

# Comparative Population Biologies of North American Spruce Budworms

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Patterns of variation in traits that determine population success of the spruce and western spruce budworms are compared. The two species differ little in their biologies. Geographic variation, where documented, tends to be clinal in the spruce budworm and racial in the western species. Their respective host species vary with similar patterns. Reconstructions of Holocene host-tree histories suggest that western spruce budworm hosts have migrated little compared to spruce budworm hosts. Examination of budworm life-history traits suggests that gene flow from high-elevation western populations to low-elevation eastern populations is more probable than the reverse. A model, based on the probable Holocene history of North American coniferous forests and budworm-dispersal patterns, is proposed to explain the current patterns of variation observed.

Ce document compare les variations de caractères qui déterminent le succès des populations de la tordeuse occidentale de l'épinette et de la tordeuse des bourgeons de l'épinette. Les deux espèces diffèrent peu biologiquement. Les variations géographiques, lorsqu'on les connaît, tendent à varier par degrés insensibles chez la tordeuse des bourgeons et sont plutôt raciales chez la tordeuse occidentale. Il en va de même de leurs hôtes respectifs. Les reconstructions des antécédents de leurs hôtes, à l'holocène, portent à croire que les hôtes de la tordeuse occidentale ont peu migré comparativement à ceux de la tordeuse des bourgeons. D'après l'examen des traits du cycle évolutif des tordeuses, le flux génique des populations occidentales des habitats d'altitude vers les populations orientales de basse altitude est plus probable que l'inverse. Un modèle fondé sur l'histoire probable des forêts de conifères de l'Amérique du Nord durant l'holocène et des formes de dispersion des tordeuses est proposé pour expliquer les variations actuellement observées.

## Introduction

Few insect species have been scrutinized as much as members of the genus *Choristoneura*. Much work in the past 4 decades focused on two fir- and spruce-feeding species, which are among the most destructive defoliators in North America: the spruce budworm (*C. fumiferana* (Clemens)) and the western spruce budworm (*C. occidentalis* Freeman). Since McKnight's (1968) review, a significant body of literature on the biology of these species has accumulated. Much of this work, focused on life-history traits thought to be important in determining success of the insects, has documented the extreme variation (within and among populations) that is seldom subsumed by interspecific differences. The bewildering variation in characters traditionally used in establishing boundaries of taxonomic categories has hindered the development of a

biologically adequate classification for the conifer-feeding members of this genus (Powell 1980).

In this paper, I assess the nature and significance of this variation in the two principal pest species of the genus and describe any patterns that emerge from this analysis. Rather than provide a list of similarities and differences, I shall use these comparisons to infer the phylogenetic relation between the species and hypothesize a mechanism to explain the patterns observed. My ultimate objective is to indicate where results may validly be extrapolated from one species to the other and caution where extrapolation may be dangerous. These conclusions will be of value as we design pest-management procedures based on techniques that depend on species-specific responses for their efficacy.

Stehr (1967a) argued for a population-biology perspective in understanding relations among budworm popu-

lation size, density, quality, and dynamics. This approach synthesized the relevant information about the budworms' ecology, genetics, and evolution. Pivotal to this understanding is the concept of gamodeme: the population of interbreeding individuals limited only by the spatial and temporal boundaries of their breeding system. Establishing breeding-system boundaries is problematical and must be done experimentally, however. Despite the difficulties it presents, the solution of this problem has important practical consequences in pest management. Stehr (1967b) also recognized that the evolutionary histories of conifer-feeding *Choristoneura* would be reflected in the geological and climatological history of their hosts. This observation was tantalizingly perceptive because recent biogeographical events that could influence the evolution of this group have been extensively documented by paleontologists. Its real significance is that, although the evolutionary record of the budworm/forest system may not have a fossil record, many of these events are remarkably recent.

Maps of insect distribution and host range may be combined to delineate the known and probable spatial gamodeme boundaries of the "species" as we currently conceive them. This approach ignores any infrastructure within gamodememes occupying large areas devoid of any obvious physical barriers. The present range of *C. fumiferana* is almost continuous from the Avalon Peninsula of Newfoundland to the Mackenzie Delta on the Arctic Ocean. The range of white spruce (*Picea glauca* (Moench) Voss),<sup>1</sup> an important host species of the spruce budworm, extends to the Pacific at Cook Inlet and the Chukchi Sea in Alaska. Thus, if we assume that the spruce budworm follows its hosts' ranges, its distribution probably spans 100° of longitude and 25° of latitude. This is too large an area to be devoid of population structure. In contrast, the present range of *C. occidentalis*, which is associated with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests, extends from British Columbia to Arizona and probably into the Tropics in the Sierra Madre of Mexico (Stehr 1967b), spanning 25° of longitude and perhaps 35° of latitude. Although this area is much smaller, the effect of the West's physiography has been to produce forest distributions with obvious spatial boundaries that may be used to delimit the western spruce budworm gamodememes.

Temporal gamodeme boundaries are more difficult to establish. I shall limit this discussion to the Holocene epoch, which began 20,000 to 15,000 years before the present (BP). This probably marks the initial retreat of the North American ice sheets that developed in the Wisconsin glacial stage.

## Holocene Biogeography of Budworm Hosts

According to Flint (1971, p. 330), at the beginning of the Holocene, the coniferous forest was shifted 20° (2 220 km [1,380 mi]) south of where it survives today. This forest spanned only 2 to 5° of latitude (140 km [120 mi.] to 550 km [350 mi.]) probably because environments suitable for its survival were "compressed" between the ice sheet and the Tropics; the Tropics has changed little in extent (Holmes 1965). Continental in climate, early Holocene boreal forests occupied a narrow belt west of the Appalachians from western Pennsylvania, through Missouri, to the east slopes of the Rocky Mountains in Montana. Bryson and Wendland (1967) show this forest in the Rocky Mountain foothills of what is now Wyoming. Although *Abies* pollen is difficult to recognize (Bakuzis and Hansen 1965), fir may have been a minor component of or absent from this forest. This view is supported by Davis's (1967) and McAndrews's (1967) reconstructions of early Holocene vegetation south of the Great Lakes. On the east coast, a maritime spruce-fir forest covered an area from what is now southern Pennsylvania to northern South Carolina, and bounded by the Appalachian Mountains to the west (Flint 1970). Fir (*Abies* sp.) was always a consistent component of this region's pollen record (Wright 1971). Forest migration northward from these refugia was determined by the rate of deglaciation and physical barriers such as the Great Lakes, Lake Agassiz, the Rockies in the West, and the Appalachians in the East. The present distribution of balsam fir is probably the result of a northerly migration from the eastern refugia into New England and a subsequent westerly spread north and south around the Great Lakes. The modern distribution of red spruce (*Picea rubens* Sarg.) suggests a similar migration route without a southern Great Lakes advance but reaching the 80° meridian. Lester (1974) provides evidence of distinct balsam fir phenotypes east and west of this meridian north of the Great Lakes. This discontinuity probably resulted from the meeting of two previously isolated populations following migrations circumventing the Lakes. My conjecture is that balsam fir was not a component of an Alaskan refugium. White spruce, in contrast, would have colonized deglaciated lands across a broad front from the continental refugium. The continental spruce-dominated forest would have established contact with the eastern spruce-fir forest east of the Great Lakes between 10 and 8,000 years BP (cf. Terasmae 1974, Fig. 10). The boreal forest reached its approximate northern limits about 6,000 years BP (Nichols 1975). Balsam fir pollen appears in the stratigraphic record at 115° W longitude 2,000 to 3,000 years BP (Nichols 1975, Fig. 1), suggesting a probable date when it reached the western limits of its range.

<sup>1</sup>Throughout, host ranges are from Little (1971).

The western situation is complicated because more host species are involved and the stratigraphic record is not as complete as it is in the East. The Wisconsin Cordilleran ice sheet in western North America extended from central Alaska south to northern Washington and was continuous from the Pacific east to the Laurentide ice sheet, which it met in the foothills of the Rocky Mountains (Flint 1970). South of this front, in the mountain and Pacific states, alpine glaciers formed; their altitudinal extent depended on topography, latitude, and distance inland. Evidence from the location of cirques suggests that these glaciers may have extended down to 610 m (2,000 ft) in the northern Cascades, 1 830 m (6,000 ft) in the southern Cascades, and 2 240 m (8,000 ft) in the Sierra Nevada; in the Rockies they were at 1 830 m (6,000 ft) in the Inland Empire, and 3 660 m (12,000 ft) in northern New Mexico (Flint 1970, Fig. 18-4). As a consequence, Canada was devoid of vegetation and western forests in the United States survived at lower elevations and south of their present range. Interpretation of macrofossil evidence places these early Holocene forests about 450 km (280 mi.) south and 800 m (3,000 ft) downslope from their modern counterparts in Arizona and Utah (Cole 1982). Except for the destruction of the northern forests, forest types susceptible to the western spruce budworm expanded during the late Wisconsin age, particularly in the southern latitudes, because of this downslope migration and the more favorable climatic conditions prevailing (Flint 1970, Figs. 19-3, 16-2; Martin and Mehringer 1965).

A major biogeographical event resulting from the glacial advance into the Pacific Northwest was that Douglas-fir populations were split into what are now recognized as the coastal variety *menziesii* and the inland variety *glauca*. Just before this, Douglas-fir went through a period of explosive population growth, variously attributed to the evolution of a new karyotype or climatic change after the last pluvial period (Silen 1978). A period of rapid population growth and range expansion after deglaciation has been documented by Tsukada (1982), who concluded that contact between the two varieties was re-established some 7,000 years BP.

Associated with Douglas-fir and major hosts of the western spruce budworm are several species of true firs, spruces, and larches. The principal fir associate in the Cascade and coastal forests is grand fir (*A. grandis* (Dougl.) Lindl.) in the northern Cascades, white fir (*A. concolor* (Gord. & Glend.) Lindl. var. *lowiana*) in the southern Cascades, depending on elevation: grand fir and subalpine fir (*A. lasiocarpa* (Hook.) Nutt.) in the Canadian Rockies and adjacent states; and subalpine fir, cork bark fir (*A. lasiocarpa* var. *arizonica*), and white fir (*A. concolor* var. *concolor*), in the Southwest. Engelmann spruce (*Picea engelmannii* Parry) is a component of these forests in the northern

Cascades and Rocky Mountains, and Colorado blue spruce (*P. pungens* Engelm.) is present in the southern Rockies. White spruce is present within the range of the western spruce budworm at the Alberta-British Columbia/Montana borders. Depending on elevation, western larch (*Larix occidentalis* Nutt.) and subalpine larch (*L. lyallii* Parl.) are also components of these forests in the northern Cascades, the northern Rocky Mountain states, and adjacent Canada. Macrofossil evidence from the Southwest suggests that these associations may have been in a state of flux for most of the period under consideration (Cole 1982; Mehringer and Ferguson 1969). Individual host-tree reaction to climatic change determined the details of forest composition, but the host species of this region may have remained unchanged for as long as 300,000 years (Barnosky 1984).

## Host Relations

Marked differences occur in the patterns of geographic variation among the two budworms' host-tree species. In the East, the gentle topography and increasingly drier and cooler conditions to the west are correlated with east/west clines (Table 1). By contrast, race formation has been prevalent among the western species (Table 1), perhaps because of the patchy distribution of suitable habitats. White spruce, a boreal species, possesses an east/west cline stretching from Newfoundland to the MacKenzie and Richardson Mountains in the west. This is also the eastern boundary of the Alaskan race of white spruce. Where the ranges of similar eastern and western host species overlap, introgression is always evident (Table 1). Similarly, introgression is common among the host species of the western spruce budworm. In general, eastern and western host species have not differentiated sufficiently to become reproductively isolated. Thus, in addition to their spatial overlap, much overlap occurs in biological traits between eastern and western host species of these budworms.

Nevertheless, real genetic and developmental differences among neighboring western forest stands further complicate the patterns in host-tree variation. Thus, racial (Steiner 1979) and intertree differences (Beckwith and Kemp 1984) in the time of budburst for interior Douglas-fir contribute significantly to local variation. Similarly, genetic variation in the phenology of coastal Douglas-fir populations is associated with elevation, aspect, and distance of the provenance from the ocean (Sorensen 1983). The distances may be small: significant three-dimensional clinal variation in growth characteristics of coastal Douglas-fir populations were detected by Silen and Mandel (1983) over distances as short as 16 km (10 mi.) and elevational differences of only 310 m (1,000 ft).

Table 1  
Geographic variation in budworm host-tree species

Host species	Species code	Range	Pattern of variation	Introgresses with	References <sup>1</sup>
Principal spruce budworm hosts:					
<i>Abies balsamea</i>	1	Eastern	E/W cline	7	a
<i>Picea glauca</i>	2	Boreal	E/W cline <sup>2</sup>	8	a,b
<i>P. mariana</i>	3	Boreal	None	4	a
<i>P. rubens</i>	4	Eastern	None	3	a
Principal western spruce budworm hosts:					
<i>Abies concolor</i>	5	Western	2 races	6	b
<i>A. grandis</i>	6	Western	5 races	5	b
<i>A. lasiocarpa</i>	7	Western	2 races	1	b
<i>Picea engelmannii</i>	8	Western	Unknown	2,9	a
<i>P. pungens</i>	9	Western	Unknown	8	b
<i>Pseudotsuga menziesii</i>	10	Western	9 races	—	c

<sup>1</sup>a = von Rudloff (1975), b = Fowells (1965), c = Wright et al. (1971).

<sup>2</sup>Alaskan race also.

Several other sources of local variation are evident at many hierarchical levels — every one bearing its own peculiar seasonal and annual pattern. Within a stand, species composition, trees, and crown and canopy levels are recognized as contributing significantly to the variability in habitat characters that are important to the budworm. Shoot phenology, bud production, shoot growth and concomitant changes in the nutritional value of host tissues, and the production of secondary compounds are all known to be subject to these sources of variation. Each of these phenotypic traits have special significance in determining budworm success.

Host phenology is known to vary with respect to budworm development. This asynchrony affects budworm survival on balsam fir (Eidt and Cameron 1973) and has been identified as a correlate with the occurrence of western spruce budworm outbreaks in British Columbia (Thomson et al. 1984). Experiments in New Brunswick showed that phenological differences among white, grand, and balsam firs were not sufficient to interfere with spruce budworm development (Eidt and MacGillivray 1972). Cameron et al. (1968) found good synchrony between spruce budworm development and balsam fir shoot growth in New Brunswick. Blais (1957) and Greenbank (1963a) suggested that phenological differences between black spruce and the other host species were sufficient to explain the different patterns

of budworm survival and damage among the two sets of host species. These differences may be caused by microclimatic differences among sites rather than genetic differences among hosts. Manley and Fowler (1969) found phenological differences among black spruce, red spruce, and their hybrids to be negligible. Bean and Wilson (1964) found that accumulated degree-days were a better predictor of budworm development than balsam fir shoot growth. Apparently, cues that initiate budburst are different from those that induce budworm development. Kemp and Beckwith<sup>2</sup> found significant annual variation in the degree-day date of budburst for both Douglas-fir and grand fir in western sites. They pointed out that, although soil temperature regimes determined the date of budburst in Douglas-fir (Cleary and Waring 1969), accumulated degree-days based on effective air temperatures determined western spruce budworm emergence in the spring. No differences were detected among parameters for budworm development in the different budworm gamodemes studied by Cameron et al. (1968) in New Brunswick, Wagg (1958) in Orgeon, and other Pacific Northwest sites (Beckwith and Kemp 1984).

<sup>2</sup>W.P. Kemp, Dept. For. Res., Univ. Idaho, Moscow, Id. and R.C. Beckwith, U.S. Forest Service, Corvallis, OR, personal communication.

Much of the differences reported among species and regions may thus be explained by differences in the local environments rather than by genetic differences among gamodemes of budworm or their hosts.

Variation in host-tree phenology and the dependence on environmental cues other than those that affect the tree in initiating budburst make the spring emergence of the budworm hazardous. Overcoming the hazard of feeding-site establishment in the spring is accomplished by variation in feeding habits depending on the availability of suitable buds.

Both the spruce budworm (Thomas 1976) and the western spruce budworm (Volney et al. 1983) have protracted periods of spring emergence. The distributions of emergence times are adequately modeled by the lognormal distribution. In western spruce budworm populations, the variation is such that the variance within a family (offspring from a single female) is almost that of the population variance (Volney et al. 1983). Such a pattern is effective in spreading the risk of early-instar mortality resulting from failure to establish feeding sites. When host-tissue availability is variable and unpredictable, this pattern allows all families to be represented among individuals emerging synchronously with bud development. Thus, all families can react to the range of spring conditions experienced by the populations, and opportunity is limited for selection to reduce variation that is not associated with spring emergence time.

More significantly, perhaps, is the effect of host-tree flowering on this process. The occurrence of flowering before vegetative budburst expands the phenological window for budworm feeding-site establishment (and survival) considerably. Because the distribution of spring emergence times is skewed to the left, the expansion of the phenological window early in the season can result in more than a proportionate increase in budworm survival. Conditions associated with flowering of balsam fir are associated with elevated survival of early instars (Blais 1952; Greenbank 1963a). Although his evidence was derived from outbreak populations, Blais believed that flower production in balsam fir and elevated early-instar survival was one mechanism responsible for the release of spruce budworm populations.

Production strategies in host-tree buds can thus affect budworm survival. The spruces and Douglas-fir, which are less shade-tolerant than the firs, produce both microsporangiate and megasporangiate strobili throughout much of their crowns (Fowells 1965). In Douglas-fir, reproductive buds are known to be produced in the unshaded portions of the crown (Silen 1973). Balsam fir (Powell 1977) and other true firs (Fowells 1965) have a distinct megasporangiate zone at the crown apex immediately above a narrow microsporangiate zone, also in the upper crown. Although

the number of vegetative buds per unit branch area may not differ significantly among eastern host species (Greenbank 1963b), the number of reproductive buds per tree on the more shade-tolerant fir is probably substantially lower. The importance of bud dynamics in budworm population release was not addressed in much of the subsequent work, which continued to focus on outbreak populations.

Latent-bud production may be a factor that influences the duration of outbreaks. Douglas-fir and the spruces produce latent buds on their shoots for most of their lives. These buds are stimulated after defoliation and a second crop of buds will be produced after feeding is complete. Consequently, the size of the bud population increases for several years during an outbreak. This process may prolong the period over which outbreaks are sustained by these hosts. Balsam fir (Batzler 1973) and white fir, by contrast, lose this ability early in their lives. Only the ability of the young trees to sprout adventitiously allows the true firs to survive outbreaks.

Greenbank (1963b) considered white spruce shoot growth, which is significantly greater than in fir, another means by which white spruce sustains defoliation longer than balsam fir. Similarly in the West, Douglas-fir can sustain more defoliation (Carolyn and Coulter 1975), and its shoot growth is greater than in grand fir (Beckwith and Kemp 1984). Both species of spruce budworm are apparently similar in ability for damaging the shade-tolerant true fir component of their host stands more than the less shade-tolerant spruces and Douglas-fir.

Evaluating host preferences and suitability is difficult. An understanding of several processes, ranging from stimuli that initiate and maintain feeding to the influence of host tissue on fitness, is required to assess a true preference. Experiments have clearly shown that all four major host plants of the spruce budworm present adequate feeding stimuli (Albert 1983; Albert and Parisella 1983). Detailed work of this nature has not been done on the western species, but because Douglas-fir, spruces, firs, and even larches are fed on extensively (Fellin and Dewey 1982), the assumption that they all have phagostimulants — which function in initiating and maintaining feeding by the western spruce budworm — is reasonable.

Food quality, represented by the various host tissues used, influences budworm productivity. Caloric intake and caloric intake per milligram of protein consumed are correlated with spruce budworm survival, developmental rate, and pupal weights. Pupal weights are correlated with  $F_1$  survival (Shaw et al. 1978). These indexes are used because several nutritional components interact in as yet unknown ways to determine budworm performance. Nutritional components include sugars (Harvey 1974), crude fat, protein (correlated with total nitrogen in the diet), and moisture content

(Shaw et al. 1978). All these components vary annually, seasonally, and locally, but not significantly among plots separated by 224 km (139 mi.) (Shaw and Little 1977) in New Brunswick. Mattson et al. (1983) obtained similar results for spruce budworm reared on all major hosts found in Minnesota. They also found that pupae derived from larvae reared on balsam fir and upland black spruce were larger than those from white and lowland black spruces. Thomas (1983), however, obtained heavier pupae from white spruce than from balsam fir. These discrepancies indicate the nature of variation that might be expected to be induced by the complex interaction of biotic and abiotic factors that determine food quality in the several hosts of the spruce budworm. Further, food quality can be manipulated through fertilizer treatments. Thus, over a range of 8.8 to 17 percent foliar nitrogen in trees treated with inorganic fertilizers, female pupal weights generally increased in spruce budworm reared on balsam fir trees in New Brunswick (Shaw et al. 1978).

Similarly, over a broad range of foliar nitrogen concentration, both white fir and Douglas-fir are adequate hosts for the western species; only at uncommonly high or low concentrations were deleterious effects detected (Brewer et al., in press). In the Southwest, the western spruce budworm developed faster on Douglas-fir than on either white or cork bark firs, but no effect was found in pupal weights (Wagner and Blake 1983). Beckwith (1983) found Douglas-fir and Engelmann spruce to be slightly better hosts than subalpine fir, but western larch — although fed on by larvae — was distinctly inferior. Thus, the cues that initiate and sustain feeding are not always associated with nutritionally superior hosts. Western spruce budworm growth rates also differ among populations, and they are altered by extreme concentrations of nitrogen, bornyl acetate, and beta pinene incorporated in artificial diets (Cates et al.<sup>3</sup>). These experiments also demonstrated that each population of the western spruce budworm reacted in its own way to the variable dietary components; significant two-factor interactions occurred between nitrogen and terpenes to influence growth rates; and survival was determined by concentrations of nitrogen and bornyl acetate. Thus, terpenes may interact with nutritional components to influence budworm success, but, terpene concentration is known to vary geographically, annually, seasonally, and locally in all budworm hosts that have been examined (von Rudloff 1975). It is not surprising, therefore, that the budworms are extremely tolerant of large differences in food quality.

## Life-History Traits

To be successful, an organism must feed, grow, mate, reproduce, and avoid natural enemies. Success sometimes involves dispersal induced by environmental modifications of commonly observed behavior (Wellington 1980). Species comparisons would be most successful if matrices containing correlations of life-history traits — obtained under identical conditions — could be contrasted. Unfortunately, this has never been done for spruce and western spruce budworms; consequently, individual traits must be compared one at a time.

Fecundity is often used as a measure of population success, but it is subject to considerable environmental control. Potential fecundity (Thomas et al. 1980) of field populations, while variable, does not differ between the two species (Table 2). On average, dead spruce budworm females found in the field have laid 70 to 80 percent of their potential egg complement; populations seldom realize their full potential (Thomas et al. 1980). No comparable data are available for the western spruce budworm, but they are also unlikely to lay their full egg complement in nature. Because the full egg complement is seldom deposited in their native stands, egg-deposition rates and variation in egg quality associated with deposition order must be recognized as traits that can influence population success in these species. Egg-deposition rates of the western spruce budworm have not been studied in detail, which makes comparisons impossible. Harvey (1977), however, has shown that, in the spruce budworm, mean egg weight declines with deposition order, that individuals from the latter half of eggs deposited emerge later, survive to the second instar better, and more females occur among them than in the first half. An east/west cline has been demonstrated in the mean egg weight of the first eggs laid (Harvey 1983a), which is largely unchanged by variations in temperature and diet, and its heritability is high (Harvey 1983b) and thus susceptible to rapid selection. Harvey (1983b) suggests that the heavier eggs in western populations of the spruce budworm endow larvae with greater food reserves, which allows survival over the longer western winters.

Some measures have been made of initial mean egg weights of the western spruce budworm that permit comparison. Harvey (1983b) found the mean initial egg weights on one of the western spruce budworm populations (Montana) and a spruce budworm population (Ontario) to be 0.182 and 0.161 mg, respectively. Based on the relation between latitude and mean initial egg weight, the Montana estimate is anomalously high and corresponds to a latitude 7° north of the insects' origin. Other estimates of mean initial egg weights have not been determined for the western spruce budworm. Data from Brewer et al. (in press) allows estimation of the mean initial egg weights of the western spruce

<sup>3</sup>R.G. Cates, C. Henderson, and R.R. Redak, Dept. Biology, Univ. New Mexico, Albuquerque, NM, personal communication

Table 2  
**Mean field fecundity of the spruce budworm (SB)  
 and the western spruce budworm (WSB)**

Species	Locale	Mean	Reference
SB	Ontario	195.3	Harvey (1983b)
SB	NW New Brunswick	162-209	Miller (1963)
SB	NW Ontario	157-182	Blais (1953)
SB	New Brunswick	201-255	Thomas et al. (1980)
WSB	Colorado	154.4	McKnight (1971)
WSB	SW Oregon	125-237	Volney et al. (1984)
WSB	New Mexico	159-215	Volney (unpubl.)
WSB	Pacific Northwest	100-200	Campbell (in press)

budworm. The mean weight of eggs produced by females, which laid only a small number of eggs in these experiments may be assumed to approach Harvey's initial egg weight. These values range from 0.164 to 0.174 mg, suggesting an origin at least 3 to 4° north of where the insects used in the experiment were originally collected. Such comparisons confound species effects with elevational effects in the place of origin; nevertheless, they suggest that western spruce budworm populations from higher elevations produce larger eggs in the first masses than their spruce budworm counterparts from the same latitude but at lower elevations and further east.

Diapause synchronizes development after hatching in both species. Some populations live in environments where development is not completed in a single growing season. Some budworm populations are adapted to this condition by being able to enter a second diapause. The two-year-cycle budworm (*C. biennis* Freeman) is distinguished from the spruce budworm and the western spruce budworm by the high incidence of a second diapause. In several respects, the two-year-cycle budworm is intermediate to the other two. A second diapause in the spruce budworm and the western spruce budworm is variable and subject to artificial manipulation, however (Harvey 1967). This may be a character that shows clinal variation in response to increasing elevation, latitude, or both.

Growth rates differ among species in detail only. The median postdiapause development time is shorter in the spruce budworm than in any of the four fir- and

spruce-feeding budworms of North America (Stehr 1964). In addition, other studies show that development time varies little in the different populations of the spruce budworm and the western spruce budworm (Table 3). Despite these differences, a substantial degree of overlap in development times remains among the species (cf. Stehr 1964), but the spruce budworm population is more variable than any of the others examined. The general pattern of postdiapause development does not differ between species. For the western spruce budworm, no detectable difference in development between the sexes has been found up to the end of the fifth instar; females spend a substantially longer time in the sixth instar than males, but their pupal stadia are only slightly shorter. Thus males eclose before females.<sup>4</sup> Similarly, spruce budworm females spend a shorter time in the pupal stage (Sanders 1975), but are preceded by males at eclosion by 1 to 2 days (Stehr 1964). Clearly, the two species would react the same to a given environment and would not be seasonally isolated should they become sympatric.

Slight differences in the daily patterns of mating activity have been observed. Half the spruce budworm females maintained at 20°C on a 17-h photoperiod began calling 3½ to 4½ hours before lights were turned out (Sanders 1971a; Sanders and Lucuik 1972), but

<sup>4</sup>W.J.A. Volney and A.M. Liebhold, Dept. Entomological Sciences, Univ. California, Berkeley, CA. Unpublished data

Table 3  
Median postdiapause development times

Species	Rearing temperature (°C)	Development time		Reference
		Females	Males	
<i>C. fumiferana</i>	Unspecified	29.5	26.5	Stehr (1964)
<i>C. occidentalis</i>	Unspecified	32.5	29.5	Stehr (1964)
<i>C. retiniana</i>	Unspecified	37.5	30.8	Stehr (1964)
<i>C. occidentalis</i>	25	34.4	32.2	Volney and Liebhold <sup>a</sup>
<i>C. retiniana</i>	25	36.8	33.9	Volney and Liebhold <sup>a</sup>
<i>C. fumiferana</i> <sup>b</sup>	21	29.0	27.5	Harvey (1975)
<i>C. occidentalis</i> <sup>b</sup>	23-26	29.5	29.5	Lyon et al. (1972) <sup>c</sup>

<sup>a</sup> Unpublished data.

<sup>b</sup> Mean.

<sup>c</sup> Insects not sexed.

western spruce budworm females did not react similarly until 2 h before lights out (Liebhold and Volney, 1984). The spruce budworm is intermediate between the western spruce budworm and the two-year-cycle budworm (Sanders et al. 1977). Both spruce budworm and western spruce budworm females begin calling earlier at lower temperatures (Liebhold and Volney 1984; Sanders and Lucuik 1972). The circadian periodicity of this behavior in the western spruce budworm can be modified by selection (Liebhold and Volney 1984). In general, the diel distribution of male response to artificial attractants is similar to the distribution of female calling, except that it is less protracted.

Where they have been tested in the field, the two species are cross attractive (Sanders et al. 1977) and laboratory bioassays support this conclusion (Sanders 1971b). The two species share the same major pheromone components (Sanders and Weatherston 1976; Silk et al. 1982). The response of spruce budworm males to western spruce budworm females is only half of what it is to conspecific females, however, which suggests subtle differences in the pheromone chemistry of the two species. Silk et al. (1982) attribute this to detectable quantities of E/Z 11-tetradecenyl acetate and E/Z 11-tetradecanol mixed with the principal pheromone components (E/Z 11-tetradecenal) in western spruce budworm virgin-female effluvia. The function of the minor components in long-range attraction of conspecific western spruce budworm males to females is unknown (Cory et al. 1982). Whatever the reason, cross-attraction is asymmetric; matings between spruce budworm males and western spruce budworm females occurs less frequently than the reciprocal cross, but this degree of incompatibility is

unlikely to be significant in preventing interspecific matings in nature.

Both species are dispersed as larvae (Beckwith and Burnell 1982; Régnière and Fletcher 1983). Whether this results in significant long-range (>100 km, 62 mi.) dispersal is unknown, but this process is important in redistributing insects within stands and may be exploited in silvicultural control (Jennings et al. 1983). Adult dispersal is significant in moving insects over great distances. In dense populations, spruce budworm females make vertical flights after laying a variable portion of their eggs. This behavior may be repeated nightly under the appropriate environmental conditions (Greenbank et al. 1980). Moths have been recovered as far as 450 km (280 mi.) from their native stand in a single night of nonstop flight (Dobesberger et al. 1983). Flight capacities reported by Greenbank et al. (1980) suggest an upper limit of 800 km (497 mi.) for moths in a single night. Although long-range dispersal of the western spruce budworm has not been documented in such detail, massive moth flights associated with storms have been reported on several occasions in British Columbia and the adjacent states (Carolyn, in press).

## Synthesis

An examination of all life-history traits studied in detail so far suggests that no barriers exist to gene flow between the two species. Variability within and among host trees is sufficient that variability in host quality among locations is comparatively trivial over distances at least as great as 225 km (140 mi.) for the spruce budworm.



Ample evidence exists that local and geographic variation in host traits are matched by an impressive array of variable life-history traits, allowing each budworm species to thrive in its own habitat. With the patterns of host-species variation described above, one would expect each species to be capable of colonizing the other's hosts. Not surprisingly, Harvey (1983b) reared western spruce budworm larvae on balsam fir foliage, and the spruce budworm does well on western firs (Eidt and MacGillivray 1972). The two host-tree groups are not sufficiently distinct to present much of a barrier to gene flow between the two insect species.

Deficiencies in food quality, if they are relatively small, are ameliorated by two physiological mechanisms that tend to buffer population changes. Development time is often extended on marginally inferior host trees and female pupae are produced as heavy as those from slightly better hosts. Slight deficiencies in host quality are thus overcome by what appears to be compensatory feeding in both insect species. The second mechanism produces eggs of almost uniform size in the first egg masses laid regardless of the female's nutritional history. Although fecundity can be altered by varying food quality, mean initial egg weights are almost completely under genetic control (Harvey 1983b). This control effectively buffers eggs from the vicissitudes of the female's environment. Furthermore, dispersal flights are often made only after the first eggs have been laid (Greenbank et al. 1980). If egg size is associated with overwinter survival and the optimum egg size varies clinally (Harvey 1983a), this peculiar combination of dispersal and oviposition traits ensures that locally adapted progeny are left in the egg-laying female's native stands. The consequences of smaller mean egg sizes and higher proportion of females among the last laid eggs carried by dispersing females are discussed below.

Neither species has distinctive life-history traits or host requirements that would preclude their establishment within the other's range. All critical life-history traits examined so far are plastic, may be changed rapidly by selection, or are variable and inherited so that variation is conserved. Were detection possible (no suitable characters distinguish the species), the two species would doubtless hybridize in nature where they occur sympatrically. This assumption is based on the observation that some sympatric populations of *C. occidentalis* and *C. retiniana*, which are only marginally cross-attractive (Liebhold et al. 1984), successfully hybridize in nature and produce viable offspring (Volney et al. 1984).

Attempts to establish an evolutionary relation between these species are frustrated by a lack of suitable fossil evidence. That they are close phylogenetically is suggested by the extreme patterns of within — relative to among — species variation. Further, isozyme analyses show the remarkable similarities among all

conifer-feeding *Choristoneura* species (Harvey 1985). By combining information on their biology with modern climatological and vegetation patterns, we can reconstruct prehistoric environmental patterns to arrive at reasonable conjectures as to the course of their evolution.

Gene flow would be effected by adult dispersal and reproduction. After dispersal, two routes are possible to successful budworm establishment in distant stands. Either colonizing males would have to mate with local females, or the eggs deposited by migrating females would have to survive. Except for seasonal differences between the source and the destination, western spruce budworm males would be more likely to be successful in mating with spruce budworm females than the reverse cross because of the asymmetry in cross-attractiveness. The larger eggs transported by western spruce budworm females from populations at higher elevation would be laid in milder winter environments at the lower elevation of eastern destinations. If Harvey's (1983a) conjecture is right, the larger eggs of the western spruce budworm have a better chance of surviving in the East than those of spruce budworm moved to the West. Both routes to gene flow favor a west-to-east flow between populations.

Both species are transported by storm systems (Carolin, in press; Greenbank et al. 1980). Current circulation patterns in North America track from west to east (Wellington 1954). Paleoclimatic reconstructions (Bryson and Wendland 1967) suggest that Holocene changes in these patterns would also have transported moths from the montane coniferous forest to the western boreal forest. The source populations in the Rockies, however, would have changed as the location of the boreal forest changed in latitude with climatic fluctuations. The biological and physiographic evidence thus suggest that gene flow would be adequately described by a riparian model with a western source, at high elevation, in which colonists are driven east/northeast by the prevailing circulation patterns. Today, movements are probably between *C. biennis* and *C. fumiferana* in the northern Rocky Mountains. Migration in the opposite direction, although possible, would be less likely to be successful in effecting gene flow.

The absence of a fossil record cannot be used as evidence for the recency of the association between the insects and their hosts (for a variety of reasons, the recent North American lepidopteran fossils are poorly known [Howden 1975]). Several other lines of evidence support — or, at least, are not at odds with — the hypothesized model, however.

The results of isozyme studies reported by Stock and Castrovillo (1981) and Harvey (1985) indicate that distance, rather than substantial differences in biological traits, is a better indicator of isozyme-related

genetic difference among taxa. Western pine-feeding and fir- and spruce-feeding *Choristoneura* live in sufficiently similar environments or sufficient genetic exchange occurs between them to produce isozyme patterns that make them very dissimilar from the spruce budworm populations from Maine. The western spruce budworm populations tend to be highly variable genetically (Willhite and Stock 1983). Such a pattern probably results from a selection for locally adapted populations coupled with occasional environmental impediments to successful gene flow under current climatic and biotic conditions within their range. The development of clines in a few isozyme frequencies and apparently patternless variation in others of the spruce budworm (Harvey<sup>5</sup>) are not inconsistent with the model of combined gene flow and selection. Finally, repeated infusion of western genes from several genetically distinct sources would explain the larger variance in certain biological traits of the spruce budworm populations than those in the West. In a sense, the eastern gamodeme has become the estuary of the North American budworm genetic river.

Although eastern maritime coniferous forests of the early Holocene may have had a budworm population, the current behavior of populations in the modern forest (Blais 1985) suggests that the association is relatively new (Stehr 1964). The western spruce budworm also fluctuates in density (Shepherd, 1985), but chronic problems with this insect seem to be restricted to regions where the forest has become re-established on recently deglaciated lands. The reconstructions presented here suggest that the budworm-forest association may be only 8,000 to 10,000 years old in eastern North America and 7,000 years in the Pacific Northwest and adjacent Canada. From the meager records available, the Douglas-fir forests on the west side of the southern Cascades and the adjacent coastal ranges in California and Oregon — which remained unglaciated — do not seem to sustain protracted budworm outbreaks. This region, with its variation in physiography and biotic communities, may provide the setting in which to test our theories on budworm population biology.

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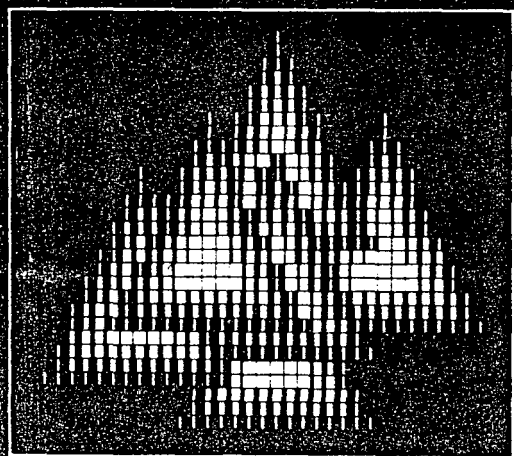
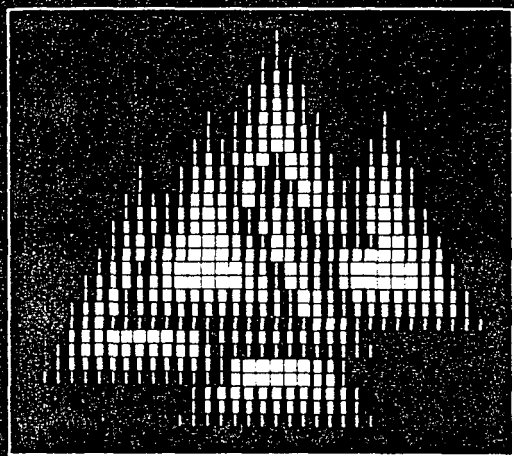
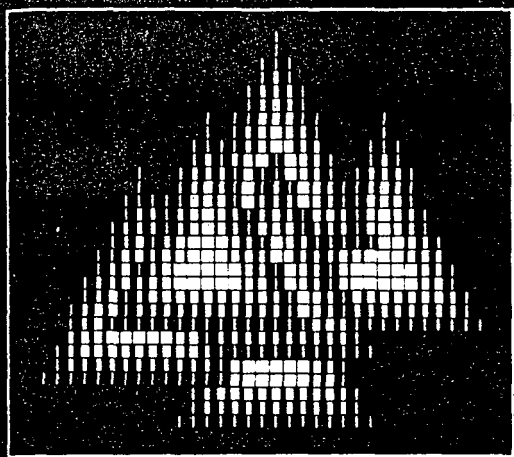
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