentages change again and by mid-June have reached the high levels typical of fall and mid-winter foliage. Entirely different sequences in the change were recorded for other major terpenes. Bornyl acetate rose from trace amounts in the buds to an early maximum in the shoots late in May and thereafter the relative amounts dropped gradually to low relative percentages which are typical of fall and winter foliage. Two weeks after the rise in bornyl acetate, the relative percentage of camphor rose dramatically to about 35 percent of the total terpene content and remained at that level thereafter. Thus, small changes in the time of feeding could make large differences in the types of terpenes with which the larvae have to contend. Cates et al. (1983a), using synthetic diets, showed that bornyl acetate had adverse effects upon *C. occidentalis* larvae but β -pinene had favorable effects.

Cates et al. (1983a, 1983b) also investigated foliage chemistry and found significant correlations between the terpene content of Douglas-fir trees and larval density and dry weight of adult female western spruce budworm. They did not sample at different times and so could not measure the effects of synchronization between these factors, but they found the time of budburst to be significant in a multiple regression, so an interaction was probably present. They also found that trees on

a moisture-stressed site had less suspected feeding-resistant terpenes in their foliage than needles of nonstressed trees growing on a north-facing slope.

Mattson et al. (1983) found significant negative correlations between terpene levels in foliage and weight gain of *C. fumiferana* larvae, and Heron (1965) found that pungenin, which has a deterrent effect on feeding by *C. fumiferana* larvae, occurs at low levels in new shoots and at high levels in mature needles. A review of the role of terpenes in tree resistance has been given by Hanover (1975) and Stark (1965). Similarly, Durzan (1968), Durzan and Lopushanski (1968), and Durzan and Steward (1963), have shown that there are large changes in seasonal and diurnal amounts of amino acids and related compounds in foliage. Greenbank (1956) found *C. fumiferana* that were delayed in their emergence and fed on older current foliage, were smaller and less fecund. More recently, Kay (1983) found that current foliage of a resistant Douglas-fir, when cut and fed to a geometrid defoliator, resulted in the death of the insects. Larvae fed 1-year-old or 2-year-old foliage from the same tree or all years of foliage from adjacent nonresistant trees survived well and grew to normal pupal weights. This indicates a biologically active chemical is probably being synthesized in actively growing tissue.

Budworm Strategies

I have mentioned that dispersal aids the insect in coping with wide variations in weather, date of budflush, and food quality. Similarly, larval dispersal helps the insect contend with the wide range in phenology and terpene levels exhibited by individual trees by spreading the risks of survival over many trees. In a variable environment, each year there is a strong selection pressure in favor of larvae which emerge during a specific time period when the buds are receptive. There is a continuous shifting of genetic selection for early or late emergence. What is favorable one year will be unfavorable another year. Budworm populations would be rapidly reduced were it not for their strong dispersal characteristics. The mixing of the population maintains a high degree of heterogeneity and a wide range in the time of larval emergence (Volney et al. 1983), enabling the insect to cope with environmental conditions.

We have noted that moths and larvae which spread over the area help ensure that, under severe conditions, at least some will find an acceptable habitat and survive. The strategy is to overproduce and accept high losses to ensure that some will succeed. However, in years when conditions are favorable over most of the stands, there can be an explosion in numbers because populations are being generated over a much larger area in conjunction with an increase in survival rates for any particular location.

Forest Management Strategies

Forest management requires the prediction, in time and place, of budworm trends. This is not easy, because under the driving influence of weather, timing of events could be just as important as the magnitude of the event. Different elements of prevailing weather are important at different times and indirect effects of weather are largely unknown. For instance, high temperatures through September and October could be deleterious to overwintering larvae (Ives 1974; Thomson et al. 1984) but high temperatures between budflush and moth emergence could be advantageous to feeding larvae by reducing the length of the exposed period. Perhaps weather, as a regulating factor, only comes into play during years of extremes, causing dramatic population changes (Thomson et al. 1984). Other factors may have more impact in average years, making trend analysis difficult. A pheromone moth trapping system capable of measuring low budworm levels may help indicate where and when outbreaks might occur.

Agricultural programs to minimize the effects of budworm are being formulated. Generally, the forester would like to reduce the amount of budworm-susceptible foliage and increase the amount of nonsusceptible foliage. He can do this in two ways: convert to a nonhost species or convert to resistant strains of trees selected from among normal host species. Conversion to a nonhost species is a good strategy, provided the site is suitable for that species and growth rates and economics are acceptable. For instance, proposals have been made to reduce the amount of susceptible climax species on the warm dry sites of the forests of northern Idaho and western Montana (Carlson et al., in press) by planting seral species, such as lodgepole or ponderosa pine, in place of the susceptible climax species. Provided these replacement species are managed on an appropriate rotation, there should be a minimum of other pest problems so that one is not just shifting problems rather than solving them. Often, though, there is little choice of alternative species on budworm-susceptible sites as the loss in growth rates or values is too great to be acceptable. In budworm-susceptible Douglas-fir forests of British Columbia, for example, no other acceptable species seem ecologically adapted to these sites. The only answer, in this case, for a long-term reduction of budworm, is to identify and propagate resistant strains.

Agriculture has been successfully using resistant strains for a long time (Painter 1966), and McDonald (1979, 1980, 1981) has carried out some interesting studies in this direction for budworm. At the same time, a study of historical defoliation patterns should reveal those sites where significant defoliation occurs most frequently. Planting resistant strains within those sites could reduce moth damage and the downwind spread of populations. We are not attempting complete eradication by such a

procedure. A reduction of impact of perhaps 50 to 80 percent may be quite attainable and acceptable.

The usual argument against this approach is that the insect can adapt to strains faster than we can produce them because of the large number of generations it passes through during only one generation of its host plant. But, as I previously suggested, the budworm is highly dependent on maintaining a heterogenetic population: it is a necessity to survive in a variable environment. There are sufficient forests which will not be cut because of inaccessibility, wilderness, park reserves, etc., to maintain the heterogeneity of the budworm and prevent the establishment of an insect population adapted to the resistant trees. Therefore, let us take advantage of this characteristic and turn it against the budworm by identifying, propagating, and planting resistant trees on the susceptible, productive sites.

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