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Case History of Population Change in a *Bacillus thuringiensis*-Treated Vs. an Untreated Outbreak of the Western Spruce Budworm

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Abstract

Larval densities of the western spruce budworm *(Choristoneura occidentalis* Freeman) were monitored for 12 years (1984-95) on permanent sample plots in northeastern Oregon. The time series spanned a period of general budworm infestations when populations increased rapidly from low densities, plateaued for a time at high-outbreak densities, and then declined suddenly. Midway through the period (1988), an area with half of the sample plots was sprayed with the microbial insecticide *Bacillus thuringiensis {B.t.)* in an operational suppression project. The other sample plots were part of an untreated area. In the treated area, *B.t.* spray reduced numbers of larvae by more than 90 percent; however, populations returned to an outbreak density within 3 years. In the untreated area, populations remained at outbreak densities and continued to fluctuate due to natural feedback processes. Natural decline of the population (1992-95) in the monitored area was largely unexplained and coincided with an overall collapse of the budworm outbreak in the Blue Mountains.

Keywords: Western spruce budworm, *Choristoneura occidentalis, Bacillus thuringiensis,* insect defoliators, monitoring populations, population dynamics.

Introduction

Outbreaks of western spruce budworm *(Choristoneura occidentalis* Freeman) are regular phenomena in the interior mixed-conifer forests of the Pacific Northwest. Most budworm outbreaks are relatively long lived, sometimes lasting many years before ending from natural causes (Stipe 1987, Swetnam and others 1995). To prevent damage and mortality of trees, attempts often are made to suppress on-going infestations by spraying with chemical or biological insecticides (Dolph 1980, Fellin and Dewey 1980, Sheehan 1996a). Direct suppression usually is initiated after budworm populations have reached high densities and tree defoliation is

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already severe. Although suppression efforts can have immediate benefits, experience has shown that they may afford only a brief "window of protection" because populations often rebuild in a short time to cause more defoliation (Fellin arid Shea 1985, Sheehan 1996b, Torgersen and others 1995). Eventual termination of outbreaks and lasting control of populations at low densities is achieved only over time by natural processes.

In 1988, we recorded such a resurgence when 164,371 acres (66 521 ha) of budworm-infested stands in the northern Blue Mountains were sprayed with the biological insecticide, *Bacillus thuringiensis* Berliner *(B.t).* This infestation was an extension of a massive budworm outbreak that began in northeastern Oregon in 1980, and at its peak in 1986, affected over 6 million acres in Oregon and Washington (Hadfield 1988; USDA 1988b, 1995). A series of permanent sample plots established for long-term monitoring of defoliator populations was located near the 1988 suppression project. By chance, half of the plots were within a spray unit that was treated with *B.t* and half were outside of the unit. Because we continued to monitor populations despite the suppression project, results from these plots provided a unique case history of outbreak trends in treated and untreated areas. Monitoring of the "untreated" plots was terminated eventually in 1992 when they became part of another spray program (Hadfield 1992). Paradoxically, after 1992, all outbreak populations of budworm in the Blue Mountains collapsed simultaneously from natural causes (Scott and Schmitt 1994, USDA 1995).

Methods

Description of Monitored Area and Sample Plots

Location of the monitored areas was ca. 25 miles (40 km) northwest of La Grande, Oregon, on the Umatilla National Forest. Forest composition was a mixture of grand fir *(Abies grandis* (Dougl. ex D. Don) Lindl.), Douglas-fir *(Pseudotsuga menziesii var. glauca* (Beissn.) Franco), ponderosa pine *(Pinus ponderosa* Dougl. ex Laws.), lodgepole pine *(Pinus contorta* Dougl. ex Loud.), western larch *(Larix occidentalis* Nutt.), and Engelmann spruce *(Picea engelmannii* Parry ex Engelm.). Sampled stands were dominated by grand fir and Douglas-fir, the primary hosts of western spruce budworm in the area. Elevation was ca. 4,000 to 5,000 feet (1200 to 1500 m).

Twelve permanent 5-acre (2-ha) plots were sampled in the monitored areas. Six plots fell in the southwestern part of the treated Tollgate Analysis.Unit (USDA 1988a), and six plots were in an untreated area east of the Meacham Analysis Unit (USDA 1988c) (fig. 1). The plots were spaced such that each group provided a representative sample of budworm populations on ca. 20,000 acres (8000 ha) of both a treated and untreated area.

Sampling Methods

The primary sampling unit on each plot was 25 to 50 host trees (grand fir and Douglas-fir). Density of budworm larvae was estimated annually in mid to late June by beating three 18-inch (45-cm) branch tips in the lower crown of each tree over a drop cloth. The mean number of larvae per three-branch unit for all trees was then calculated and converted by standard correction factors to mean density per square meter (1,550 in^2) of branch area in the, midcrown. .This "plot density" is a common index for expressing the abundance of budworm populations (Mason and Paul 1994). The mean of all plot densities in a monitored area constituted an index-of."population density each year for the respective area.

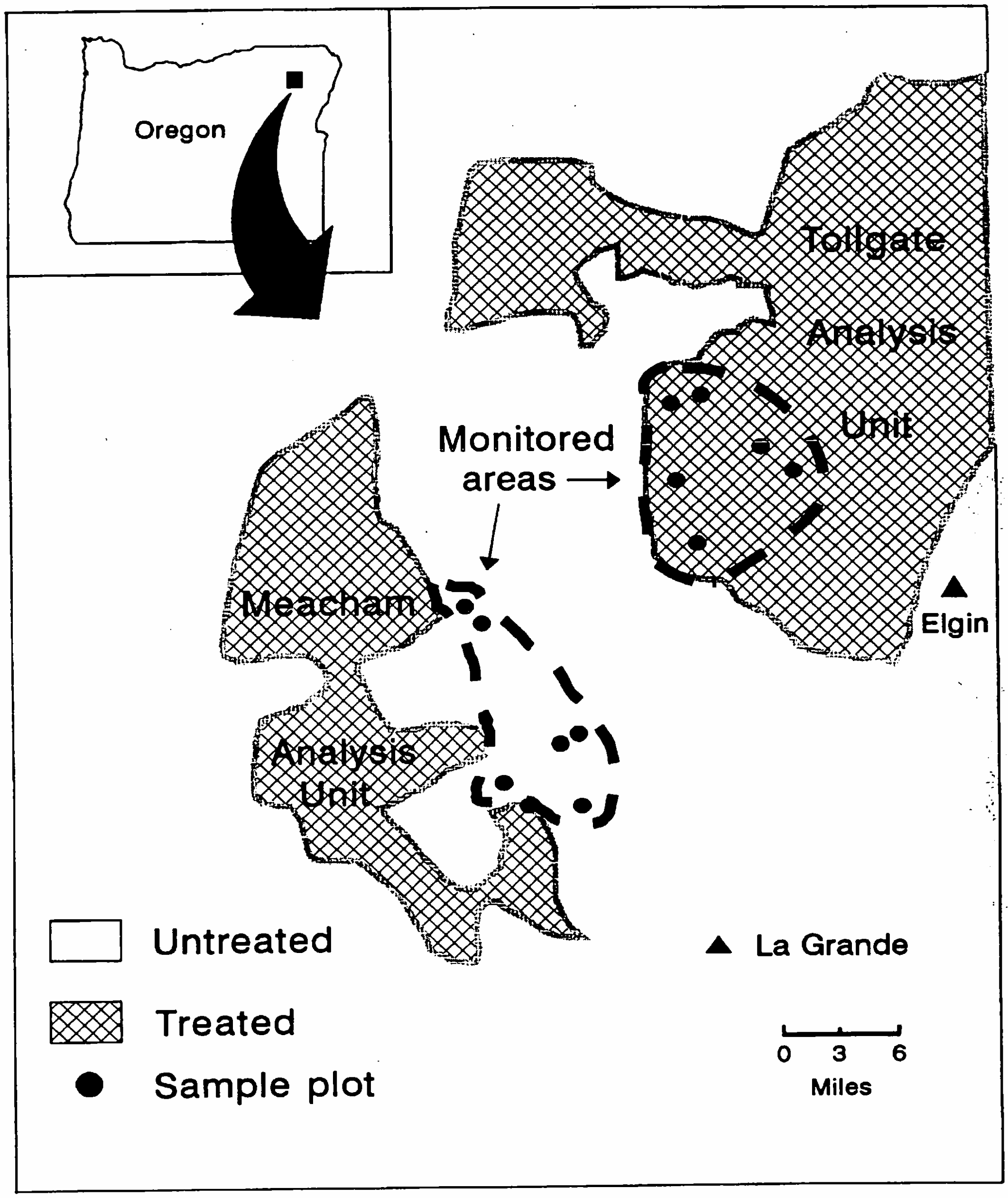

Figure 1—Geographic location of sample plots and monitored areas of *B.t.*-treated and untreated western spruce budworm populations.

Annual monitoring of budworm densities was initiated in 1984 and continued for untreated plots until 1992 and for treated plots until 1995 when budworm populations had virtually disappeared. Sampling was timed each year to coincide with the presence of a majority of instar IV larvae (nominal fourth instars). In 1988, plots were sampled in the third week of June immediately before treatment with *B.t* so that estimates of population density did not reflect the effects of spray.

Insecticidal Treatment

Bacillus thuringiensis is a microbial insecticide that after ingestion produces toxins fatal to budworm larvae. It has no contact toxicity or epizootiological characteristics (Fellin and Shea 1985). Treatment of the Tollgate Analysis Unit consisted of undiluted *B.t* (Thuricide 32LV)[1] applied at the rate of 16 BIU (billion international units)in 64 ounces per acre (4.7 L per ha). Application was by helicopter from June 15 to July 1, 1988 (USDA Forest Service 1988a).

Analyses

Trends of budworm density over time in treated and untreated areas were compared graphically by plotting data on a semilogarithmic scale. No analyses were made of data beyond 1992 when the "untreated" area became part of a new suppression project. Rate of change in density between two successive generations was estimated for each plot by an index of population trend in which the "trend index" in any year, t, was the simple ratio of plot density at t+1 to plot density at t (Southwood 1966). Dynamics of the untreated population were summarized during its release and outbreak mode by a phase plot of log rates of change over mean density and by fitting a nonlinear logistic model to the data (Berryman 1991, Berryman and Millstein 1990).

Results

Sampling Errors

Most population densities and trend indices in the monitored areas were estimated with standard errors less than 25 percent of the mean. The highest percentage standard errors were associated with the smallest mean values and, therefore, were less important because the magnitude of error was also small on a numerical scale (table 1).

Release Phase (1984-86)

Time-series plots of larval densities show that populations in both monitored areas grew steadily from very low densities in 1984 to peak outbreak densities by 1987 (fig. 2). Each population declined slightly between 1987 and 1988. During the period before treatment (1984-88), larval densities were slightly higher in the untreated area, but population growth rates were nearly the same for both areas (table 1):

Outbreak Mode in Untreated Area (1986-92)

Between 1986 and 1992, larval densities in the untreated area reflected the numerical behavior of populations in an outbreak mode as densities fluctuated above the defoliation threshold (30 larvae per square meter). The clockwise spiral of the phase diagram in figure 3A shows how population increases in this mode were limited at high densities, thereby causing fluctuations around a temporary equilibrium of ca. 160 larvae per square meter. This density probably reflected a threshold at which larvae competed seriously for food. Populations could be sustained only briefly above the equilibrium before depletion of foliage apparently generated a negative feedback that quick[y caused-numbers to return to a lower density. The dominant density-dependent effect during this stage of the outbreak was a direct feedback from initial density and accounted, for 80.4 percent of the variation in rate of change (fig. 3B).

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[1]The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product of service

Table 1—Mean densities and trend indices of western spruce budworm larvae (nominal fourth instars) in *B.t.*-treated and untreated monitored areas, 1984-95 (N = 6)

	Treated (1988)				Untreated			
Year	Mean midcrown density[a]	(SE)	Mean trend index[b]	(SE)	Mean midcrown density[a]	(SE)	Mean trend index[b]	(SE)
1984	2.00	(0.31)	7.62	(1.53)	2.58	(0.61)	21.22	(10.53)
1985	13.34	(0.75)	2.91	(0.29)	30.03	(6.23)	1.98	(0.44)
1986	38.23	(3.15)	4.40	(0.41)	45.86	(1.63)	3.67	(0.37)
1987	165.12	(15.24)	.48	(0.04)	166.59	(14.91)	.74	(0.09)
1988	81.29	(12.34)	.17	(0.04)	117.80	(9.62)	.84	(0.22)
1989	12.83	(3.54)	1.89	(0.36)	103.70	(30.70)	1.89	(0.17)
1990	22.74	(6.23)	5.58	(0.83)	173.75	(41.00)	1.85	(0.32)
1991	122.38	(29.22)	1.53	(0.38)	257.52	(10.26)	.76	(0.08)
1992	140.17	(17.39)	.02	(0.01)	193.31	(20.15)	—	
1993	2.48	(0.99)	.15	(0.06)	—[c]		—	
1994	.30	(0.12)	.35	(0.21)	—		—	
1995	.00	(0.0)	—		—		—	

[a] Number of larvae per square meter of branch area in the midcrown.
[b] Ratio of consecutive plot densities.
[c] Monitoring discontinued after 1992.

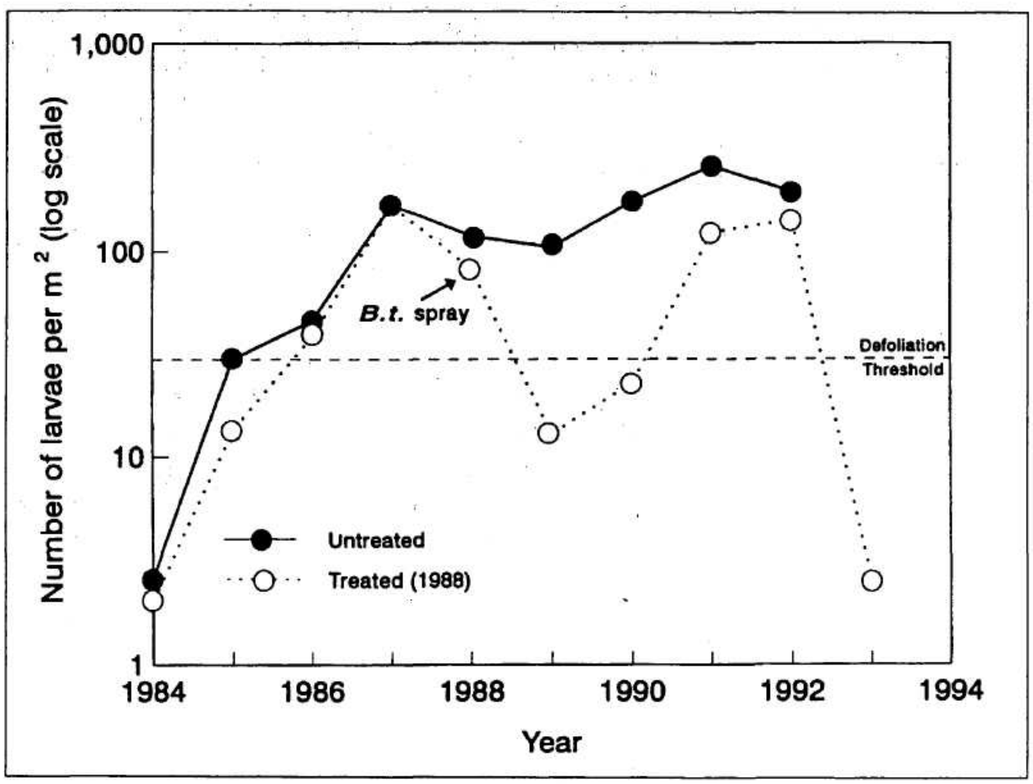

Figure 2—Time-series plots of mean densities of western spruce budworm populations in *B.t.*-treated and untreated areas.

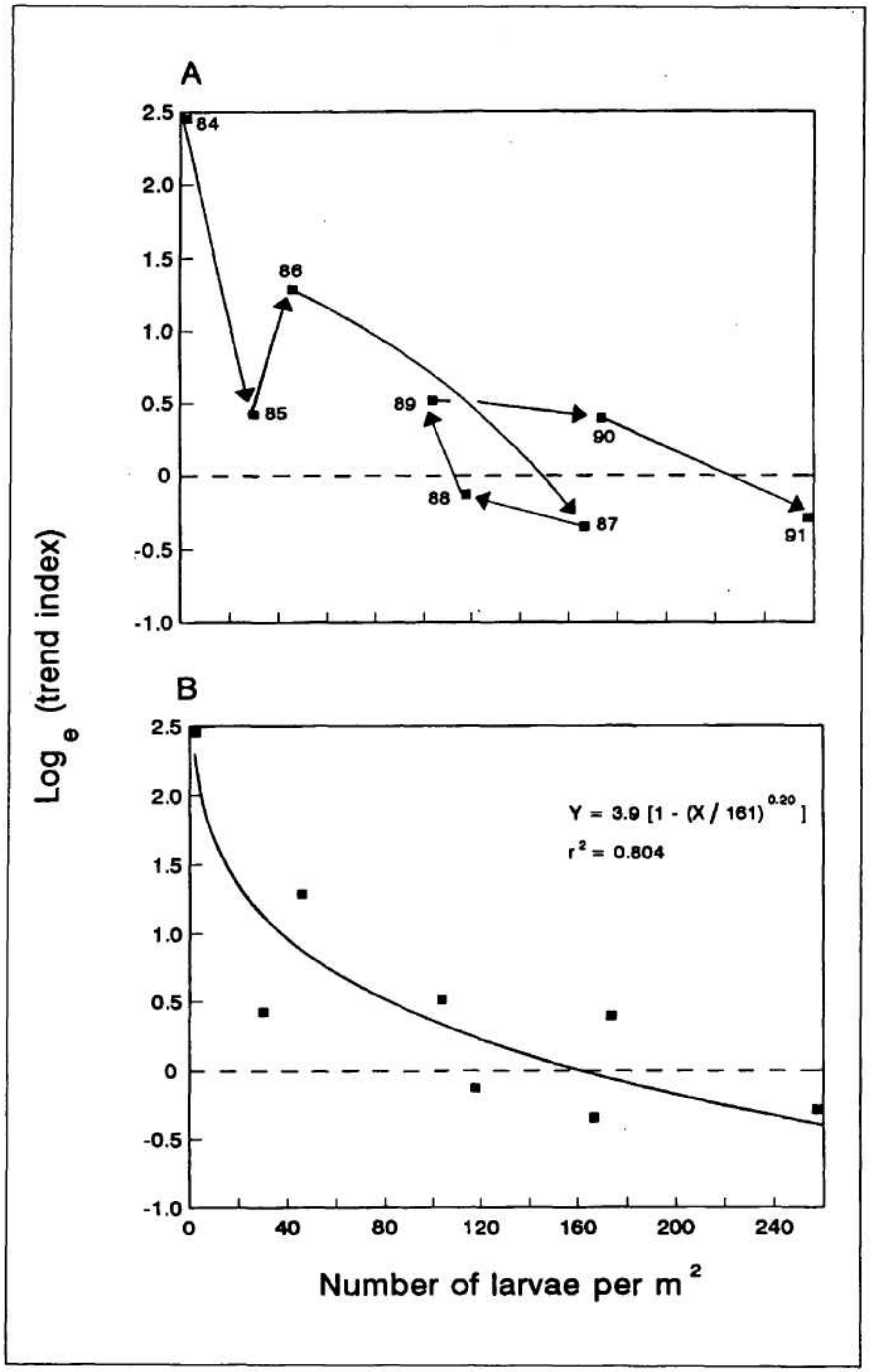

Figure 3—Dynamics of western spruce budworm population in untreated-monitored area: (A) phase diagram of population change, (B) feedback effect of initial density on rate of change.

Suppression of Treated Population (1988-89)

Our 1988 density estimate of 81.3 larvae per square meter (table 1) was identical to the prespray estimate for the southern portion of the Tollgate Analysis Unit made by independent project crews (Bridgewater 1988). After the unit was sprayed with *B.t.* in late June, postspray sampling by the same crews in July indicated a more than 90-percent reduction in larval density. Effectiveness of spray in the treated area subsequently was confirmed by an 84-percent drop in budworm densities between the 1988 and 1989 generations (table 1) and a significant decrease in the percentage of area defoliated (Sheehan 1996b). Populations declined only slightly during the same period in the untreated area (fig. 2).

Recovery in Treated Area (1989-92)

Except for the first year after treatment, population increases during the recovery period were higher each year in the treated area than in the untreated area. After the sharp decline between 1988 and 1989, density of the sprayed population increased again in 1990. This was followed in 1991 by a dramatic upsurge to a higher density than was originally treated in 1988 (fig. 2). Rates of population change as reflected by trend indices in 1989 and 1990 were not unlike those during the release phase 5 years earlier when populations were first building up (table 1). Density increased further between 1991 and 1992, although at a slower rate. After being temporarily checked by the *B.t.* treatment, populations returned in just 3 years to the equilibrium density of the outbreak mode.

Decline Phase (1992-95)

The last year of outbreak populations in both monitored areas was in 1992. At this time, the previously untreated area was included in a new suppression project (Hadfield 1992), and further monitoring was discontinued. Numerical trend of the untreated population was slightly down after peaking in 1991, but this change did not differ from normal fluctuations expected at high-outbreak densities (table 1, fig. 3B). As noted above, population density in the treated area was still increasing from 1991 to 1992 when the final leg of recovery after spraying was completed. The sharp downturn in 1993, therefore, was nothing short of a natural "population crash" as densities in the former treated area decreased 98 percent between 1992 and 1993 (table 1). This decline continued at nearly the same rate for the next 2 years until no larvae were recovered on any of the sample plots in 1995 (table 1).

Discussion

The quick return of the treated population to outbreak numbers raises a question about the extent to which colonizing individuals from outside the control area contributed to the recovery. Resurgence of western spruce budworm populations after insecticide treatment has been observed often (Marsden and others 1985, Stipe and others 1984, Torgersen and others 1995). It also is well known that gravid moths in outbreaks tend to disperse from defoliated stands and oviposit on trees with more foliage (Campbell 1993). Newly treated stands in which foliage has been protected temporarily, therefore, are especially susceptible to reinvasion by moths from adjacent untreated stands. Such moth inflights sometimes have cancelled the beneficial effects of .control programs within 1 to 2 years of treatment (Stipe and others 1984).

Resurgence also could originate primarily from the surviving population already in place after treatment. The findings in this study clearly show that posttreatment recovery rate was similar to the rate of initial population buildup in the monitored areas when mass moth immigration, presumably, was not as strong a factor in affecting population change. Rapid recovery would seem to be capable of springing from the residual population alone, particularly if the number of density-dependent natural enemies had not increased. A return to outbreak density in 2 to 3 years, therefore, may not be that different from what occurs during the release phase in a conventional population buildup (Campbell 1987). It is more likely, however, that recovery usually will be accelerated by moth immigration whenever untreated infestations are adjacent to treated areas.

The dominance of fast-acting negative feedback in the untreated area indicates that population trend during release and the outbreak mode was not strongly influenced by insect parasitization which normally has a delayed response to host density. Budworm populations apparently were less constrained by biotic regulation during this period than by physical factors related to overcrowding like competition for food and space. Analyses of longer time series spanning periods of low- as well as high-density populations are needed to evaluate the contribution of higher order delayed feedback in budworm systems (Berryman and others 1986).

The data set reported here is a rare quantitative record of a complete budworm outbreak in one locality. It further demonstrates the necessity of monitoring populations continuously to document all phases of an infestation (Mason and Paul 1993). Monitoring data provide much insight into the numerical behavior of populations; however, they are inadequate by themselves for detecting the specific processes that actually determine changes in density. The 1993 crash, for example, was completely unexpected insofar as prior population trends gave no clue of the downturn that followed. The steady decline of densities after 1992 was part of a general collapse of budworm populations that occurred in the Blue Mountains and throughout much of the Pacific Northwest (Scott 1994, Scott and Schmitt 1994, USDA Forest Service 1995). Synchronous collapses of budworm *(Choristoneura* spp.) outbreaks like these have long been an enigma and still are largely unexplained. Detailed information on the complex interrelations affecting survival in key life stages likely will be required before their causes are revealed (Campbell 1993, Royama 1992).

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