1987

Western Spruce Budworm

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In 1977, the United States Department of Agriculture and the Canadian Department of the Environment agreed to cooperate in an expanded and accelerated research and development effort, the Canada/United States Spruce Budworms Program (CANUSA), aimed at the spruce budworm in the East and the western spruce budworm in the West. The objective of CANUSA was to design and evaluate strategies for controlling the spruce budworms and managing budworm-susceptible forests to help forest managers attain their objectives in an economically and environmentally acceptable manner. This manual is one in a series on the western spruce budworm.

canusa

Canada
United States
Spruce Budworms
Program

May 1987

Western Spruce Budworm

Martha H. Brookes, Robert W. Campbell, J. J. Colbert,
Russel G. Mitchell, and R. W. Stark, Technical
Coordinators[1]
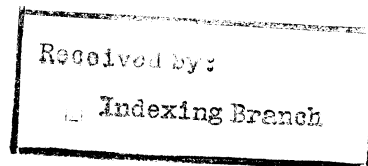
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Experiment Station in Corvallis, OR, and is now a consulting entomologist in Syracuse, NY. J. J. Colbert
and Russel G. Mitchell are Program Manager and Applications Coordinator, respectively, of CANUSA-
West in Portland, OR. R. W. Stark was formerly Program Manager of CANUSA-West and is now at the
University of Idaho, Moscow.

Despite extensive aerial spraying, outbreaks of the spruce budworm in the East and the western spruce budworm in the West have caused considerable damage to susceptible forests and show no signs of abating. As many as 900 million acres (365 million ha) have been infested in 1 year in the eastern part of the continent. About 5 million acres (2 million ha) are infested annually in the West, and about 247 million acres (100 million ha) of western forests are considered susceptible. A new approach to budworm problems was clearly needed—one that could include direct suppression but would emphasize forest management to reduce susceptibility.

In 1977, the United States Department of Agriculture and the Canadian Department of the Environment agreed to pool the expertise and facilities of both countries; together they embarked on a 6-year research and development program in 1978. Objectives were to design and evaluate economical and environmentally acceptable strategies to suppress the budworms and to manage forests susceptible to them. Part of the planning was to assure that new information and technology would be available for application by forest managers as soon as possible.

So that the information would be in forms most useful to forest managers, administrators in the western segment of the program (CANUSA-West) appointed a working group (see appendix 1) to plan the distribution of research results to all appropriate audiences. Meeting annually, the group identified the major audiences and developed a framework for reaching them. A major part of the effort is a series of three books. This book is a synthesis of current knowledge about the insect and its hosts. It summarizes most of the known information on the western spruce budworm and provides background for the recommendations contained in two management books: *Managing Trees and Stands Susceptible to Western Spruce Budworm*, and *Western Spruce Budworm and Forest-Management Planning*. These management books are intended to stand alone to provide easy access to just the information needed by their specialized audiences—forest managers and planners—to support decisions related to budworm. When detailed information is sought, the user can consult the comprehensive index in this volume. The many citations provide a key to the technical and scientific literature.

> For convenience, "budworm" or "western budworm" in this book means the western spruce budworm, *Choristoneura occidentalis* Freeman. The spruce budworm, *C. fumiferana* (Clemens), is called "eastern budworm."

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Chapter 1

History

1.1 Introduction
Lawrence E. Stipe[1]

The first budworm outbreak reported in the West was in 1909 in British Columbia (Mathers 1931, Unger 1983). It was preceded by nearly 100 years of recorded eastern budworm activity; thus, many of the sampling techniques and management practices used in the West had their origins in the East. Although host differences between the East and West were well known from the start, only recently have the many biological differences between the eastern and western budworms been recognized.

1.2 Outbreak Chronology

Because budworm is a native insect, its outbreaks are nothing new to western forest ecosystems. From 1922 through 1946, outbreak information came from ground surveys and rangers' reports (Johnson and Denton 1975). These reports mainly described the general locality of outbreaks, with only scattered data on size and trend. From 1947 to the present, most areas have a fairly complete defoliation history from aerial detection surveys. Many infestations lasted only a few years, but others have persisted for over 25 years.

1.2.1 1922 to 1946

Most outbreaks from 1922 to 1946 were small and widely scattered. Early outbreaks subsided quickly and resulted in little or no damage. These infestations interested forest entomologists, but land managers had no means for suppression nor did they consider action necessary.

Several small outbreaks in the Pacific Northwest were reported in 1929, 1932, 1941, and 1942 (Dolph 1980); all subsided naturally. The first extensive outbreak developed in 1942 in the Okanogan National Forest in northeastern Washington. Over 200,000 acres (over 80 000 ha) were defoliated before a natural collapse in 1948. In 1944, an outbreak began in the Blue Mountains of northeastern Oregon and, before subsiding, covered the entire host type in the Blue Mountains.

The first budworm outbreak reported in the northern Rockies of the United States was in the early 1920's near Priest Lake, Idaho, and many others occurred over the next 25 years throughout the region. This long string of outbreaks began in Yellowstone National Park during 1922 and was followed in 1924 by outbreaks on the Clearwater, Nezperce, and Coeur d'Alene National Forests in Idaho. Then in 1925, outbreaks appeared in the Lewis and Clark, Beaverhead, Gallatin, and Helena National Forests in Montana, followed in 1926, 1927, and 1930 by outbreaks in the Bitterroot, St. Joe, and the Lolo National Forests, respectively. Although most of these outbreaks subsided quickly, the Nezperce and Helena outbreaks endured until 1946. Many other outbreaks occurred from time to time—in the Bitterroot (1930–31, 1934–35, and 1938), Custer (1935–40), Deerlodge (1945–46), Flathead (1933 and 1942–46), Kootenai (1939), and Lolo (1938–41) National Forests.

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[1]Authors' affiliations are given in appendix 2.

In the central Rocky Mountains, an outbreak began in 1922 in Cody Canyon in the Shoshone National Forest; it subsided in 1936. Except for small outbreaks in the Bighorn (1931) and San Juan National Forests (1935–36), no reported outbreaks occurred until 1941, and all subsided by 1945.

In the Southwest, the first outbreak occurred in northern New Mexico from 1922 to 1935 in the Carson National Forest. It was followed by an outbreak in the Santa Fe National Forest from 1924 to 1930 and isolated infestations in the Cibola National Forest during 1934 and 1935. The next major outbreaks occurred from 1940 through 1946 in the Carson National Forest and from 1941 through 1945 in the Cibola National Forest. An isolated infestation was recorded in the Cibola National Forest in 1949.

The early outbreak history in the intermountain region is similar to that in the northern U.S. Rockies. From 1922 through 1931, outbreaks occurred almost annually in the Boise and Payette National Forests and less frequently in the Challis, Sawtooth, Targhee, and Bridger–Teton National Forests. No significant outbreaks were reported from 1932 until the mid-1950's.

After the first report in 1909 in western Canada, no other outbreaks occurred until 1926, when scattered defoliation was reported in the Vancouver region. Later outbreaks occurred during 1927–30, 1938, 1943, and 1944. The first outbreak in the interior region occurred during 1943–46 near Kamloops.

Western budworm outbreaks have never been reported from Alaska.

1.2.2 1947 to 1982

Aerial-survey techniques were first developed during the late 1940's. Aerial detection gave entomologists a means of tracking outbreaks over time, providing not only an important historical record of occurrence by geographic area but also defining areas for biological and impact-evaluation surveys. The oldest continuous aerial survey began in Oregon and Washington in 1947 (Dolph 1980). Most National Forests and Regions have nearly complete aerial-survey records since 1968. The value of the data collected from aerial surveys increases as new data are added.

Acres of visible defoliation, determined by aerial survey, can be used to show outbreak trends from 1947 through 1982. Combining similar areas—with boundaries based on defoliation trend, forest type, and climate—resulted in 16 zones (fig. 1-1) that include the following National Forests, plus adjacent Federal, State, and private forest lands:
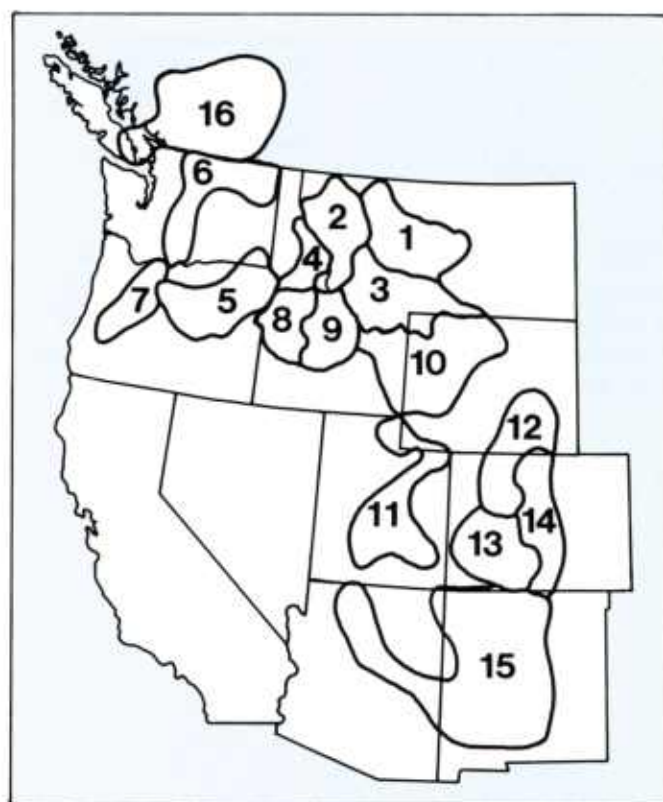
Figure 1-1—Zones of infestation based on aerial defoliation trend, forest type, and climate.

Zone	Zone name	National Forest
1	North Central Montana	Helena, Lewis and Clark
2	Clark Fork	Lolo, Bitterroot, Flathead, Kootenai
3	Yellowstone	Deerlodge, Beaverhead, Gallatin, Custer, Yellowstone National Park
4	Clearwater	Clearwater, Nezperce, St. Joe
5	Blue Mountains	Malheur, Ochoco, Umatilla, Wallowa–Whitman
6	Inland Washington	Okanogan, Wenatchee, Kaniksu, Colville
7	Central Cascades	Willamette, Mt. Hood, Deschutes
8	Boise– Payette	Boise, Payette
9	Upper Salmon River	Salmon, Challis, Sawtooth
10	Upper Snake River	Bridger–Teton, Targhee, Shoshone
11	Intermountain	Dixie, Manti–LaSal, Fishlake, Ashley
12	Central Rockies	Medicine Bow, Routt
13	Southern Rockies	Grand Mesa, Uncompahgre, Gunnison, Rio Grande, San Juan
14	Front Range	Roosevelt, Arapahoe, Pike, San Isabel
15	Southwest	Kaibab, Coconino, Sitgreaves, Apache, Gila, Fremont, Cibola, Santa Fe, Carson, Lincoln, Grand Canyon National Park
16	Canadian	Vancouver, Kamloops, Nelson

Visible defoliation trend from aerial-survey data is shown by zone for the period 1947 to 1982 (fig. 1-2). A composite map shows host type and combines all defoliation data recorded from aerial surveys between 1947 and 1983 (fig. 1-3).
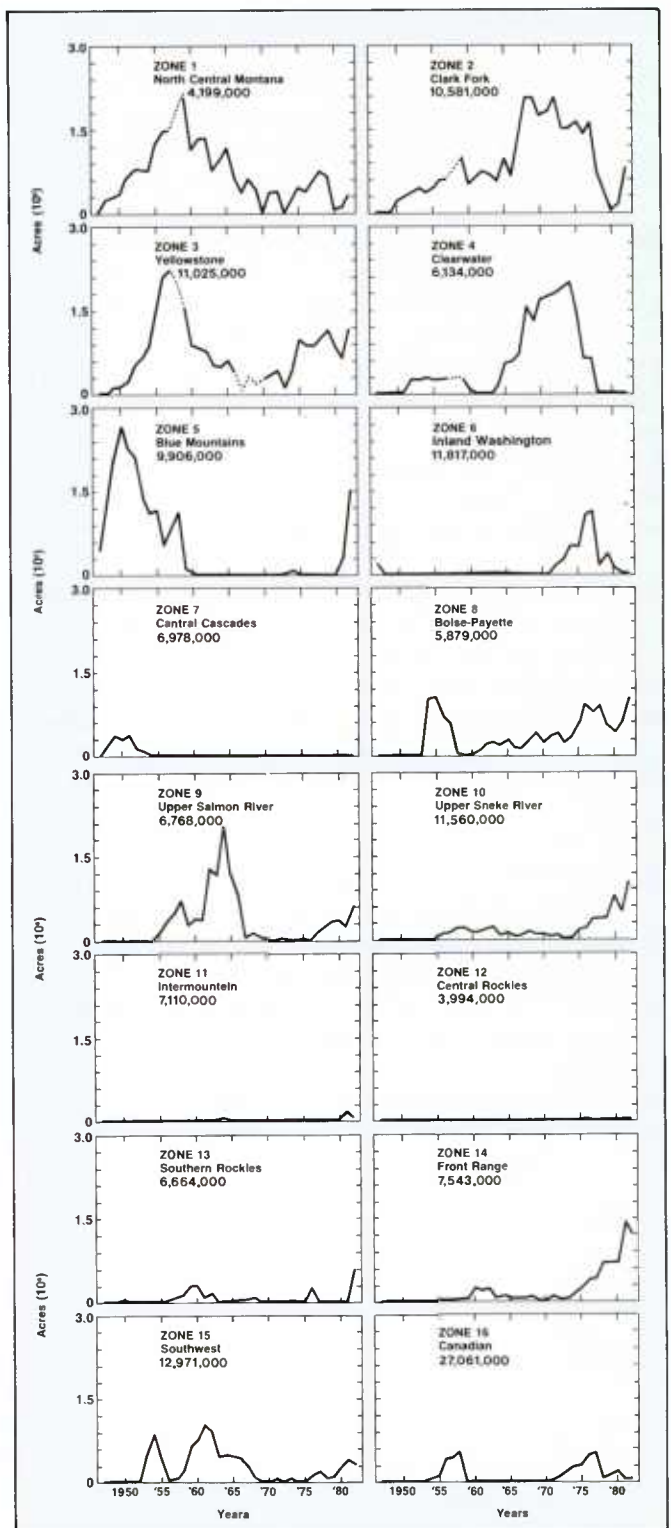
Figure 1-2—Defoliation trend by zone (interpolated missing data are indicated by dotted lines). Acreage of host type is given for each zone.

Figure 1-3—Area of host type and defoliation recorded from aerial surveys, 1947 to 1983.

The sporadic nature of early outbreaks, weighed against widespread outbreaks of tree-killing bark beetles, left budworm low in research priority. A serious and widespread outbreak that began in Oregon in 1944 stimulated research in the Western United States. In 1953, an analysis of forest-insect research needs by the Oregon State Board of Forestry assigned priority to economic suppression of the budworm. Although limited studies on budworm biology were conducted at USDA Forest Service Experiment Stations in the United States and at Forest Insect Laboratories (later Forest Research Centres) in Canada, primary interest was in detecting outbreaks by ground and aerial surveys and applying direct suppression when serious tree damage appeared imminent. In fact, no major change in resources devoted to budworm research occurred in the United States until the advent of CANUSA.

What follows is a brief outline of research history. Other historical information is contained in chapters 2, 3, and 7.

1.3.1 Early Work

Many early observations on budworm outbreaks are found in reports by the Canadian Forest Insect and Disease Survey, the Cooperative Economic Insect Report, and in Hopkins U.S. file records maintained at western USDA Forest Service Experiment Stations. Early observations were recorded on outbreaks in lodgepole pine in Wyoming (Balch 1930 unpubl.) and on subalpine fir in British Columbia (Mathers 1932). Early suppression of budworm was attempted in Wyoming by Evenden (1932 unpubl., 1933 unpubl.) and in Colorado by Orr and Wygant (1945 unpubl.).

Starting in 1943, mass collections of budworm were made in British Columbia, Colorado, and Oregon for propagation and introduction of parasites into infestations of the eastern budworm (Wilkes 1946, Wilkes and others 1948). Several later papers described larval characteristics and adult habits of dipterous parasites (for example, Coppel and Maw 1954a, 1954b) and provided a key to adults (Coppel 1960).

With the rapid increase of infestations in Oregon, top priority was given to development of an aerial-spray method for direct suppression. A pilot test in eastern Oregon during 1948 showed that applications of 1 lb of DDT in 1 gal of fuel oil per acre (1.1 kg/9.3 l per ha) caused high budworm mortality (Eaton and others 1949). Based on this test, operational suppression began in Oregon in 1949, in Montana in 1952, and in other regions subsequently.

Budworm development, host phenology, and parasitism were studied in connection with the 1948 test, and mass collections were made in 1949 of large larvae and pupae to assess parasite abundance. In 1950, fixed plots were established for measuring population trends and changes in budworm parasitism. Similar but less intensive studies were begun in sprayed areas in 1951 and continued through 1959 (Carolin and Coulter 1971). As outbreaks appeared, attempts were made to define densities of overwintering larvae (Denton 1951 unpubl., McKnight 1969a, Terrell 1959, Whiteside and Gruba 1955 unpubl.). Egg-mass sampling was found to be more reliable than sampling overwintering larvae for estimating the spring population in buds (Carolin and Coulter 1959 unpubl.).

Ecological studies were rare during these early outbreaks. Wagg (1958) investigated effects of temperature and relative humidity on rate of growth of budworm larvae in Oregon. In British Columbia, studies were made on ecological factors affecting the 2-year budworm; Shepherd (1961) compared its developmental requirements with those of the western budworm.

Around 1955, an ambitious study was initiated at the Sault Ste. Marie Laboratory, Canadian Forestry Service, in cooperation with the Entomology Research Institute, Canada Department of Agriculture, to characterize different forms of budworms in North America. Using larval collections from many outbreaks, the investigators employed innovative genetic techniques along with traditional taxonomic research to separate many of the forms into species and species groups (Freeman 1967, Stehr 1967).

Also starting around 1955, small expansions in the USDA Forest Service research and development programs in the West led to a more unified and intensified effort to solve budworm problems. Developing improved sampling techniques was emphasized. As DDT fell into disfavor, efforts increased to find a suitable substitute. Aerial-spray tests were resumed in 1963 and continued through 1981. This struggle for safe but effective insecticides gave emphasis to the need for an insecticide-screening project, which was set up at the Pacific Southwest Forest and Range Experiment Station, Berkeley, CA, in 1963.

In Canada, insecticide screening and recommendations for field use were the responsibility of a centralized national institute—in the early years, the Chemical Control Research Institute, Ottawa. In the 1970's, it was combined with the Insect Pest Management Institute to form the Forest Pest Management Institute at Sault Ste. Marie, ON.

As of 1973, budworm outbreaks were at low ebb in most of the Rocky Mountain area, but they were showing signs of increase in the Pacific Northwest. A new sequence of outbreaks was underway by 1975, new insecticide tests were being conducted, and a new approach to budworm research was sorely needed.

1.3.2 Centralized Planning

In Canada, forest-insect research by the Forest Biology Division of the Department of Agriculture dominated forestry research for many years, and planning was much more centralized than in the United States. When the division was placed in the Canadian Forestry Service, the emphasis on insect research was reduced, but centralized planning continued.

Starting in 1945, preliminary research results were published in the Forest Insect Investigations Bimonthly Progress Report; budworm research was well represented. In the United States, forest-insect research was mainly in the Bureau of Entomology and Plant Quarantine; after 1953, the work was shifted to the USDA Forest Service. Studies were directed toward current regional problems, which fragmented effort and limited scope.

6

Around 1955, the budworm problem in the United States led to similar study assignments at several Forest Service Experiment Stations, and the work was coordinated by the Intermountain Forest and Range Experiment Station. A workshop in 1965 brought together eastern and western researchers, who recommended a centralized, coordinated, countrywide approach.

The USDA Forest Service recommended in 1973 that forest-insect research be consolidated on a few insects of major importance (Cutler 1978). The Department of Agriculture unveiled plans for accelerated research on three forest insects—the gypsy moth, the Douglas-fir tussock moth, and the southern pine beetle. As these programs ended, budworm outbreaks were expanding in both eastern and western North America; the stage was set for an international effort.

1.3.3 CANUSA Program—A Coordinated Approach

Objectives of the CANUSA Program were briefly described in the introduction. Several steps were taken to coordinate and stimulate activities as CANUSA started and as it progressed.

The program provided an extensive bibliography on the budworms (Jennings and others 1979, 1981, 1982, 1983), and an annual list that included abstracts of progress reports and an index of investigators cross-referenced by research activity.

The main goal of CANUSA-West was to develop a decision-support system to collect, process, and display the information required for management decisions (Twardus and Brookes 1983 unpubl.). Because facilities, data collection, and objectives are unique to an organization, CANUSA sought advice from resource managers to assure that the information would reach, fit into, and improve an organization's decision-support system.

Directing research and development activities included planning for getting their results to users. A working group, representing a wide spectrum of potential users plus communications experts, continually monitored research and developed plans for assuring that applicable research results would get to those who need them. The working group reviewed and updated the technology transfer plan when appropriate. This group—and the five working groups responsible for the other target areas—played a significant role in coordination of activities through constant communication and regular meetings.

CANUSA-West has sponsored 20 to 30 studies each year, about half within the USDA Forest Service and Canadian Forestry Service and half at 11 universities in the United States and Canada. An evaluation of an earlier accelerated program on the Douglas-fir tussock moth concluded that two to four times the results were obtained than would have been expected if a business-as-usual approach had been taken (Allen and others 1982). Major advantages include increased funding, enhanced cooperation between research and application institutions, and the synergism that occurs when a critical mass of scientists addresses a specific problem (Allen and others 1982).

1.4 Budworm Management
Lawrence E. Stipe

Forest managers have had three broad options for dealing with western budworm: do nothing, use direct suppression, or treat silviculturally (USDA Forest Service 1977 unpubl.). Emphasis and use of these options has varied greatly as a result of research findings, management experience, and changes in public interest. More recently, these three options are used in concert in what is called integrated pest management (IPM). In any given area, implementation of IPM may include any combination of these options. Site-specific objectives determine how the options will be used.

After World War II, aerial-application technology was improved and DDT, a broad-spectrum chlorinated hydrocarbon, was available. These developments led to a technique that provided foliage protection over large areas. Management actions to suppress budworm began in the late 1940's; by the early 1950's, several million acres had been sprayed with DDT.

1.4.1 Rationale and Objectives

After a successful test of DDT against budworm in 1948, pest managers were quick to dismiss the do-nothing option (Eaton and others 1949, Fellin 1983). Because silvicultural options were not well defined or understood, the only alternative considered was spraying. Because budworm was native and widespread, no attempt was ever made to eradicate it. Although eradication was suggested, the primary objective was to return outbreaks to innocuous densities.

Two strategies considered during the DDT era were foliage protection and population reduction. Population reduction, in which success is determined by percent mortality and not by the residual population, was generally selected. Mortality figures were generally not adjusted to account for natural mortality. Although foliage protection continues to be widely used in the East, it has found little use in the West. Population reduction is still the main strategy used in the West, but project success is sometimes determined by reaching a targeted residual density. If mortality rates are used, they are adjusted for natural mortality.

1.4.2 Chemical Insecticides

Most pesticides used in managing forest pests were originally developed for use in agriculture. Before DDT, materials tested for budworm suppression were generally ineffective or not suited for large-scale use.

DDT is a broad-spectrum pesticide with long residual activity. These qualities made it attractive for suppression of many forest insects.

Through improvements in application technology and reduced costs after World War II, DDT at 1 lb/acre (1.1 kg/ha) soon became the standard treatment. By the mid-1940's, DDT had been used against the Douglas-fir tussock moth and the eastern budworm. It was tested against budworm in 1948 near Heppner, OR, and first used operationally in 1949. The operational use of DDT for budworm suppression in the Western United States from 1949 through 1964 is summarized by Forest Service Region and year (table 1-1). DDT was never used operationally in Western Canada.

In the early 1960's, concern about the widespread use of DDT began to build, with ever-increasing opposition to large-scale aerial spray programs. In 1963, the President's Science Advisory Committee recommended that Government agencies curtail the use of persistent insecticides (Carlson and others 1983). No operational programs were conducted from 1967 through 1975. The period was characterized by decreased budworm activity in most areas, reevaluation of suppression philosophy, extensive testing of ultralow-volume application technology, and increased public concern. The DDT controversy climaxed in 1972, when DDT could no longer be used without special approval from the Environmental Protection Agency (EPA).

Table 1-1—Operational use of DDT from 1949 to 1964 in the Western United States[1]

	USDA Forest Service Region					
Year	Northern	Rocky Mountain	Southwestern	Intermountain	Pacific Northwest	Total
	Acres					
1949	—	—	—	—	267,000	267,000
1950	—	—	20,400	—	933,300	953,700
1951	—	—	—	—	926,600	926,600
1952	—	—	—	—	664,200	664,200
1953	135,210	—	4,000	—	369,200	508,410
1954	—	—	6,400	—	67,700	74,100
1955	372,650	—	453,133	837,210	620,900	2,283,893
1956	885,250	—	6,000	475,890	—	1,367,140
1957	784,680	—	—	660,630	—	1,445,310
1958	—	—	100,000	—	818,000	918,000
1959	126,880	—	—	—	—	126,880
1960	117,850	—	—	—	—	117,850
1961	—	—	—	—	—	—
1962	451,760	84,885	444,790	—	46,200	1,027,635
1963	415,120	5,280	568,970	190,000	—	1,179,370
1964	—	—	—	526,980	—	526,980
						12,387,068

[1]DDT was never used operationally for budworm suppression in Western Canada.

The Forest Service initiated an intensive screening program to evaluate alternative insecticides. This work and that of many manufacturers and others resulted in registration of several other materials by EPA. Chemical insecticides currently registered for aerial application for budworm suppression are acephate, carbaryl, malathion, mexacarbate, and methomyl. Methomyl and naled are registered for ground application. These products have relatively short residual lives and are far less damaging to nontarget organisms than was DDT. In Canada, acephate, aminocarb, carbaryl, fenitrothion, and triclorfon are registered for aerial application.

Malathion was the first insecticide to replace DDT for budworm suppression. It was used in 1966 in the Carson, Beaverhead, and Gallatin National Forests. Further testing and operational use ended in 1966, except for an operational project in eastern Washington during 1976. Poor results with malathion have been common; further use is unlikely without additional testing. Carbaryl quickly replaced malathion for operational use. First used operationally in 1976 in Forest Service Region 6 (Pacific Northwest), carbaryl is currently the most widely used material for budworm suppression in the West.

Acephate is attractive for use near streams and lakes because of its safety. It was first used operationally in Idaho in 1979 and in Oregon in 1982. Mexacarbate was extensively field tested from 1966 to 1972 but was not used operationally until 1983 in Oregon.

1.4.2.1 Experimental Projects—Except for two small field tests with toxaphene and dieldrin in 1949, DDT was the only material tested until 1963. Since 1963, many insecticides have been field tested using aerial and ground application. These projects not only provided the efficacy data for many materials but also gave managers an opportunity to test and improve application technology. Table 1-2 summarizes the experimental use of aerially applied chemical insecticides for budworm suppression from 1948 to 1980.

Except for the early work with lead arsenate and DDT, ground-application techniques were generally ignored until recently. Since 1976, experiments with ground application have evaluated carbaryl, acephate, pyrethrins, and diflubenzuron. Tests in 1979 and 1980 also showed that early ground applications of carbaryl and acephate were effective in protecting Douglas-fir cones and seeds from budworm damage (Stipe and Green 1981, Stipe and Hard 1980).

An inoculation technique was first tested in 1978 near Cascade, ID (Markin 1979b unpubl.). A powdered formulation of acephate, implanted in the lower trunk before budburst, was translocated through the tree to the expanding bud tissues. Further tests with both powder and liquid formulations of acephate have used both implants and pressurized injectors (Reardon, personal communication).

Table 1-2—Experimental use of aerially applied chemical insecticides from 1948 to 1980 in the Western United States

Year	National Forest	Pesticide	Rate/acre[1]	Acres
1948	Umatilla	DDT	½, 1, 2	4,200
1949	Willamette	DDT	½, ¾, 1	3,600
	Umatilla	Toxaphene	1	900
	Umatilla	Dieldrin	¼	300
1951	Wallowa–Whitman	DDT	¼, ½, ¾	12,000
1952	Bitterroot	DDT	1	12,000
1958	Helena	DDT & Genite	1 + 1, 1 + ½	18,200
1963	Carson	Dimethoate	⅛, ¼	395
	Bitterroot	Malathion	½, 1	13,550
	Salmon	DDT	½	16,500
	Targhee	Carbaryl	.8, 1.6	5,000
	Lolo	Phosphamidon	1	5,000
1964	Helena	Malathion	¾	26,290
	Deerlodge/Lolo	Malathion	¾	131,410
	Lolo	Malathion	9 oz	160
	Salmon	Dimethoate	¼	1,080
	Salmon	Mexacarbate	1.6 oz	60
	Salmon	Pyrethrins	.01, .03	60
	Salmon	Dichlorovos	.1	20

Table 1-2—Experimental use of aerially applied chemical insecticides from 1948 to 1980 in the Western United States (continued)

Year	National Forest	Pesticide	Rate/acre[1]	Acres
1965	Bitterroot	Mexacarbate	2.4 oz	1,080
	Bitterroot	Naled	6.4 oz	1,160
	Gallatin	Malathion	13.0 oz	640
	Lewis & Clark	Malathion	9.0, 13.0 oz	2,910
	Salmon	Malathion	9.0, 13.0 oz	8,150
1966	Bitterroot	Mexacarbate	2.4 oz	5,360
	Salmon	Mexacarbate	2.4 oz	4,860
1967	Sawtooth	Mexacarbate	2.4 oz	2,300
1968	Lolo	Mexacarbate	1.0 oz	6,080
1969	Nezperce	Mexacarbate	2.4 oz	6,000
1971	Nezperce	Mexacarbate	2.4 oz	9,000
1972	Lolo	Mexacarbate	2.4 oz	500
1975	Okanogan/Wenatchee	Fenitrothion	2–3 oz	7,500
	Okanogan	Acephate	1	1,200
	Okanogan	Matacil	.15–.3	1,200
	Beaverhead	Carbaryl	1	3,500
	Beaverhead	Trichlorfon	1	3,800
	Wenatchee	Trichlorfon	1.5	100
	Wenatchee	Carbaryl	2.0	120
	Wenatchee	Acephate	1	100
1976	Helena	Acephate	1	3,000
	Helena	Trichlorfon	1	3,000
	Targhee	Acephate	¼, ½, 1	400
1977	Payette	Acephate	½	4,000
	Payette	Chlorpyrifosmethyl	⅛, ¼, ½	750
1978	Payette	Chlorpyrifosmethyl	⅛, ¼, ½	750
	Payette	Carbaryl	⅛, ¼, ½	750
	Payette	Sulprofos	⅛, ¼, ½	750
	Boise	Methomyl	⅛, ¼, ½	750
1979	Lewis & Clark	Phosmet	.12–.5	750
	Lewis & Clark	Permethrin	.25–1.4	750
	Lewis & Clark	Carbaryl	¼–1	750
	Lewis & Clark	S.I.R. 8514	⅛	150
1980	Payette	Phosmet	½, 1, 1½	750
	Payette	S.I.R. 8514	¼	150
	Payette	Sulprofos	⅛, ¼, ½	750

[1]Pounds, unless otherwise specified.

1.4.2.2 Operational Projects—The first attempt to suppress a budworm population with chemicals began in 1929 in a small campground in the Shoshone National Forest, WY (Evenden 1930 unpubl.). A formulation made of lead arsenate, fish oil, and water was applied with high-pressure ground equipment to late instars. These ground treatments continued through 1932, but the infestation subsided naturally. Later, as outbreak size and frequency increased, ground techniques were found inadequate and generally abandoned. The success of the first aerial test in the Western United States in 1948 marked the beginning of many years of DDT use (table 1-1). Operational suppression programs using chemical insecticides are summarized by area and year from 1966 to 1983 (table 1-3).

1.4.3 Biological Agents
David G. Fellin

Environmental problems with chemicals have stimulated considerable interest in biological agents for suppression of both eastern and western budworms. Agents receiving the most attention have been a bacterium *(Bacillus thuringiensis)*, viruses, and pheromones. Investigations have also been conducted on insect growth regulators (IGR's), feeding deterrents, nematodes, microsporidia, and entomopathogenic fungi.

Table 1-3—Operational suppression programs using chemical insecticides from 1966 to 1983 in the Western United States

Year	Location	Pesticide	Rate/acre	Area
			Pounds	*Acres*
1966	Carson	Malathion	1	60,800
	Beaverhead	Malathion	0.8	64,400
	Gallatin	Malathion	.8	20,590
1976	Wenatchee/Okanogan	Malathion	.8	358,000
	Okanogan	Carbaryl	1	7,700
1977	Wenatchee/Okanogan	Carbaryl	1	356,700
	Santa Fe	Carbaryl	1	37,450
	Gallatin	Carbaryl	1	200
1978	Gallatin	Carbaryl	1	200
1979	Gallatin	Carbaryl	1	1,000
	Warm Springs Indian Reservation	Carbaryl	1	34,400
	Boise	Acephate	1	47,897
	Boise	Carbaryl	1	92,270
1982	Malheur/Umatilla	Carbaryl	1	169,354
	Malheur	Acephate	.5	9,195
	Carson	Carbaryl	1	61,351
1983	Malheur/Umatilla	Carbaryl	1	501,994
	Malheur	Mexacarbate	.125	10,095
	Carson	Carbaryl	1	36,000

1.4.3.1 Bacteria—*Bacillus thuringiensis* Berliner (B.t.) occurs in nature, and many different variants or serotypes have been isolated. Some commercial brand names used in the United States and Canada are Bactospeine, Dipel, Futura, Sok-Bt, and Thuricide. All of these formulations contain the highly potent strain HD-1.

B.t. is an aerobic spore- and crystal-forming pathogen that, in most serotypes, is specific to insects in the order Lepidoptera. Larvae are infected by eating B.t. from contaminated foliage; the digestive juices interact with crystals and spores, which ruptures the gut wall. Feeding ceases within a few hours of infection, although the insect may not die for several days (Hulme and others 1983).

Initial field tests with B.t. began in the East in 1959 (Smirnoff 1963), and later tests between 1971 and 1976 demonstrated the feasibility of using B.t. to suppress budworm populations and protect host trees (Smirnoff 1979). But before B.t. could be considered operational, serious problems had to be resolved on timing of application, volume and dosage, spray systems, and spectrum of droplets.

Western investigators began laboratory and field studies with B.t. in the mid-1970's. Retnakaran and others (1983) found that B.t. alone reduced or stopped larval feeding. In simulated aerial application bioassays, budworm reductions were increased from 37 to over 60 percent by the addition of molasses and an ultraviolet screen; but the molasses reduced the sticking properties of the spray mixture.

The first field application of B.t. on western budworm was a ground test in 1960 in Montana (Denton 1960 unpubl.). Since then, several experimental and operational aerial programs have used B.t. throughout the West (table 1-4) (Bennett 1982, Hodgkinson and others 1979, McGregor and others 1976, Ragenovich 1983, Shepherd and others 1982, Stipe and others 1983, Thompson and others 1977).

B.t. persistence from one year to the next was reported in Maine by Dimond and Spies (1981) and in Canada by Morris and Moore (1983). No carryover effect was found in tests conducted in Montana and New Mexico (Thompson, personal communication).

Table 1-4—Experimental and operational use of *Bacillus thuringiensis* Berliner (B.t.) from 1975 to 1983 in the Western United States

Year	Region and forest	Use	Rate per acre	Acres
			BIU	
1975	6, Wenatchee	Experimental	8	405
1975	1, Gallatin	Experimental	7.28	3,500
1978	British Columbia	Experimental	—	395
1980	3, Kaibab	Experimental	8	1,200
1981	1, Deerlodge	Experimental	8	16,750
1981	3, Carson	Experimental	8	13,469
1982	3, Carson	Operational	8	3,996
1983	3, Carson	Operational	12	2,000
1983	6, Malheur	Operational	12	12,472

Early results were inconsistent in both eastern and western tests, but recent work has improved confidence in the value of B.t. Eastern tests showed greatly increased insect mortality and consistency in the efficacy of B.t. when the dosage was increased to 12 BIU/acre (30 BIU/ha) (Grimble and Morris 1983). Populations surviving treatment with B.t are considerably less vigorous than the populations surviving chemical treatments with organophosphates and carbamates (Smirnoff and Valero 1983).

The following are general conclusions based on investigations on the use of B.t.:

• When applied correctly, B.t. can provide an effective and efficient pest-management option (Hulme and others 1983, Ragenovich 1983).
• The effectiveness of B.t. increases as spray deposit increases, and decreases as prespray larval density increases (Morris 1980).
• The per-acre cost of B.t. treatment is somewhat higher than that for chemical treatment, but B.t. treatments will eventually cost no more than treatments with chemical insecticides (Hulme and others 1983).
• No evidence has been found of any resistance being developed by the budworm against the bacterium, and none is expected (Hulme and others 1983).
• When applied correctly, B.t. is environmentally safe (Hulme and others 1983).
• B.t is now available for operational use against the eastern budworm, and guidelines have been published (Morris and others 1984).

1.4.3.2 Viruses—Four kinds of viruses are found in natural populations of eastern and western budworms. Two of them—a nucleopolyhedrosis virus (NPV) and a granulosis virus (GV)—have shown some promise in the laboratory as biological insecticides.

Larvae must ingest virus to become infected. Larval tissues such as fat cells, epidermal cells, and tracheal matrix cells are destroyed. Larvae with sublethal virus infections can develop into pupae and adults.

Carryover of virus from one generation to the next has been documented (Cunningham and others 1974, 1975; Shepherd and others 1982), although transmission in or on eggs has not yet been demonstrated with any budworm virus.

Western budworm viruses have been studied and their characteristics in the laboratory described (Arif and Krywienczyk 1982). Both GV and NPV have been shown in the field to provide population reduction and foliage protection in the year of treatment (Cunningham and others 1983, Hodgkinson and others 1979, Shepherd and others 1982). In general, though, test results with budworm viruses have been inconsistent, population reductions have been unacceptably low, and foliage protection poor. Even if virus were effective, its use would be unlikely at the current stage of technology—virus is not available commercially and is extremely expensive to produce.

1.4.3.3 Nematodes—One or more species of nematodes may provide an alternative for suppression of budworm populations. Laboratory studies indicate that western budworm larvae and pupae are highly susceptible to one species of nematode—*Neoaplectana carpocapsae* (Kaya and others 1981, Kaya and Reardon 1982). Field applications in Idaho in 1980 were unsuccessful, however. Another nematode species is known to kill both larvae and pupae of the eastern budworm (Finney and others 1982).

1.4.3.4 Microsporidia—*Nosema fumiferanae* is the most common microsporidian parasite of the spruce budworm. In Ontario, it is extremely abundant; as the age of budworm infestations increases, so does the incidence of microsporidiosis (Hodgkinson and others 1979).

The disease adversely affects larval and pupal vigor and reduces longevity and fecundity of adults. The addition of *Nosema* spores to naturally infected budworm enhances these effects. These protozoans may be transmitted by infected females to their offspring.

Although numbers of microsporidia are low in western budworm populations, a high incidence of a naturally occurring *Nosema* species was recently noted in western Montana (Carlson and others 1983).

Another microsporidian, *Pleistophora schuberai*, has been shown to be an effective parasite of the spruce budworm in laboratory studies. Spores applied to the larval diet have resulted in 100-percent and 70-percent mortality of second and fifth instars, respectively. Susceptibility of the budworm to the parasites decreased with age of the host (Wilson 1982). Prospects of developing this agent for field use are considered promising.

1.4.3.5 Entomopathogenic Fungi—Moderately heavy natural infections of entomopathogenic fungi have been recorded in the Maritime Provinces, but widespread epizootics are rare (Dimond 1976). Several species of fungi have been recorded from budworm throughout its range, and investigations are underway on methods of mass production. Their potential in suppression is unknown.

1.4.3.6 Pheromones—The western budworm's sex attractant provides a chemical message that permits the male moths to find female moths for mating. The principal components of the attractant are the same as those of the eastern budworm and have been identified as E- and Z-11-tetradecenal (Weatherston and others 1971). Although pure E-11-tetradecenal is only marginally attractive to western budworm males, maximum attraction is achieved by a 92:8 blending of the E:Z stereoisomers of 11-tetradecenal (Cory and others 1982, Silk and others 1982). The pheromone system also contains secondary compounds in the form of alcohols and acetates, but the behavioral significance of these materials is unknown (Cory and others 1982, Silk and others 1982).

Sex attractants are best known for their use in traps as sensitive, inexpensive devices for surveying budworm populations. But sex pheromones may also be used to disrupt mating behavior by saturating the atmosphere with attractant. This approach to reducing populations has been successful with the western pine shoot borer and the Douglas-fir tussock moth (Sower and others 1982, 1983). Research on mating disruption with the eastern and western budworms began in the early 1970's, and several large-scale trials have been conducted in the last decade. Trials have met with limited success (Palaniswamy and others 1982), but investigators have concluded that the technique has shown enough promise to warrant continued research.

1.4.3.7 Feeding Deterrents—For some insect species, the selection or rejection of a particular host plant for feeding is influenced by feeding deterrents in the foliage. Scientists at the University of Maine in Orono have developed a convenient and reproducible bioassay with which they have tested more than 100 plant extracts with encouraging results (Bentley and others 1982). Prospects for isolating a material that satisfies all criteria for acceptance is difficult to assess, but the principle presents an intriguing possibility.

1.4.3.8 Insect Growth Regulators—Insect growth regulators (IGR's) are hormones or hormonal mimics that disrupt the metamorphosis of insects and affect their ability to develop normally, survive, and reproduce. In 1969, natural juvenile hormones and their synthetic analogues (JHA's) showed inhibitory effects on nerve cord metamorphosis and adverse effects on survival and reproduction of eastern budworm (Robertson 1979a).

Research on IGR's in the West has been pioneered by Robertson and her colleagues in Berkeley, CA. Robertson and Kimball (1979a) determined that some JHA's applied to full-grown larvae would kill at dosages similar to those of several conventional insecticides. The LD_{50}'s of some JHA's to sixth instars are actually less (that is, more toxic) than those of acephate and carbaryl—two conventional chemical insecticides registered for use against budworm.

Robertson and Kimball (1979b) also found that, with few exceptions, most of the JHA's significantly reduced the number of eggs laid and the number of eggs hatching. When third rather than sixth instars were treated, reductions in number of eggs laid and hatched were neither as frequent nor as extensive.

Further studies (Robertson and Kimball 1981) determined that to achieve maximum reduction of F_1 populations, the primary target should be the sixth instar; pupae would be a possible secondary target. Weight and sex of individuals may influence the effectiveness of JHA's (Robertson 1982).

Although JHA's demonstrate many qualities that could be useful in managing budworm when properly applied and could be as effective as some chemical toxicants with a minimum of environmental disruption, several problems with both JHA's and molt inhibitors remain to be investigated. They are not specific to target species and could adversely affect nontarget arthropods, including the predators and parasites of the budworm.

1.4.4 Silvicultural Practices

Before 1977, most silvicultural prescriptions ignored budworm (Schmidt and others 1983). Thus, although past silvicultural practices have greatly influenced budworm, the history of silviculture intentionally applied to affect budworm is very short. In 1977, an Environmental Impact Statement was prepared for Region 1 of the USDA Forest Service (Northern Region), in which nearly 1 million acres (about 405,000 ha) were selected for silvicultural treatment to minimize budworm damage. In 1978, the Boise and Payette National Forests (Forest Service Region 4, Intermountain) also elected to use a silvicultural option, with the added protection of sprayed buffer zones. The decisions reflect important policy changes in budworm management through emphasis on using silvicultural treatments to alter the site and stand toward a more seral condition. As the interaction between site and stand characteristics and budworm population dynamics becomes better understood, silvicultural treatments can be modified to further reduce impacts from budworm (see chapter 7).

Long-standing policies of fire control and harvesting techniques have had a great impact on forest succession and thus on susceptibility to budworm. Silviculturists have known for many years that site-specific prescriptions can be used to manipulate environmental conditions. Fire control has caused a gradual shift toward climax vegetation—increasing the proportion of shade-tolerant species, which we now know are preferred by the budworm. Stands can be converted to or maintained in a more seral, and less susceptible, condition through silvicultural treatments.

Chapter 2

Taxonomy of Spruce Budworms and Recognition of Associates

2.1 Budworm Taxonomy

V. M. Carolin, J. A. Powell, G. E. Daterman, and
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2.1.1 Historical Review

Budworms are placed in the tribe Archipini of the
family Tortricidae (Lepidoptera). Species of long
standing were listed in one or more of the genera
Tortrix, *Harmologa*, and *Archips* (= *Cacoecia*) before
being assigned to *Choristoneura* by Freeman (1947,
1958). This assignment included both eastern and
western species feeding mainly on true firs, Douglas-
fir, and spruces, as well as others known or assumed
to feed on pines and one on juniper.

During the course of revisions of the Archipini,
various kinds of *Choristoneura* received taxonomic
attention. Obraztsov (1962) redescribed *retiniana*
(Walsingham), named two new species—*spaldingiana*
and *subretiniana*, and added two subspecies to *C.
lambertiana* (Busck), a pine-feeding species. Powell
(1964), working in California, applied the name
fumiferana (Clemens) broadly to include all fir- and
spruce-feeding populations. He also named
californica, believing it to be a pine-feeding race. He
treated it, *carnana*, and *subretiniana* as subspecies of
lambertiana, and relegated Obraztsov's subspecies
lindseyana, which had been conceived as a race of
lambertiana, to synonymy with *fumiferana*.

From 1955 through 1967, entomologists at the
Canadian Forestry Service, Insect Pathology
Research Institute, Sault Ste. Marie, ON, made a
major effort to define genetic, physiologic, and
morphologic characteristics of distinctive budworm
populations. During this period, 287 larval collections
were made from localities distributed throughout most
of the range of *Choristoneura* in North America
(Stehr 1967); about half these localities were in the
West. Larvae were reared under controlled conditions
to the adult stage; offspring were then reared from
single-pair matings. These colonies were characterized
taxonomically and used experimentally. Freeman
(1967) named four new western species that feed on
firs and spruces: *occidentalis*, *biennis*, *orae*, and
viridis (which was relegated to synonymy with
retiniana by Powell 1980) (fig. 2-1). The status of
western species on pines was left unchanged. Other
results included the description of characters of
immature forms (Harvey and Stehr 1967),
identification of aspects of mating behavior affecting
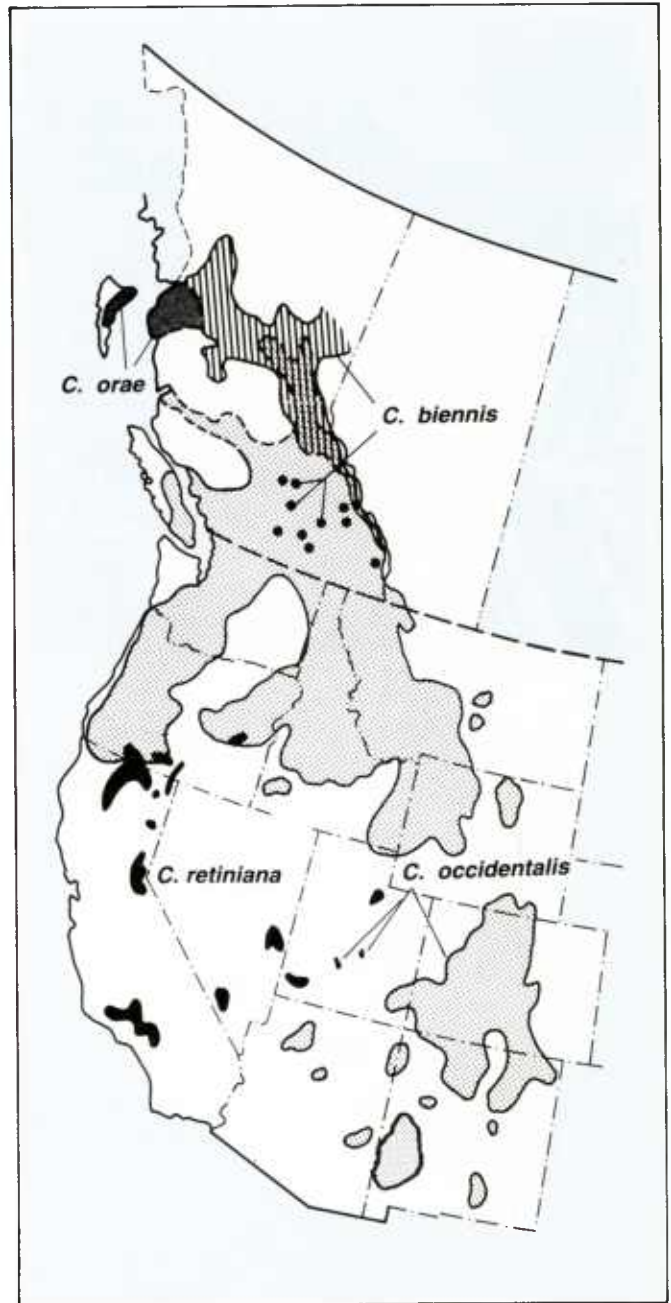species isolation (Campbell 1967), and validation of

Figure 2-1—Distribution of fir-feeding
Choristoneura species in the West. (*C.
fumiferana* occurs in Alberta and Saskatchewan.)

second diapause as a species character (Harvey 1967). Early results on hemolymph polymorphism (Stehr 1959) aided in interpretation of color variation in and among populations.

The major result of these efforts was recognition of a widespread and economically important western species, *C. occidentalis,* as distinct from *C. fumiferana,* a species that had ravaged boreal forests in eastern North America for more than a century. Reliable distinguishing characters in male or female genitalia were not found (Freeman 1967), however, so species recognition was still somewhat arbitrary. Many questions remained, particularly on the identity of forms with green larvae in later instars, and also with named species for which the relation with host plant was not clarified. Further revision of *Choristoneura* could thus be anticipated.

2.1.2 Taxonomic Problem and Research Approach

Stability of nomenclature is essential to communication between entomologists and coordination of their efforts. In *Choristoneura,* a major problem is the complexity of variation among populations. Powell (1980) elaborates:

> Sympatric populations exhibit varying degrees of reproductive isolation, and allopatric populations show geographic variation in size and color of adults, larvae, and pupae, and in preference for host plants. There are both polymorphic and continuously variable features, and characters conventionally used by taxonomists in defining species in moths are not sufficiently differentiated in this group to provide indicators of genetic and behavioral compatibility among populations.

2.1.3 Nomenclature

Changes in nomenclature for the conifer-feeding *Choristoneura* were made and explained by Powell (1980). As a result, seven described species feeding on western conifers and two on eastern conifers are recognized in the recent checklist of Lepidoptera in North America (Powell 1983). Of the western species, five feed primarily on true firs, Douglas-fir, and spruce. One feeds on pine, and another is of uncertain status. A species feeding on juniper was transferred to a different genus (Powell and Obraztsov 1977). A synopsis of western species, as currently recognized (Powell 1980), follows.

Fir- and spruce-feeding species:

occidentalis Freeman, western spruce budworm—This name is applied to Abietoideae-feeding populations having a broad western range including southwestern, central, and northern Oregon, Washington, southern British Columbia, and the Rocky Mountain States south to New Mexico and eastern Arizona. Adults, host preference, and phenology differ considerably over its range. Late instars of most populations range from olive to heavily marked with red-brown.

retiniana (Walsingham) (syn. *lindseyana* Obraztsov, 1962; *viridis* Freeman, 1967), Modoc budworm—This form feeds on fir, principally white fir, in the southern Cascade Range, at Mt. Shasta, and in the Warner Mountains of Oregon and California. Similar populations occur in the Sierra Nevada, Tehachapi Range, and mountains of southern California, in the isolated ranges of eastern and southern Nevada, and in central and southern Utah. Adults are polymorphic, including both pale tan, unmarked, and mottled or checkered forewings. Larval and pupal integuments are weakly sclerotized; thus, late instars and pupae appear green.

biennis Freeman, 2-year budworm—This species has a 2-year life cycle; it occurs in the mountainous areas of western Alberta and eastern and central British Columbia. Food plants are subalpine fir, white spruce, and Engelmann spruce. Adults are generally larger and darker than in other species; occasional specimens resemble either *fumiferana* or *occidentalis* (Freeman 1967). Cool temperatures at high altitudes were shown to be the likely cause for the selection and maintenance of these 2-year-cycle populations (Shepherd 1961). Laboratory rearing of consecutive generations under extended photoperiod indicates that the second diapause is genetically fixed (Harvey 1967).

orae Freeman—This form is found in the coastal forests of British Columbia and southeast Alaska. Food plants are Pacific silver fir and Sitka spruce.

carnana (Barnes and Busck)—The typical form is known from the San Gabriel and San Bernardino Mountains of California, where it feeds on bigcone Douglas-fir. Populations exhibiting a similar monomorphic phenotype occur along the west slope of the Sierra Nevada, where they have been reared from Douglas-fir. The subspecies *carnana californica* Powell in the Coast Range of California also feeds on Douglas-fir. Larvae from both the Sierra Nevada and Coast Ranges are heavily marked and brick red.

Pine-feeding species:

lambertiana (Busck)—This species is divided into three subspecies: *l. lambertiana* (Busck), *l. subretiniana* Obraztsov, and *l. ponderosana* Obraztsov. The type series of *l. lambertiana* was reared from sugar pine near Ashland, OR. The typical race has since been recorded only once, from nearby Siskiyou County, CA. The race *l. subretiniana* occurs on lodgepole in the eastern Sierra Nevada, in the Warner Mountains of Oregon and California, and, in a slightly different phenotype, in Harney County of eastern Oregon. Northward from the California border, the phenotype loses the gray coloration between the rust-red banding on the forewings. A distinctive race, *l. ponderosana*, is distributed along the eastern flank of the Rocky Mountains in Colorado, Wyoming, Montana, and South Dakota, mainly on ponderosa pine with one recovery from limber pine (Stevens and others 1977); populations of varying phenotypes occur in northern Arizona, southern Nevada, Utah, and northward (Powell and DeBenedictis 1982 unpubl.). Adult forewings have indistinct, dull yellow-orange markings over a silvery-white background; hindwings are grayish white.

Uncertain status:

spaldingiana Obraztsov—The type locality of this form was Provo, UT, at the western edge of the Wasatch Range. No host plant was indicated. Evidence from pheromone trapping of adults at Mt. Timpanogos, UT, and in south-central Utah in 1981 indicates this name was based on the mottled form of *retiniana*.

2.1.4 Interrelations of *Choristoneura* and Host Species

Some of the western *Choristoneura* are sympatric, and two or three species are sometimes found together in the same stands but on different host plants. Specific cases are cited by Powell and DeBenedictis (1982 unpubl.) for California and Utah.

C. occidentalis and *retiniana* occur together in the Schell Creek and Snake Ranges of Nevada, and in north-central and southwest Utah. Association of *occidentalis* and one or more forms of *lambertiana* is common, but is specifically recorded only with *lambertiana ponderosana* in Colorado, southwest Utah, and northern Arizona. Trapping records show *occidentalis, retiniana,* and *l. subretiniana* occur together in the southern Cascades.

C. retiniana and *carnana* occur together in California, in the San Gabriel Mountains, parts of the central and northern Sierra Nevada at mid-elevations, and the southern Cascade Range. *C. retiniana* and *lambertiana subretiniana* inhabit the same stands in the Warner and Manzanita Mountains and high elevations in the central and northern Sierra Nevada of California; *retiniana* and *l. ponderosana* are found together in the Charleston Mountains of southern Nevada and in southwest Utah.

C. retiniana and either *carnana* or *occidentalis* normally occur together only in mixed stands of true fir and Douglas-fir, with *retiniana* feeding on fir and *carnana* or *occidentalis* feeding primarily or exclusively on Douglas-fir. Where fir is present alone, either *occidentalis* or *retiniana,* but not both, occur. In the absence of fir, only *occidentalis* or *carnana* are found. Either *occidentalis* or *carnana* may be present in mixed Abietoideae stands, but to date *retiniana* has not been found exclusively occupying the mixed sites. Over most of its broad range, in the absence of *retiniana, occidentalis* feeds on whatever species of Abietoideae are present.

In an area of sympatry between *C. occidentalis* and *C. retiniana* in southwestern Oregon, both species were found on either Douglas-fir or white fir. The relative frequency of the two species within a stand was strongly associated with the relative basal areas of Douglas-fir and white fir (Volney and Waters 1983 unpubl.).

2.1.5 Sex Pheromones

Reproductive isolation resulting from differences in components of the female sex pheromone appears to be the primary mechanism in separation of western species. Most conifer-feeding *Choristoneura* will crossmate in confinement, but not necessarily in the field. Previous work on cross-attraction indicates some strong similarities in sex pheromones of some named species, based on male response. Virgin females of *fumiferana, occidentalis,* and *biennis* attracted *fumiferana* males; however, virgin females of *retiniana* (= *viridis*) failed to attract *fumiferana* (Sanders 1971). Field trials in British Columbia and Oregon by Sanders and others (1974) demonstrated that trans-11-tetradecenal, a powerful attractant for male *fumiferana* and *occidentalis* (Weatherston and others 1971), is also a sex attractant for male *biennis,* and that trans-11-tetradecenyl acetate is attractive to *retiniana.*

Recent research has focused on differences, often subtle, in the balance of chemical components in pheromones of various *Choristoneura.* Although the principal attractant for males of *fumiferana* and *occidentalis* is the same, differential responses suggest the presence of different ''secondary'' pheromone components (Sanders and others 1977). Thus, recent studies have emphasized recognition of the balance between trans (E) and cis (Z) isomers of aldehydes, acetates, and alcohols in analyzing male responses under field conditions. This approach in characterizing species (or populations) will have broad application in survey or trapping programs with pheromones as bait.

Chemical analyses of the sex attractant of *C. occidentalis* showed the active components to be the aldehydes E- and Z-11-tetradecenal in a ratio of 92:8 (Cory and others 1982, Silk and others 1982). In field bioassays, synthetic baits releasing these components at rates approximating those of female moths were at least as attractive as the females. Hexane extraction of female abdominal tips showed that these aldehyde components were present in relatively low quantities in the pheromone gland; E-11-tetradecenyl acetate was the most abundant component. Air collection of pheromone emissions and hexane washes of the external surface of female abdomens showed that the

aldehydes were the predominant materials released by the females. The E- and Z-11-tetradecenals at the 92:8 ratio were clearly responsible for long-range attraction in field bioassays. The addition of 11-tetradecenyl acetates or alcohols to trap baits did not significantly inhibit nor enhance attraction. These secondary components may have some role in close-range reproductive behavior that is not reflected by trap captures.

Pheromone identification studies on other western *Choristoneura* have confirmed that pheromone differences are important in maintaining at least some degree of reproductive isolation among species. *C. carnana californica* has a pheromone that is virtually indistinguishable from the *occidentalis* pheromone (Daterman and Sower 1984 unpubl). *C. retiniana,* however, coexists over parts of its range with both of these species and has a distinctly different pheromone. The major component of the *retiniana* pheromone is E-11-tetradecenyl acetate, with a lesser amount of the Z-isomer necessary to induce male response (Daterman and others 1984). A 92:8 ratio of the E:Z-acetates appeared optimal. When the corresponding 11-tetradecenyl alcohols were added to the acetates at 10 percent of the total mix, attraction was enhanced.

At least two subspecies of pine-feeding *Choristoneura* coexist with *occidentalis, retiniana,* or *carnana californica.* The pheromone systems of *lambertiana subretiniana* and *lambertiana ponderosana* are similar—the former's consists primarily of a 60:40 ratio of E:Z-11-tetradecenyl acetate, and the latter, a 70:30 split of the same compounds (Daterman and others 1983 unpubl.). When 10 to 15 percent of the corresponding 11-tetradecenyl alcohols are added to the synthetic mixture, the degree of attraction increased significantly.

Pheromone components of *C. orae* have recently been determined from material collected in southeast Alaska. An 82:9:9 ratio of E-11-tetradecenyl acetate, Z-11-tetradecenyl acetate, and E-11 alcohols provided an effective attractant for trapping male moths (Gray and others 1984).

These pheromone differences among taxa probably serve to maintain reproductive isolation most of the time. *Choristoneura* spp. often interbreed in the laboratory, however, an indication that some crossbreeding could occur under field conditions. The presence of intermediate individuals in field populations in mixed Douglas-fir/white fir stands of southwest Oregon (Volney and Waters 1983 unpubl.) suggests that this occurs. Further, virgin females reared from intermediate larval morphs attracted males whose forewing coloration was similar either to that of males attracted by *C. occidentalis* or of males attracted by *C. retiniana* females (Liebhold and others 1984).

Field trapping during 1981 (Powell and DeBenedictis 1982 unpubl.) tested cross-attraction of virgin females, as well as synthetic lures, between *retiniana* and *carnana* populations at sites in California, and among *retiniana, occidentalis,* and *lambertiana* populations at sites in Nevada and Utah. Results confirmed that the *occidentalis* pheromone used as a lure in field traps was highly attractive both to this species and *carnana.* No cross-attraction was found between *Choristoneura lambertiana subretiniana* and *retiniana* at sites in California where both occurred, or between *l. ponderosana* and *retiniana* at sites in the Great Basin (Powell and DeBenedictis 1982 unpubl.). In similar tests in Colorado, no cross-attraction was found between *l. ponderosana* and *occidentalis* (Daterman and others 1983 unpubl.). Flights of the sympatric species always took place concurrently. Occasionally some apparent cross-attraction to nonspecific pheromone baits occurs, although the number of responding insects is generally low. Powell and DeBenedictis (1982 unpubl.), for instance, reported that traps baited with *occidentalis* pheromone caught 97.5 percent of all *occidentalis* males captured, and *retiniana* males were attracted only by *retiniana* lures.

2.1.6 Genetic Variation

Resolution of systematic problems caused by extensive variation among populations, as in *Choristoneura,* is abetted by new techniques in molecular genetics. Of these, electrophoresis is near ideal for comparing subspecies, species, and closely related genera because of its sensitivity and ease of analysis (Avise 1974). Because a relation usually exists between the electrophoretic phenotype and genotype of an individual, this method, which can detect variation at single gene loci, removes the ambiguity inherent in other, more traditional approaches (Stock and Castrovillo 1981). The method permits comparisons of gene frequencies at a large number of loci, providing a direct but conservative estimate of genetic differentiation.

Relations Among *Choristoneura* Species—In a 1-year study, Willhite and Stock (1983) uncovered enough genetic differences among 14 collections of *C. occidentalis* from Idaho and Montana to group them into three genetically similar units. These groupings were based primarily on genetic relations at 16 gene loci and on the presence of rare alleles shared among populations. The genetic data, combined with analysis of historical records of outbreaks over the area, indicate that dispersal may play a significant role in the spread of infestations in some locations.

In a preliminary study, Stock and Castrovillo (1981) compared single populations of five species: *C. occidentalis, biennis, retiniana, fumiferana,* and *lambertiana ponderosana.* The highest similarity occurred among *occidentalis, biennis,* and *retiniana.* *C. fumiferana* and *lambertiana* were genetically most distant from the other three species.

Castrovillo (1982) analyzed collections of seven *Choristoneura* species, adding populations tentatively identified as *orae* and *pinus* to the species examined earlier by Stock and Castrovillo (1981). High genetic similarity occurred among all species; as a result, no diagnostic loci could be identified for separating individuals or small samples belonging to different species. In spite of this similarity, however, cluster analysis showed that multiple collections of the same species from different parts of their range were more similar to each other than to collections of other species (fig. 2-2), and that simple geographic proximity or distance cannot explain the differences, however subtle, that do occur among most collections.
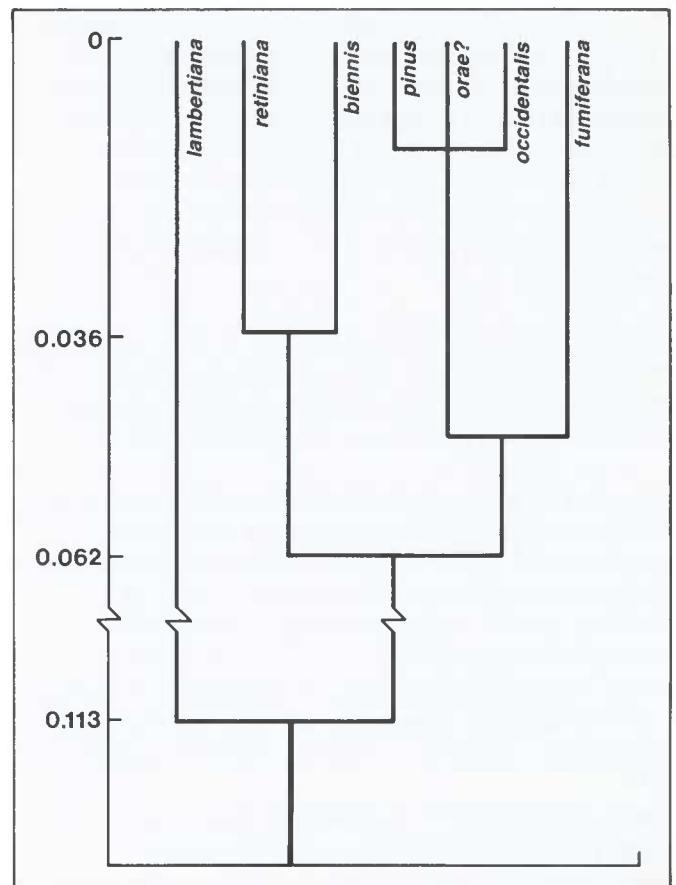

Figure 2-2—Phenogram illustrating relations of seven *Choristoneura* species, based on Nei's genetic distance values. ? = tentative identification.

Castrovillo (1982) also studied an outbreak in central Idaho for possible associations between the genetic structure of *C. occidentalis* and physical variables of infestations, such as defoliation intensity, outbreak age, host species, outbreak trends, and location within an outbreak. Subtle differences in allele frequency were associated with outbreak age, host species, outbreak history, and geographic location of the collection.

Similar studies are being conducted in budworm infestations in Canada, from Alberta through the eastern provinces, by G. Harvey, Canadian Forestry Service, Great Lakes Forest Research Centre.

Variation in Response to Insecticides—Within-species differences in response to pesticides have been demonstrated. Within-species variation in response to acephate, applied topically, may be as large as between-species variation among *C. occidentalis, retiniana,* and *fumiferana* (Stock and Robertson 1980). The greatest difference in population responses occurred between laboratory and field populations of *occidentalis*, rather than between different species.

Further studies on *C. occidentalis* (Stock and Robertson 1982) showed that dose-mortality regressions were not significantly different for acephate sprays applied to second through sixth instars, but that those for carbaryl sprays applied to second through sixth instars differed significantly, both in response thresholds and change in response per unit dose. Thus, for prespray electrophoretic monitoring, second through sixth instars may be equally useful before application of acephate, and sixth instar most suitable before carbaryl application.

In a survey of responses of *C. occidentalis* populations to carbaryl (Robertson and Stock 1985), preliminary results based on toxicological analyses alone indicate that apparent resistance to carbaryl occurs among *C. occidentalis* populations.

2.2.1 Background

Distinguishing between larvae of spruce budworms and those of associated Lepidoptera is particularly important where results are based on counts of larvae on foliage samples. Many associates superficially resemble western budworm larvae, but most can be separated by use of simple characters viewed with a $10 \times$ hand lens. Carolin (1980) concluded that about 20 species occur with sufficient regularity to justify identification by field crews.

2.2.2 Field Keys for the West

An interim key to larvae up to 12 mm long was prepared for 18 species, including 2 species of *Choristoneura* (Carolin and Stevens 1979). A second key, including new material from the Southwest, was made for larger larvae; it covered 24 species, including 3 of *Choristoneura* (Carolin and Stevens 1981). Notes on life histories of associates in Arizona and New Mexico were prepared by Stevens and others (1983). A summary publication (Stevens and others 1984) consists of revised and expanded keys, life-history information, and illustrations of both larvae and adults for most of these species.

2.2.3 Common and Occasional Associates

Of 40 associates of *Choristoneura occidentalis* in buds or on new shoots, about half were either common or occasional in any particular study. Only two species, *Dioryctria reniculelloides* (Mutuura and Munroe) and *Zeiraphera hesperiana* Mutuura and Freeman, were common associates of *occidentalis* in all areas studied. Larvae of some of these associates are shown in figure 2-3.

In Oregon and Washington during 1951–62 (Carolin 1980), common associates on Douglas-fir included *Acleris gloverana* (Walsingham), *Argyrotaenia dorsalana* (Dyar), a *Coleotechnites* sp., *Epinotia radicana* (Heinrich), *Dioryctria* (probably) *reniculelloides,* and *Zeiraphera hesperiana.* On grand fir, *Z. hesperiana* was replaced by a smaller unidentified *Zeiraphera,* and *Coleotechnites* sp. partially by a *Chionodes* species. Occasional associates on Douglas-fir and true firs were one or more species of *Chionodes, Eupithecia annulata* (Hulst), *Achytonix epipaschia* (Grote), and *Egira* (= *Xylomyges) simplex* (Walker).

Figure 2-3—Larvae of some associated
Lepidoptera. A = *Zeiraphera*, probably
hesperiana. B = *Dioryctria* species. C =
Epinotia radicana. D = *Chionodes* species. E =
Acleris gloverana. F = *Nematocampa limbata*.

E

F

In the northern Rocky Mountains, *Dioryctria reniculelloides* (then called *D. reniculella* Grote) was a common associate of the budworm in the 1950's (Johnson and Denton 1975). In 1965, the same species continued to be the most populous of the associated insects on Engelmann spruce, subalpine fir, and Douglas-fir (Williams and Walton 1968). Densities of other Lepidoptera, with the occasional exception of *Zeiraphera hesperiana* (recorded as *Z. griseana* Hübner), were very low; included were *Epinotia radicana*, *Lambdina fiscellaria lugubrosa* (Hulst), and an unidentified looper. In 1981, Markin (1982 unpubl.) identified nearly all of 68,458 larvae (budworm and associates) found on Douglas-fir foliage. *D. reniculelloides* was again the most abundant associate, representing 15.6 percent of all larvae, followed by *A. gloverana* (7 percent), *E. radicana* (5 percent), *Z. hesperiana* (1 percent), and miscellaneous associated species (1 percent).

In southeastern Idaho in 1976, an outbreak of lepidopterous defoliators in Douglas-fir stands was studied by Markin (1982). The complex of associates included six species: budworm (48 percent), *D. reniculelloides* (18 percent), *Z. hesperiana* (17 percent), *Nematocampa limbata* (Haworth) [= *filamentaria* Guenée] (8 percent), *E. radicana* (2 percent), *A. gloverana* (1 percent), and unidentified larvae and pupae (6 percent).

In Arizona and New Mexico during 1978–81, at least 16 species of associates were recorded on Douglas-fir and white fir (Stevens and others 1983). As in the Northwest, *Argyrotaenia dorsalana*, *Acleris gloverana*, *Epinotia radicana*, *Dioryctria reniculelloides,* and *Zeiraphera hesperiana* were common. In addition, *Argyrotaenia klotsi* Obraztsov, *Dioryctria pseudotsugella* Mutuura and Munroe, *Enypia griseata* Grossbeck, and *Ypsolopha nella* (Busck) were collected; *Y. nella* is a common associate in the Southwest. The species of *Eupithecia* represented in this area was *catalinata* McDunnough, rather than *annulata* as in the Northwest.

In California during 1979–81, searches of true fir and Douglas-fir foliage for the budworms *Choristoneura carnana* and *retiniana* indicated *E. radicana*, *Dioryctria* spp., *Acleris gloverana,* and various species of *Coleotechnites* to be prominent associates, particularly of *retiniana* (Powell and DeBenedictis 1982 unpubl.). In addition, two general feeders were common, *Archips argyrospilus* (Walker) in some collections from Douglas-fir, and *Sparganothis senecionana* (Walsingham) associated with *C. retiniana*. More than 20 other species were collected as rarities. Species of *Zeiraphera,* common or occasional in other regions, were scarce. All of these collections were made in areas of relatively sparse budworm populations.

Comparisons of the diversity of species of associated Lepidoptera among different western forest areas are difficult. The number of common and occasional species appears highest in the Pacific Northwest, lowest in the northern U.S. Rocky Mountains, and somewhat variable in the Southwest. Competition from species that erupt spasmodically, such as the Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough), did not occur during these periods.

2.2.4 Ecological Significance of Associates

Competition for food and space by associated species plays an important role in budworm survival. During the bud-opening period, larvae of some associates feed in the same places as budworm; others feed in different places, such as the base or tip of the opening bud. Competition for the same food in the same place may lead to predation. *Dioryctria reniculelloides* competes directly with budworm and is known to prey on pupae and prepupae (McKnight 1971). *Epinotia radicana* feeds at the tip of the expanding shoot, not in direct competition with the budworm, but later, at larval maturity, wanders about and occasionally feeds on budworm pupae. A few associates harbor parasites that also attack the budworm, thus maintaining a reservoir of these parasites when budworm populations are very low.

Tree damage may be intensified when both the
budworm and its associates are abundant. In an
outbreak in Douglas-fir stands in southeastern Idaho
in 1976, the budworm constituted 48 percent of the
larvae and pupae found (Markin 1982). In a similar
study by Markin (1982 unpubl.) on Douglas-fir in
Montana, the budworm represented 71 percent of all
larvae found on foliage samples. Carolin (1980) found
a lower proportion of associates, ranging from 3 to 28
percent; the lowest proportion of associates was
found in stands that had severe bud damage.

Insecticide applications could change the proportions
of the resident defoliators. Markin (1982) speculated
on the possibility of increased selectivity of an
insecticide because of different life histories and
developmental rates for various associates. After
DDT was sprayed in Oregon in 1958, three
associates—*Zeiraphera hesperiana* (recorded as *Z.
griseana*), *Argyrotaenia dorsalana,* and *Epinotia
radicana*—showed markedly better survival than the
budworm (Carolin and Coulter 1971). In 1965,
mexacarbate was more toxic to budworm than to
other lepidopterous species; two loopers—one
unidentified and the other *Lambdina fiscellaria
lugubrosa*—were the least affected of the associates
(Williams and Walton 1968). Applications of naled
were very toxic to all associates except *E. radicana*
and *L. fiscellaria lugubrosa*. Results are affected not
only by the particular activity of an insecticide and its
persistence but also the timing of application.

Chapter 3

Life History and Behavior
V. M. Carolin

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3.1 Life Stages and Description

3.1.1 Egg

A budworm egg is oval, light green, and about 1.2 mm long. Eggs are laid in masses on the undersides of needles, and overlap each other like scales on a fish. Average number of eggs per mass varies considerably among regions and sometimes from place to place within a region (table 3-1). Some variation in egg-mass size has been recorded among tree species (Washburn and Brickell 1973), but an extensive study in three regions showed no significant difference between Douglas-fir and grand fir (Campbell and others 1984e). Number of rows per mass ranges from one to five, and various investigators have correlated egg-mass length and number of rows with number of eggs. The relations are quite consistent within a particular area and year, but may differ dramatically among areas and years, or both (Campbell and others 1984e).

Table 3-1—Average number of eggs per mass reported on three budworm host species in the West

Species and place	Eggs per mass	Reference
Douglas-fir		
British Columbia	45	Silver (1960)
	38	Harris and Dawson (1982)
Colorado	24	McKnight (1969b)
	32	McKnight (1969b)
Idaho	37	Klein (1972 unpubl.)
	44	Washburn and Brickell (1973)
	51	Campbell and others (1984e)
Oregon	42	Carolin and Coulter (1972)
	40	Campbell and others (1984e)
Montana	42	Terrell (1961 unpubl.)
	41	Terrell (1961 unpubl.)
	50	Campbell and others (1984e)
Washington	36	Eldridge and Egan (1983a unpubl.)
	50	Beckwith (personal communication)
Wyoming	33	Klein (1972 unpubl.)
Grand fir		
Idaho	40	Washburn and Brickell (1973)
	52	Campbell and others (1984e)
Oregon	46	Campbell and others (1984e)
Subalpine fir		
Idaho	50	Washburn and Brickell (1973)

Before hatching, individual eggs swell slightly; they are green with black dots that are the head capsules of developing larvae. After hatch (fig. 3-1), egg masses are transparent or translucent; the majority remain on the foliage for 1 year (Buffam and Carolin 1966, Carolin and Coulter 1959 unpubl.). Procedures for separating new from old egg masses are described by Twardus and Carolin (1984).

Figure 3-1—Newly hatched first instars on egg mass (photos for figures 3-1 through 3-6 courtesy of R. Ladd Livingston, Idaho Department of Public Lands, Coeur D'Alene, ID).

3.1.2 Larva

In the forest, the larva normally has six, and rarely seven, instars. In laboratory colonies, larvae fed artificial diets sometimes have more instars; in such rearings by Schmidt and Lauer (1977), 13 percent of the males and 29 percent of the females had seven instars and a few had eight.

Each of the first six instars looks different and has a different head width; sixth and seventh instars are similar in color and markings and have overlapping head widths. The first measurements of head widths were made by C. F. Speers in 1948 (Eaton and others 1950 unpubl.), using field-collected larvae reared on foliage. Subsequent measurements on field material and laboratory stock differ only slightly; however, in the fifth and sixth instars, head widths for female larvae were found to be generally greater than those for males (Stein 1981). Measurements of head widths by different regions are shown in table 3-2.

Stunting of late instars and their head widths is caused by the presence of the internal parasites *Apanteles fumiferanae* Viereck and *Glypta fumiferanae* (Viereck), as shown for the eastern budworm by McGugan (1955). For identification by instar, relying entirely on head widths can be misleading. The following simplified larval descriptions are given by Stevens and others (1984).

First instar—The larva (fig. 3-1) is about 2 mm long and light green, with a light-brown head and prothoracic shield. It does not feed or increase in size.

Second instar—During its spring feeding, the larva ranges from 2 to 4 mm long, is yellow orange with tiny, dark setal areas, and has a dark brown, squarish head and a lighter brown prothoracic shield. Its anal shield is barely discernible as a few dots of sclerotization.

Third instar—The orange-brown larva ranges from 4 to 7 mm long. Its head is brown black with lighter adfrontals, a black mark on each side of the upper head, and a pale clypeus. Its prothoracic shield is brown with a central liplike undulation at its rear margin. The anal shield, barely visible, is pale brown with 12 to 16 dots of sclerotization.

Fourth instar—The larva is 6 to 10 mm long and light brown to cinnamon brown, with small, pale ivory setal areas. Its head, including the clypeus, is brown black. The prothoracic shield is brown black and has a straight rear margin. The anal shield is easily visible as ivory-colored dots in the shape of an anchor.

Table 3-2—Mean head widths of western budworm instars

Place, reference	1st	2d	3d	4th	5th	6th	7th
				Millimeters			
Colorado, McKnight (1967)	—	0.34	0.44	0.67	1.17	1.86	—
New Mexico, Jennings (1962 unpubl.)	—	.35	.47	.71	1.17	1.87	—
Oregon, Eaton and others (1950 unpubl.)	—	.35	.48	.76	1.26	2.02	—
Washington, Stein (1981)	0.27	.34	.46	.73	1.20	1.86	—
Montana–Idaho—diets							
Lyon and others (1972)	.24	.31	.46	.76	1.24	1.87	—
Schmidt and Lauer (1977)	—	.30	.46	.74	1.20	1.76	1.98

Fifth instar—The larva (fig. 3-2) is 10 to 16 mm long and two toned. Its upper body is olive brown with conspicuous pale ivory setal areas; its lower sides are light tan to pale orange. Its head is reddish brown or occasionally light chestnut-brown, with two black triangles on each side of the upper head. The prothoracic shield is black and has a partial longitudinal split centrally located at its base. The anal shield is orbicular and ivory colored, with uniformly distributed brown dots.

Sixth instar—The larva is 16 to 30 mm long and two toned; its upper body is olive brown or occasionally light reddish-brown and rarely yellowish brown, with large, conspicuous, ivory setal areas (fig. 3-3). Its lower sides are pale yellow or pale orange. Its head and prothoracic shield are yellow brown to light chestnut-brown with variable small black markings; the prothoracic shield is divided by a median longitudinal line or split. The anal shield is large, orbicular, and ivory colored.

3.1.3 Pupa

The pupa (fig. 3-4) is 12 to 16 mm long, broad at the head end, bulging in the wing-pad area, and then tapering rapidly to the rear. In fresh pupae, coloration is predominantly brownish yellow and occasionally brownish green, later turning amber brown or reddish brown, with dark (melanized) spots, stripes, bands, or rings. The polymorphism evident in fresh pupae is sex controlled; females are predominantly brownish yellow; males are equally divided between brownish yellow and brownish green (Freeman and Stehr 1967). As in most Lepidoptera, the last two abdominal segments are fused in the female.

3.1.4 Adult

Wingspread in the male is 24 to 28 mm, and in the female 25 to 30 mm (Freeman 1967). The predominant forewing and body color (fig. 3-5) is rust or orange brown, and occasionally grayish. In the female, the ground color of the forewing is almost always bright orange-brown, rarely gray or grayish. A basal patch, median band, and subapical patch are found on the forewing of both sexes but are more distinct in the female. Hindwings are brownish gray (Freeman 1967).

Figure 3-2—Fifth instar.

Figure 3-3—Sixth instar.

Figure 3-4—Pupa.

Figure 3-5—Adult.

3.1.5 Color Variation

Color of larvae and pupae varies over the range of the budworm. An example is provided by research in south-central Oregon, where the range overlaps with that of the Modoc budworm (Volney and others 1983a, 1983b, 1984). On a series of plots where the ranges of Douglas-fir and white fir overlap, both typical and intermediate forms of both species were found on both tree species. Analysis of the relation of stand composition, as measured by basal area, to the proportion of different color morphs in each population suggested that the frequency of these morphs might be determined by the abundance of host foliage to which each morph was principally adapted. In subsequent laboratory rearings, color of late instars, pupae, and adults was related to temperature, sex, and genetic background. Although color of larvae is associated with adult forewing color (Volney and others 1983a), color alone cannot be used to identify the moths.

3.2 Life Cycle

3.2.1 Seasonal Behavior

Generalized information (Carolin and Honing 1972, Fellin and Dewey 1982, Ruth 1980) is used as a framework for recent results. The parts of the year the budworm spends in the various life stages is shown schematically in chapter 8 (fig. 8-3).

3.2.1.1 Sequential Behavior—Moths usually emerge late in July or early in August. Females mate and begin laying eggs soon after emergence. For eastern Washington, an average of 141 eggs per female was recorded, with some females laying fewer than 50 eggs (Pitman 1963). For southwest Oregon, number of eggs per female ranged from 117 to 216, and for northern New Mexico, 176 to 196 (Waters and Volney 1982 unpubl.). Females stay more or less in place to deposit the first and largest egg mass, then make short- to long-distance flights, after which they deposit smaller egg masses. Eggs hatch in about 10 days.

Behavior of larvae immediately after hatching is assumed to be similar to that of eastern budworm, as reported by Henson (1950). All larvae left an individual egg mass within 3 minutes; no hatching took place at an air temperature lower than 60.1 °F (15.6 °C) or at relative humidities below 50 or above 75 percent. At low air temperatures, the larvae are photopositive and move to the outside of the tree canopy, spinning silk as they travel; at high air temperatures or under strong solar radiation, they move to the interior of the canopy. They spin silken shelters in branch scars, under bark scales, and among lichens on the limbs and boles of the host tree, and molt into the second instar. With lowering temperatures, they become dormant and overwinter. The larvae hibernate deeper in the canopy than do eastern budworm larvae.

Larvae break diapause with warming temperatures in spring. In western budworm species, considerable variation occurs in the threshold development temperature among populations, but these temperatures are considerably higher than the 36.5 °F (2.5 °C) cited for eastern budworm (Volney and others 1983b). The cold period to which budworm larvae are exposed affects the rate and pattern of the breaking of diapause. The longer diapausing larvae are kept at 35.6 °F (2 °C) (up to 35 weeks, at least), the sooner larvae leave their hibernacula when higher temperatures occur; also, variation in the rate of exiting decreases and survival increases with duration of the cold period (Schmidt 1977). In the northern Rocky Mountains, dispersing second instars have been trapped over periods of 47 to 65 days, indicating a very gradual breaking of diapause (Fellin 1981 unpubl.).

Most emerging larvae move to foliage and tunnel into needles; here they feed for 7 to 14 days and molt into the third instar. Larvae leave needles and bore into swelling vegetative buds. Some larvae go directly from hibernation into developing pollen cones and seed cones, later moving to opening buds or new shoots. Late-emerging larvae move directly to opening buds. As the new shoots unfurl, larvae spin loose webs among the needles and feed until disturbed or until new needles are completely destroyed. Larvae become full grown 30 to 40 days after entering buds and pupate either in their feeding webs or in webs elsewhere on foliage.

3.2.1.2 Dispersal—Larval and adult dispersal, which redistributes budworm populations within and between tree crowns and stands, results in significant loss (Beckwith and Burnell 1982). Horizontal dispersal may take place during the first instar and in the second, after hibernation. Larvae of the eastern budworm are known to be transported by wind (Henson 1950, Wellington 1945). Adults also disperse horizontally, either over a short distance by flight or air updrafts or over a long range associated with frontal passages.

Intensive studies on horizontal larval dispersal were made in Montana by Fellin (1981 unpubl.) with the use of sticky traps to capture wind-blown larvae. Off-tree dispersal of first instars proved minor. Dispersal of second instars was extensive and occurred over several weeks. Various silvicultural treatments had different effects on subsequent dispersal; selection cuttings resulted in significantly higher numbers of dispersing larvae and differences in the number of larvae trapped at the edges and the center of the treated area.

Vertical distribution during spring was studied in north-central Washington by Beckwith and Burnell (1982). They deployed sticky traps at four heights— 33, 20, 6.5, and 1.6 ft (10, 6, 2, and 0.5 m)— in small openings in the canopy and found that the 33-ft traps consistently caught more larvae than traps at other heights. The smaller numbers caught on the lower traps were attributed in part to the filtering effect of adjacent tree crowns. Traps placed close to the ground clearly do not give accurate counts of dispersing populations, except possibly in large openings such as clearcuttings. Of the total catch of 3,746 larvae, dispersal of second instars accounted for only 62 percent. Third and fourth instars represented 38 percent, indicating greater off-tree dispersal than would be expected for these instars. The chance of dispersing larvae finding suitable feeding sites depends on several factors, particularly stand characteristics and air turbulence; however, larvae trapped within 6.5 ft of the ground would probably not have survived.

Pheromone-baited traps have been tested as a means of sampling local moth populations and may be useful in measuring local dispersal of adults. Catches of male moths with very low pheromone concentrations showed only small variation within 164- by 164-ft (50- by 50-m) plots in tests by Sartwell and others (1983 unpubl.). Study site had a significant effect on trap catches (Liebhold and Volney 1984). On 15-acre (6-ha) plots with different silvicultural treatments, Fellin (1981 unpubl.) found that the number of moths trapped at a location varied considerably. In small plots, baits may alter dispersal patterns. Widely spaced traps over a gradient in elevation might be effective in detecting dispersal.

The potential of x-ray energy spectrometry in identifying the source of dispersing adults has been described by McLean and others (1979). The method is based on patterns shown by amounts of detectable elements in the new foliage and in the insect. Moths collected as large larvae and reared on the same tree foliage could be separated from moths from other plots 0.6 mi (1 km) away, but not from moths from adjacent trees in the same plot. A special technique was devised to characterize egg-laden females. Injection of Douglas-fir needle tissue with rubidium chloride resulted in detectable concentrations being found in egg masses from females from these trees, thus providing a basis for separating resident and immigrant egg production within a stand (McLean and others 1981 unpubl.).

Long-range dispersal of budworm moths has rarely been observed in the West. In Montana during August 1951, however, spectacular mass flights from stands in the Helena National Forest descended on the city of Helena, deluging the outside lighting (USDA Agricultural Research Service 1952). In John Day, OR, on August 18, 1955, aggregations of moths were noted on store windows, and females were laying eggs. North of this town, on August 8, 1957, a large flight was observed along a forest highway in the Malheur National Forest, but its course was undetermined. In British Columbia, mass flights of the 2-year budworm are commonly attracted to street lights of cities in the south interior; records for 1940, 1944, and 1948 indicate that, where weather conditions are known, moth flights were associated with unsettled weather featuring thunderstorms and showers (Mathers 1948).

3.2.1.3 Reproduction—Male moths occasionally flit about during the day, but their principal flight begins around dusk, in response to a sex pheromone emitted by the sedentary, unmated females. Temperatures of about 60 °F (about 16 °C) during the period of 2000 to 2300 hours are essential to their activity (McKnight 1971).

At both pheromone- and female-baited traps, female calling and male response reached their peaks at about 2100 (0.5 h after sunset) at a New Mexico site, and about 2200 (1.5 h after sunset) at a southern Oregon site. Male activity mostly ceases after midnight, but female calling continues through the night (Liebhold and Volney 1984). During their searches, males orient to foliage; either host or nonhost foliage was found to enhance catches at pheromone-baited traps, in contrast to those suspended in midair (Liebhold and Volney 1984). After a male finds a female, and after brief overtures, copulation occurs for a variable period, often overnight. Under adverse climatic conditions, copulation may continue for an extended period (McKnight 1971). Females normally commence egg-laying the next day.

Fecundity diminishes if adults are not mated within 24 h after they emerge (Lyon and others 1972). Fecundity may also be affected by the quality and quantity of food during the larval stage. In studies by Shore and McLean (1982 unpubl.), the heaviest females reared on three kinds of host foliage and those reared on an artificial diet were not characterized by higher fecundity, egg viability, or survival. Those fed on Engelmann spruce laid more eggs on the average than those fed on Douglas-fir and grand fir. Egg production by adults under confined conditions is suspect, however, because it is considerably less than the number of eggs contained in the abdomen of a female. Studies by Kirkbride and Wagner (1983a unpubl.) used potential fertility to determine whether pupal and adult characteristics were useful predictors of number of eggs in a female, and whether the host species had any effect on number of eggs. Fresh pupal weight was found to be a good predictor of total number of eggs, number of large eggs, and total number minus the very smallest eggs. Other useful predictors were pupal abdominal width, dry weight of pupal abdomen, and dry weight of adult. Some differences according to tree host were noted: fresh pupal weights for budworms reared on subalpine fir were significantly lower than those reared on Douglas-fir, white fir, and Engelmann spruce.

The proportion of female moths in a population may vary from year to year. In Colorado during two generations, female proportions ranged from 0.30 to 0.62; the proportion was higher on all plots in the 1965–66 generation than in 1964–65 (McKnight 1971). In 20 of 24 populations sampled in Montana, Idaho, and Oregon during 1980–81, Campbell and others (1983b) found that the proportion of females was not significantly different from 0.50; estimates for individual populations ranged from 0.41 to 0.63. Because males are capable of mating with more than one female (Campbell 1961), a drastic deviation would be required to affect fertilization.

3.2.2 Feeding Habits

The budworm feeds on many coniferous species but causes its greatest damage in forests of Douglas-fir, true firs, or mixtures of both. The hosts are described in chapter 4 and impact from budworm feeding is described in chapter 5. Old reports of pines as hosts apply to *C. lambertiana*, and northerly collections in Canada on fir and spruce are most frequently *biennis*. The budworm, along with its eastern counterpart, is amenable to large-scale rearing on artificial diets (Lyon and others 1972, Robertson 1979b).

The feeding sequence begins in spring with larvae mining old needles (fig. 3-6a) or pollen cones, continues with mining of expanding buds (fig. 3-6b), and gradually concludes with feeding on the new foliage, with larvae partially concealed by their webs (fig. 3-6c). Small larvae spin silken webs before entering needles, pollen cones, or buds; and large larvae spin sizable shelters, often tying two tips together and feeding on both of them.

Large larvae cut or damage as many or more needles than they consume (Blake and Wagner 1983b unpubl.). By the end of the feeding period, the damaged new growth, now webbed together in clumps, turns reddish or reddish brown and is highly visible. Fall rains wash off the damaged foliage, and the amount of needle loss becomes clearly evident.

Figure 3-6—Feeding habits. A = needle-mining,
with silken threads and frass around entrance
hole. B = bud-mining, with webbing and frass
around entrance hole. C = feeding on new shoot
by sixth instar in web.

Foliage consumption rates, feeding efficiency, and growth rates of larvae on major hosts in Arizona were studied by Wagner and Blake (1983 unpubl.); also see Blake and Wagner (1983b unpubl.). In limited tests, larvae ate less foliage, by weight, of Engelmann spruce and white fir than of Douglas-fir and corkbark fir. Larvae feeding on Engelmann spruce wasted less foliage by clipping needles than did larvae on white fir, corkbark fir, and Douglas-fir. Age of foliage affected survival; larvae feeding on late season foliage died before reaching maturity (Blake and Wagner 1983a unpubl.). Growth rate and efficiency of conversion of ingested food decreased with foliage age (Blake and Wagner 1983a unpubl.).

Foliage of occasional hosts may not provide late instars with proper nutrition for normal development. Beckwith (1983) found that survival on larch, after terminal shoots had started to elongate, was much lower than on Douglas-fir, subalpine fir, and Engelmann spruce, and that male and female pupae from larch weighed significantly less. Early feeding (before terminal shoots elongate) results in near-normal survival and pupal weight.

Some larvae go directly from hibernation to developing pollen cones and seed cones, particularly in good flower years. Larvae web pollen cones together and then bore into the bottom of the pollen-cone buds; they feed on the pollen, cutting some of the pollen-forming appendages in the process. Time spent in pollen cones depends on how moist the cones are. As many as 30 days may elapse before larvae move to new shoots (Carolin and Coulter 1972).

In the northern U.S. Rocky Mountains, part of the budworm population feeds on and in developing seed cones of Douglas-fir (Dewey 1970) and western larch (Fellin and Shearer 1968). Early instars kill conelets by mining or girdling cone axes near their bases; later instars consume seeds while mining Douglas-fir cones. Up to eight larvae may be found in a cone. Signs of insect feeding in small cones include silking and frass, excessive resin production, and distorted shape. In unsprayed seed orchards, cone survival may be reduced to 1 percent (Stipe and Hard 1980). With low budworm populations and a large Douglas-fir cone crop, 5 percent or less of the cones may be killed (Shearer and Tiernan 1981 unpubl.). Some damage to cones of Engelmann spruce and subalpine fir has been reported in this same region (Shearer and Tiernan 1981 unpubl.).

3.2.3 Stability of Life Stages for Sampling

Timing of sampling is based on separation of the life cycle of the insect into life-stage intervals when effects of specific mortality factors can be measured. During the sampling period, consideration is given to habits of the insect, life cycles of biotic control agents, and physical factors.

Sampling periods for estimating budworm populations designated by Carolin and Coulter (1972) were eggs, second instars in hibernacula, second instars in needle mines, larvae (mostly fourth instar) in buds, fifth and sixth instars, pupae, and moths. These are similar to periods described for the eastern budworm by Morris (1955), except that the principal parasites attacking large larvae are more likely to complete their development in pupae. The term "residual pupae" is used by Campbell and others (1984b) to describe pupae surviving predation as the life stage to be sampled when emergence is about 95 percent.

Two stages, eggs and larvae in buds, are the most stable for sampling because hatched egg masses persist for several months and because larvae in buds stay in place and suffer little mortality. Late pupae offer an opportunity for sampling but only for a few days. Other stages present serious sampling problems. For egg-mass sampling, standards for separating new from old egg masses are provided by Twardus and Carolin (1984). Sampling schemes have been devised for surveys (Carolin and Coulter 1972) and population research (Srivastava and others 1984). Sequential sampling plans based on distribution of life stages are available for classifying prespray and postspray larval populations to evaluate suppression results (Cole 1960) and egg-mass populations during surveys in the central and southern Rocky Mountains (McKnight and others 1970). A method for sampling budworm pupae was devised by Srivastava and others (1981).

3.3 Distribution on Trees

Over the past 30 years, the average size of forest trees in the West has diminished, and stand structure appreciably changed. With more of the foliage for conifer stands now found on smaller trees, intratree budworm distribution may be different from that found on larger trees sampled in the past.

Except during larval and adult dispersal, the budworm stays on its host trees, but its vertical and horizontal distribution changes from stage to stage. Waters and Volney (in press) found that at low densities, the insects appear to occur independently of one another; at higher densities, considerable aggregation occurs, and at extreme densities—when almost all available resting sites are occupied—the effects of aggregation become less apparent.

From studies in Washington, Oregon, Idaho, and Montana, Campbell and Srivastava (1983 unpubl.) found that among-tree aggregations of egg masses, eggs, fourth instars, residual pupae, and pupal cases were all inversely related to budworm density. At any given density, eggs were more aggregated than egg masses, fourth instars were less aggregated than the preceding eggs, residual pupae were more aggregated than the preceding fourth instars, and pupal cases were more aggregated than the preceding residual pupae. Within trees, aggregations of fourth instars, but not residual pupae, were also inversely related to density. Aggregations of both fourth instars and residual pupae within trees were less than those found among trees.

Strata to indicate vertical distribution are usually crown thirds (Campbell and others 1984b) and occasionally crown fourths. Horizontal strata include whole branches (Waters and Volney 1982 unpubl.), 24-inch (61-cm) branch tips (McKnight 1968), and 18-inch (45-cm) branch tips (Campbell and others 1984b). Analysis of distribution is based chiefly on two expressions: total number of budworm on a sample unit and budworm per unit of foliage area. For comparisons among tree species, number of larvae per 100 buds or new shoots has been used by several investigators, including Carolin and Coulter (1975) and Schmid (1984 unpubl.).

3.3.1 Egg Masses

Egg-mass distribution by crown thirds was found to differ between Douglas-fir and grand fir trees, 50 to 85 ft tall (15 to 25 m), in Oregon and Washington (Carolin and Coulter 1972, 1975) and between Douglas-fir and white fir trees in Colorado and New Mexico (Schmid and Farrar 1982). In both studies, density in the upper crown of Douglas-fir was higher than or similar to that in the middle third. Density was lowest in the lower third. On grand fir in Oregon and Washington, density was lowest in the lower third and increased with height in the crown. On white fir in Colorado and New Mexico, significantly higher egg-mass densities were found in the upper third. In both studies, Douglas-fir and true firs had similar densities in the upper crown, but Douglas-fir had higher densities in the lower and middle crown thirds. Thus, egg masses were more uniformly distributed on Douglas-fir trees than on either grand or white fir trees.

In recent studies in Washington, Oregon, Idaho, and Montana (Campbell and others 1984b), the distribution of egg-mass densities was similar between crown thirds of Douglas-fir and grand fir. Average densities on whole branches were a linear function of average densities on 18-inch (45-cm) terminal tips. Branches were taken from lower, mid, and upper crowns of short trees 13 to 23 ft (4 to 7 m), medium trees 23 to 46 ft (7 to 14 m), and tall trees greater than 46 ft (14 m). Egg-mass densities increased from lower to upper crowns and from short to tall trees. Egg-mass densities on short and medium trees were linearly related to densities on midcrown, 18-inch foliage tips. On tall trees, densities were described as linear functions of both an index of current defoliation and densities on midcrown terminal tips of short and medium trees.

3.3.2 Larvae in Hibernacula

Boxing limb and bole sections and then forcing larvae to light in a warm room has shown that most larvae are distributed with lichens, large bark scales, or both, on host trees. More larvae are found per unit area on the bole than on limbs of smooth-limbed trees (Denton 1953, Terrell 1959, Wright and others 1952 unpubl.). Distribution of hibernating larvae differs from stand to stand according to host-tree characteristics. For finding and counting these larvae, the light-attraction technique was superior to use of sodium hydroxide solution to dissolve the hibernacula (Egan and Beckwith 1983 unpubl.).

In moderate to heavy populations on pole-sized Douglas-fir in Colorado, larvae hibernated on boles, foliage, twigs, and branch stems at all crown levels; about 65 percent were on the branches and 35 percent on the boles (McKnight 1969a). On branches, these figures represent distribution by crown thirds: upper, 10 percent; middle, 24 percent; lower, 27 percent; and dead limbs on the lower bole, 4 percent. The following are corresponding figures for distribution on the bole: upper, 5 percent; middle, 14 percent; lower, 12 percent; and on the lower bole, 4 percent. Total percentages of larvae on branches and boles were similar for middle and lower crown thirds—38 and 39, respectively. Horizontal distribution of all larvae on branches included 11 percent on the basal 1.2 ft (30.5 cm), 25 percent on the rest of the stem, and 29 percent on foliage and twigs.

In sparse populations on dominant and codominant Douglas-fir, 31 to 62 ft tall (9.6 to 18.9 m), in north-central Washington, a higher proportion of hibernating larvae was found on the boles, compared with the Colorado study (Eldridge and Egan 1983a unpubl.): 61 percent were on the boles, 21 percent on branch stems, and 18 percent on foliated twigs. For 15 of 20 trees, highest densities per unit area for bole samples occurred on the lower half, and mostly in proximity to the lower crown. Densities on branch stems were usually highest in the lower half of the crown; densities were more uniformly distributed on foliated twigs. In these low populations, a poor correlation was found between larval densities on boles and those on branch stems.

On Douglas-fir sampled at midcrown in eastern Oregon, numbers of hibernating larvae appeared to be related to density of lichens (Carolin and Coulter 1972). Also, on trees with highest populations, limbs (branch stems) sheltered more larvae than did adjacent bole areas; on trees with low populations, more larvae were found on the adjacent bole area than on the limbs, and an increased proportion of larvae were on foliated parts. The low populations sampled by Eldridge and Egan (1983a unpubl.) appear to follow the latter distribution.

3.3.3 Fourth Instars in Buds

On 468 branches from three crown levels on 44 Douglas-fir and 8 grand fir trees 23 to 46 ft tall (7 to 14 m), densities at midcrown fell between those in lower and upper crowns in 62 percent of the cases (Campbell and others 1984b). Earlier work in Oregon with a limited number of Douglas-fir trees more than 49 ft tall (15 m) showed no significant differences among crown levels as to number on whole branches or density based on foliage area (Carolin and Coulter 1972). The middle crown appears to have average numbers per branch and average densities of larvae for the tree. Midcrown samples were also representative of fifth-instar densities on the tree (Williams and others 1971).

Schmid (1984 unpubl.) used two expressions, larvae per square meter of foliage and larvae per 100 buds, to compare larval densities on seedlings, saplings, and the lower and middle crowns of 26- to 75-ft-tall (8- to 23-m) trees of both Douglas-fir and white fir. On both species, using either unit, densities on saplings were not significantly lower than on the two crown levels on tall trees, but densities on seedlings were significantly lower than on the tall trees. On Douglas-fir, using either unit, densities in middle and lower crowns were similar. On white fir, densities per square meter of foliage were significantly higher at middle crown for two of three sampling designs. Using larvae per 100 buds, no significant differences were found between crown levels for all three sampling designs.

3.3.4 Pupae

Distribution was determined for residual pupae by crown thirds at locations in Washington, Oregon, Idaho, and Montana by Campbell and others (1984b). Pupal densities were lowest in the lower crown of short (13- to 23-ft) trees, higher (and about the same) in the mid and upper crowns of short trees and the lower crowns of medium (23- to 46-ft) ones, higher in the lower crowns of tall (greater than 46-ft) trees, still higher in the midcrowns of medium and tall trees, and highest in the upper crowns of medium and tall trees. In all height classes, average pupal density per square meter of foliage in the whole tree was consistently higher than density in the lower crown. Pupal densities per square meter of foliage in tall trees were virtually indistinguishable from densities in medium ones. Densities were generally lower, however, in short trees.

The relations of budworm development to the duration of bud swelling and rate of shoot growth are important in affecting degree of defoliation. Early studies in eastern Oregon showed that budburst on grand fir occurred about 7 days sooner than on Douglas-fir (Carolin and Coulter 1972). Subsequent observations suggest that stand exposure may affect relative time of budburst and that abnormal weather may alter normal patterns of shoot growth as well as the proportion of larvae mining old needles. In southwest Oregon, budburst of white fir occurs slightly before that of Douglas-fir (Volney and Waters 1983 unpubl.). In the northern Rocky Mountains of the United States, defoliation trend varied with mean maximum temperature and mean measurable precipitation of the previous year (Hard and others 1980).

The phenology of shoot growth on grand fir in eastern Oregon and its relation to budworm development was studied by Wagg (1958). Growth of lateral shoots was related to accumulated degree-days over 42 °F (5.6 °C) but was more rapid in open stands than in closed stands. Budworm development from the third to succeeding instars was related to the increase in accumulated degree-days. Incidence of the fourth instar was correlated with the flowering of 21 plant species.

Similar studies were conducted for both Douglas-fir and grand fir in eastern Oregon by Beckwith and Kemp (1984). Shoot-growth models, based on degree-days and mean shoot length, were generated for each crown level by tree species, and rather large differences found in growth characteristics between Douglas-fir and grand fir. Models indicated greatest shoot length in the upper crown and lowest in the lower crown. After buds had flushed, shoot development expressed as a percentage of total shoot growth was slightly ahead on Douglas-fir, but grand fir then exceeded Douglas-fir in rate of growth. At the last examination, shoot development was similar on the two species, and 93 to 95 percent complete. The numbers of degree-days required for shoot elongation and for budworm development were similar to the same parameters found by Wagg (1958).

In eastern Oregon and Washington, Douglas-fir
showed less damage than grand fir over a given
period of time; at similar budworm densities per unit
number of buds or shoots, grand fir showed more
defoliation than Douglas-fir (Carolin and Coulter
1975). In New Mexico, Douglas-fir and white fir react
differently to repeated budworm feeding. Heavy
feeding on Douglas-fir apparently induces latent buds
to flush and expand as shoots; few if any such buds
are activated on white fir (Volney and Waters 1983
unpubl.). The number of white fir buds declined
substantially during a season of intensive budworm
feeding, but the number of Douglas-fir buds did not.
Thus, high populations may persist for longer periods
on Douglas-fir than on white fir before tree mortality
occurs.

Other site and stand characteristics influence the
duration and intensity of outbreaks. The relations
among site, stand, and host characteristics as they
relate to outbreak severity are detailed in chapter 7.

Chapter 4

Description of Host Species

Richard K. Hermann

4.1 Introduction

The principal hosts of western budworm are:
Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco),
grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.),
white fir (*A. concolor* (Gord. and Glend.) Lindl. ex Hildebr.),
subalpine fir (*A. lasiocarpa* (Hook.) Nutt.),
Engelmann spruce (*Picea engelmannii* Parry ex Engelm.),
western larch (*Larix occidentalis* Nutt.).

Budworm occasionally feed on or are associated with:
white spruce (*Picea glauca* (Moench) Voss),
Colorado blue spruce (*P. pungens* Engelm.),
ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.),
lodgepole pine (*P. contorta* Dougl. ex Loud.),
limber pine (*P. flexilis* James),
western white pine (*P. monticola* Dougl. ex D. Don),
whitebark pine (*P. albicaulis* Engelm.),
western hemlock (*Tsuga heterophylla* (Raf.) Sarg.),
mountain hemlock (*T. mertensiana* (Bong.) Carr.),
Pacific silver fir (*Abies amabilis* Dougl. ex Forbes).

Although occasional hosts may be important in various ways to the population ecology of the budworm, they cannot in themselves support a continuing outbreak of the insect; therefore, here and elsewhere in this series of books, these occasional hosts are considered nonhosts.

The host species vary considerably in importance in the various forest regions of the West. Commercially, Douglas-fir is the most important. True firs are probably next in importance, followed by Engelmann spruce, western larch, and white spruce (table 4-1).

Table 4-1—Net volume of growing stock on commercial timberland of principal host species of budworm as of January 1, 1977 (source: "An analysis of the timber situation in the United States 1952–2030," Forest Resource Report 23, U.S. Department of Agriculture, Forest Service, Washington, DC, 1982. 499 p.)

Douglas-fir	True firs	Engelmann spruce	Western larch
		Million ft³ *(million m³)*	
93,502	43,496	16,705	6,444
(2 650)	(1 230)	(473)	(182)

Annual removals of growing stock on commercial timberlands			
		Thousand ft³ *(thousand m³)*	
1,964,800	503,198	———[1]618,353———	
(55 640)	(14 250)	(17 510)	

[1]Combined figure for softwoods other than Douglas-fir and true firs.

4.2 Geographic Distribution

4.2.1 Latitudinal and Longitudinal Range

Ranges of the principal host species are shown in figure 4-1. The geographic ranges of two or more of the principal host species overlap in many places (table 4-2). Overlap of ranges, however, does not necessarily imply that these species share the same sites.

Douglas-Fir   Grand Fir

White Fir   Subalpine Fir

Engelmann Spruce   Western Larch
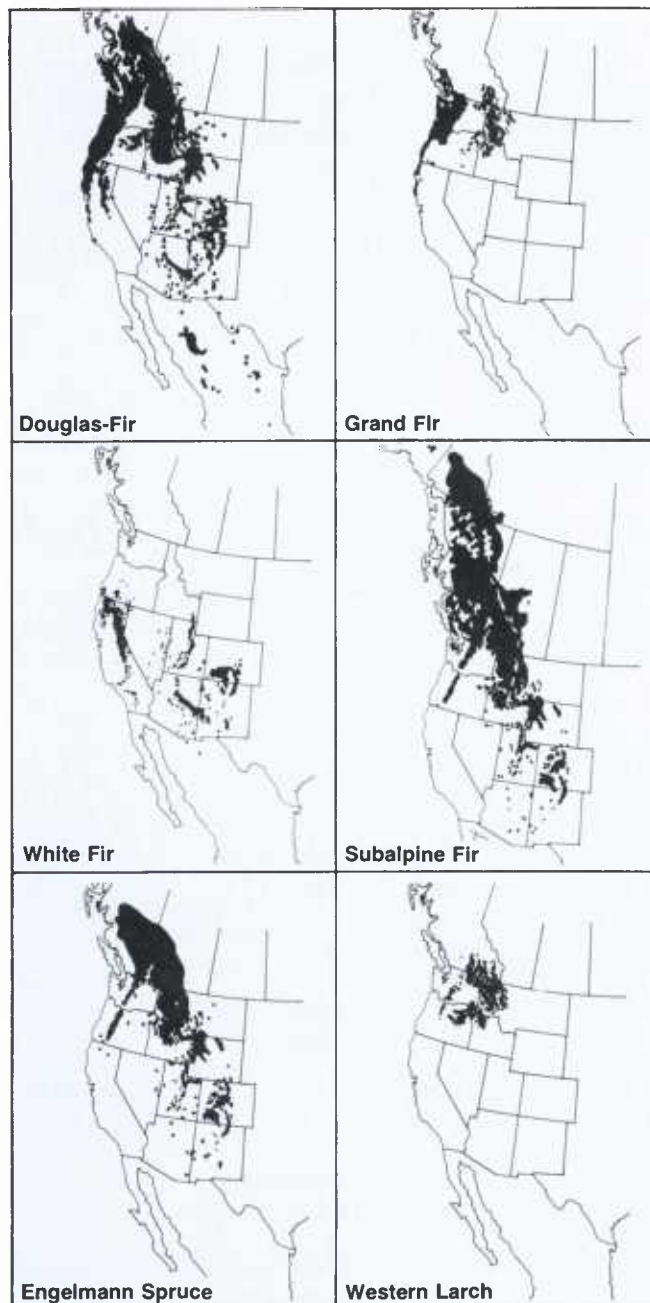
Figure 4-1—Distribution of budworm hosts (Little 1971).

4.2.2 Elevational Range

In general, altitudinal distribution of host species increases from north to south (table 4-3). This is particularly apparent in species with a huge latitudinal range.

Douglas-fir, subalpine fir, and Engelmann spruce grow to markedly higher elevations in the eastern part of their ranges. In some localities in southern and central Arizona, Douglas-fir may occur as low as 5,100 ft (1555 m) in canyon bottoms. On north-facing slopes, subalpine fir may go up to 12,000 ft (3650 m) in the southern Rocky Mountains.

A comparison of the species by regions (table 4-3) indicates that their elevational ranges are often nearly identical. Species tend to shift gradually from south- to north-facing exposures at the upper ends of their elevational ranges toward the southern limits of their distribution.

4.2.3 Genetic Variation

Considerable genetic variation may be expected in species that occupy a large range under widely differing conditions of climate, topography, and soils. Knowledge of such variation, however, is still far from complete. Dendrologists recognize two varieties of Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.), the interior variety; and *P. menziesii* var. *menziesii*, the typical coastal Douglas-fir. The taxonomic separation will probably be maintained for botanical convenience but seems not well justified in view of the clinal nature of both morphological and biochemical traits over the range of the species and the variability of types in a locality.

Studies of morphological as well as physiological traits—such as photoperiod, thermoperiod, and photosynthetic rates, biochemical determinations of monoterpenes, isoenzymes, and DNA (deoxyribonucleic acid) content—have revealed remarkable genetic variation in Douglas-fir. Such variation has also been documented for several traits—phenological, growth, form, and resistance (Silen 1978). Most traits display clinal variation, but a few vary ecotypically.

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Table 4-2—Occurrence of host-tree species in western North America

Douglas-fir	Subalpine fir	Engelmann spruce	White fir	Grand fir	Western larch
—	Alaska	—	—	—	—
—	Yukon Territory	—	—	—	—
British Columbia (Alberta)[1]	British Columbia	British Columbia	—	British Columbia	British Columbia
Washington	Alberta	Alberta	—	—	—
Oregon	Washington	Washington	—	Washington	Washington
California	Oregon	Oregon	Oregon	Oregon	Oregon
Idaho	—	(California)	California	California	—
Montana	Idaho	Idaho	(Idaho)	Idaho	Idaho
Wyoming	Montana	Montana	—	Montana	Montana
(Nevada)	Wyoming	Wyoming	—	—	—
Utah	(Nevada)	(Nevada)	Nevada	—	—
Arizona	Utah	Utah	Utah	—	—
Colorado	Arizona	Arizona	Arizona	—	—
New Mexico	Colorado	Colorado	Colorado	—	—
Texas	New Mexico	New Mexico	New Mexico	—	—
Mexico	—	—	—	—	—
	—	—	Mexico	—	—

[1]Parentheses indicate limited distribution.

Table 4-3—Elevational distribution in feet (meters) of host-tree species by region

Area	Douglas-fir	Subalpine fir	Engelmann spruce	Grand fir	White fir	Western larch
Alaska	—	0–3,500 (0–1 067)	—	—	—	—
British Columbia	0–2,500 (0–760)	2,000–5,000 (610–1 524)	2,500–3,500 (762–1 067)	0–1,000 (0–300)	—	—
Washington and Oregon	0–5,000 (0–1 525)	5,000–7,500 (1 524–2 286)	4,000–6,000 (1 219–1 829)	[1]W 3,300 (1 000) E 5,200 (1 600)	3,000–6,000 (900–1 830)	2,000–7,000 (600–2 100
Sierra Nevada	3,900–7,500 (1 200–2 300)	—	4,000–5,000 (1 219–1 524)	—	3,900–7,900 (200–2 400)	—
Northern Rockies	1,200–8,000 (370–2 450)	5,000–9,000 (1 524–2 473)	1,000–2,000 [2](610–3 352)	1,300–6,500 (400–2 000)	—	2,000–5,000 (600–1 520)
Central Rockies	6,000–8,500 (1 830–2 600)	9,000–11,000 (2 473–3 352)	9,000–11,000 (2 473–3 353)	—	5,900–8,900 (1 800–2 700)	—
Southern Rockies	8,000–9,000 (2 450–2 900)	9,500–11,000 (2 895–3 352)	9,500–11,000 (2 895–3 353)	—	6,900–11,000 (2 100–3 350)	—

[1]W = West of Cascade Crest. E = East of Cascade Crest.
[2]Westerly half 5,000–7,000 ft (1 524–2 134 m).

Adaptation of Douglas-fir to variations in annual precipitation patterns over its natural range has apparently been a major factor in differentiation of the species. Selection response to a decrease in precipitation and humidity behind successively higher north–south mountain ranges from the Coast Ranges through the Rocky Mountains is reflected by differences in growth rates. Races have the highest inherent rates of growth along the Pacific slopes, where annual moisture is generally more plentiful. Slowest growing races characterize the interior basin and east slope of the Rocky Mountains, where cyclic droughts can extend over several years. Arizona and New Mexico sources range from slow to moderately fast growing under the influence of more plentiful summer rains. This generalized clinal pattern of Douglas-fir growth over its range has long been apparent, as has a general inverse relation between growth and cold hardiness or drought resistance.

Proportions of various terpenes in needles, bark, and seeds differ considerably between races of Douglas-fir and permit distinctions among populations. Several of these terpenes have been shown to confer resistance to budworm in populations from Idaho and New Mexico (Cates and others 1983a, 1983b). Differential defoliation by budworm of neighboring Douglas-fir trees may indicate that some Douglas-fir genotypes are more resistant than others (Cates and others 1983a, McDonald 1981). Differences in susceptibility to budworm appear correlated with provenance (McDonald 1979). Content of chlorogenic acid is a highly heritable trait known to confer resistance against animals and might be important in resistance of Douglas-fir to budworm.

Proportions of terpenes apparently vary among crown levels and over time. In a single Douglas-fir tree from New Mexico, the lower crown was higher in bornyl acetate; the mid and upper crowns were highest in camphene and cadinene (Gambliel and Cates, personal communication). In another single-tree study, five samples were taken at three different times from mid-June to mid-September, 1982. The terpenes alpha-pinene, camphene, limonene, and an unidentified sesquiterpene progressively increased through the summer, while over the same period, beta-pinene, myrcene, and another unidentified sesquiterpene significantly decreased (Cates and Gambliel, personal communication).

Engelmann and white spruce are closely related species and hybridize where their ranges overlap (LaRoi and Dugle 1968) (fig. 4-2). Almost all the available information on genetic variation in Engelmann spruce comes from studies of the Engelmann–white spruce complex, rather than from studies dealing exclusively with Engelmann spruce (Fowler and Roche 1975).
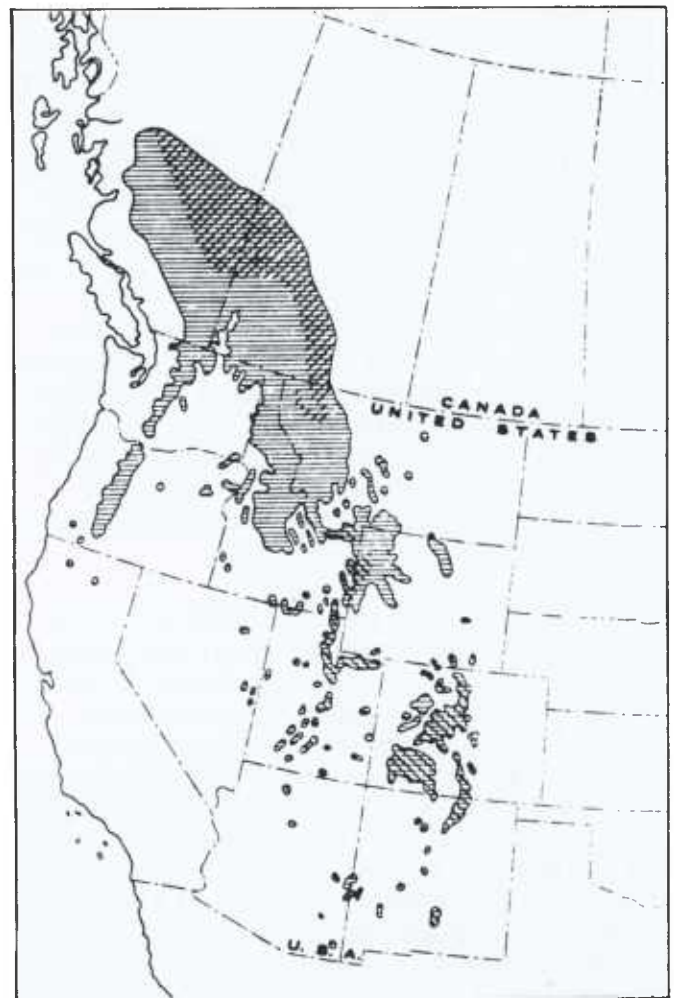
Figure 4-2— Natural range of Engelmann spruce (horizontal pattern) showing overlapping range of white spruce in the northern part of the range and blue spruce in the southern (Fowler and Roche 1975).

Cone-scale form appears to be the most useful morphological characteristic for delineating hybrid zones. Throughout the Engelmann–white spruce complex in British Columbia, cone-scale morphology varies progressively from typical low-elevation white spruce to typical subalpine Engelmann spruce. According to Roche (1969), the hybrid zone lies between 4,500 and 6,000 ft (1370 and 1830 m) in the Canadian Rocky Mountains, and in British Columbia east of the Rocky Mountains between 2,700 and 3,400 ft (825 and 1035 m). Based on cone-scale morphology, Horton (1959) classified spruce stands in the Rocky Mountains of Alberta as pure white spruce, an intermediate form, and pure Engelmann spruce. Easily definable extremes of site were recognized for each of these three taxonomic groups and were classified as hot and dry, normal and fresh, and cool and moist.

The clinal pattern of morphological variation in the Engelmann–white spruce complex in western Canada is apparently the result of introgressive hybridization, followed by habitat-correlated selection (Fowler and Roche 1975). The pattern of variation determined by physiological (Roche 1969) and chemosystematic (Hanover and Wilkinson 1970) studies parallels that found in morphological studies.

Information is scant on genetic variation in true firs. Grand fir and white fir hybridize where their ranges overlap. Müller's (1938) often-cited division of *Abies grandis* into five climatic races appears no longer tenable. Studies of morphological and physiological characteristics of grand and white fir, summarized by Steinhoff (1978), indicate that some of Müller's races represent forms that originated through hybridization and introgression of the two species. These intermediate populations occur in an area from northwestern California through Oregon into north-central Idaho (fig. 4-3). Chemotaxonomic investigations (Zavarin and others 1979) have also contributed to better distinction between grand and white fir and their intermediate forms. Surprisingly, grand fir itself shows little differentiation in its chemical constituents used for chemotaxonomic studies. Pacific coast and Rocky Mountain

populations do not appear to differ in the composition of their terpenes (Zavarin and others 1977). Provenance experiments with grand fir in Europe, summarized by Hermann and Birot (1978), point to clinal variation of the species in a north–south direction—both in the western and eastern part of its range—rather than the kind of genetic variation described by Müller (1938).

Genetic variability of white fir is considerable between populations from the Rocky Mountains and its western range. Some authors (Liu 1971, Schenck 1939) consider variation in morphological and growth characteristics between coastal and Rocky Mountain white fir large enough to recognize the former as variety *lowiana*. Genetic variability among nearby populations appears to be common; it is frequently associated with differences in soil, aspect, or elevation (Libby 1982). Evidence of clinal variation has been reported for interior white fir by Sturgeon and Mitton (1980).

Considerable genetic variability may be expected in a wide-ranging species such as subalpine fir. Pertinent studies are scarce, probably because subalpine fir has been of little commercial interest. *Abies lasiocarpa* is known to hybridize with *A. balsamea* in eastern Alberta. Hunt and von Rudloff (1979) demonstrated the existence of a coastal and Rocky Mountain type of subalpine fir on the basis of both chemical and morphological characteristics (fig. 4-4). The Rocky Mountain type has also been referred to as a separate species, *A. bifolia*. The taxonomic status, however, of the *A. lasiocarpa-A. bifolia-A. balsamea* complex needs further clarification (Hunt and von Rudloff 1983). Corkbark fir (*Abies lasiocarpa* var. *arizonica*) is the only recognized natural geographic variety of subalpine fir (Little 1979).

4.2.4 Stand Composition

Host species of the budworm occur in both pure and mixed stands. This brief account on stand composition is based largely on "Forest Cover Types of the United States and Canada" (Eyre 1980). Forest cover types are named after predominant tree species actually present. Predominance is determined by basal area, and the name of the cover type is usually confined to one or two species.
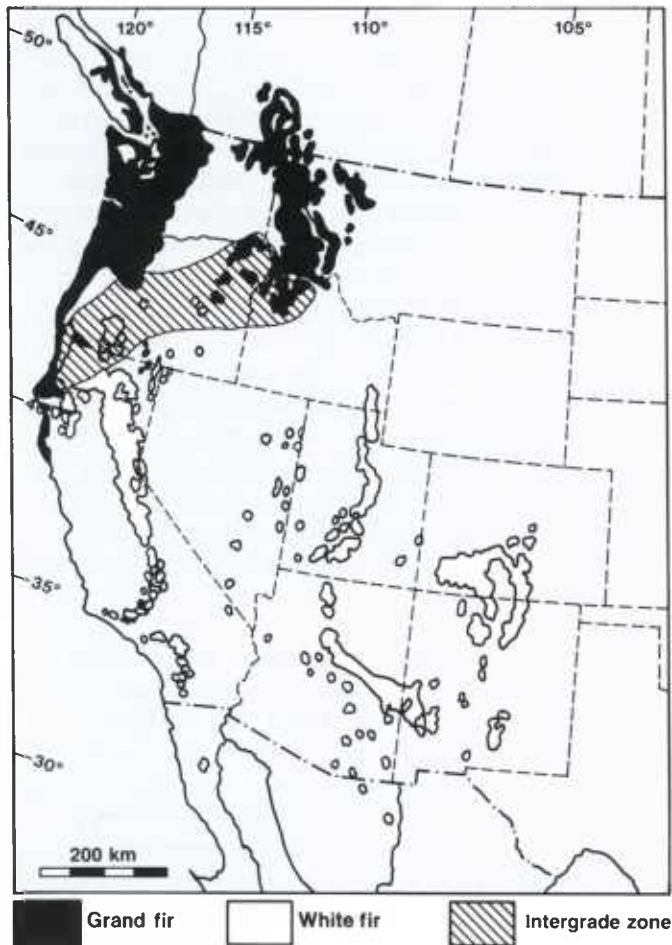
Figure 4-3—Geographic distribution of grand fir and white fir and the area where they intergrade (from Steinhoff 1978).

Figure 4-4—Range map of subalpine fir and distribution of coastal, Rocky Mountain, and intermediate forms based on terpene hybridization studies (Reprinted by permission, from Hunt and von Rudloff 1983. Population numbers refer to a table in the original source.)

Interior Douglas-fir grows in pure or nearly pure stands in parts of eastern Washington and Oregon, interior British Columbia, and the northern and central Rocky Mountains. Elsewhere it associates with most other tree species that grow in the interior mountain ranges. These include all other host species of the budworm: grand fir and western larch at low and mid elevations in the northern Rocky Mountains; Engelmann spruce, subalpine fir, and white fir at high elevations throughout the entire Rocky Mountain Range.

Coastal Douglas-fir forms extensive or almost pure stands in southwestern British Columbia and west of the crest of the Cascade Range in Washington and Oregon south to about latitude 43 °N. In these areas, western hemlock is a major associate in mixed stands. Farther south, pure stands become increasingly discontinuous. Of the many tree species found in mixture with coastal Douglas-fir, only two—grand fir and white fir—are hosts of budworm.

Douglas-fir is a major component of five forest cover types (interior Douglas-fir, coastal Douglas-fir, Douglas-fir/western hemlock, Douglas-fir/tanoak/Pacific madrone, Pacific ponderosa pine/Douglas-fir) and a minor component of 27 additional forest cover types.

Grand fir, as a rule, occurs mixed with other species. Exceptions are the Clearwater and Nezperce regions of central Idaho, where it forms pure stands. Grand fir is a major component in the grand fir forest cover type and a minor component in 18 additional cover types.

White fir forms nearly pure stands over large areas in northern and central California. In Oregon and the Rocky Mountains, it is usually present in mixed stands. White fir is a major component in the white fir cover type and a minor component in 11 additional types.

Both Engelmann spruce and subalpine fir may form pure stands, but more often they are found in association with each other or other tree species. These two species are the principal ones in the Engelmann spruce/subalpine fir cover type and are components of 13 additional ones (mountain hemlock, whitebark pine, bristlecone pine, interior Douglas-fir, western larch, grand fir, western white pine, blue spruce, aspen, lodgepole pine, limber pine, western hemlock, and coastal true fir/hemlock). Engelmann spruce is also a minor component of one cover type, and subalpine fir of four additional types.

Western larch grows rarely in pure stands except at young ages. Its commonest associate is Douglas-fir. Mixtures with grand fir or ponderosa pine are also significant. It is the principal species of the western larch forest cover type and is represented in 12 additional types.

4.2.5 Ecological Relations

Except in its youth, when it is reasonably tolerant of shade, coastal Douglas-fir ranks below most of its common associates in shade tolerance (Minore 1979). In its interior range, Douglas-fir is intermediate, being more tolerant than western larch, ponderosa pine, lodgepole pine, southwestern white pine, and aspen (Daniel 1980).

The coastal variety is seral, except on extremely dry sites in southwestern British Columbia (Krajina 1965), southwestern Oregon, and northern California. In its interior range, Douglas-fir is both climax and seral. In the northern Rocky Mountains, it replaces ponderosa pine, lodgepole pine, and western larch above the ponderosa pine belt; in turn, it is replaced by western redcedar, western hemlock, Engelmann spruce, grand fir, and subalpine fir on cooler and wetter sites. In the southern Rocky Mountains, Douglas-fir is a climax species in several habitat types of the mixed conifer forest and a seral species in the spruce–fir forests. The natural occurrence of Douglas-fir in extensive even-aged stands is mainly a consequence of catastrophic forest fires. The rapid growth, longevity, and the thick, corky bark of lower boles and main roots have enabled Douglas-fir to survive less fire-resistant associates and to remain a dominant element in western forests.

Grand fir is relatively shade tolerant and therefore often occurs as an intermediate or in the understory. In the Pacific coast region, grand fir is either a subclimax or climax species. In the lower, warmer, and drier parts of its interior range, grand fir is a climax species but seral in the upper, cooler, and moister parts. In the absence of fire, grand fir can replace intolerant and semitolerant species such as western larch, ponderosa pine, lodgepole pine, western white pine, and Douglas-fir. Grand fir is usually replaced in the course of succession, where it is associated with the very shade-tolerant western hemlock and western redcedar, unless wildfire intervenes and delays succession to the climax stage (Hall 1982).

White fir is also considered a climax species. It is rated from shade-tolerant to very tolerant, tolerance remaining strong from seedling stage to maturity. In the absence of fire, it replaces its less tolerant associates on mesic sites (Hopkins 1982). In its interior range, white fir is more tolerant than any of its associates, except Engelmann spruce and subalpine fir. Drought tolerance of white fir is not sufficient, however, for it to compete successfully with ponderosa pine on the lower, drier sites in the Rocky Mountains.

Both Engelmann spruce and subalpine fir are considered climax species in the Rocky Mountains north and south of Montana and Idaho. In the Rocky Mountains of these two States and in Utah, eastern Oregon, and Washington, however, subalpine fir is the major climax species. Although Engelmann spruce may also occur as the climax, frequently it is a persistent, long-lived subclimax species.

Alexander (1974) observed that the composition of spruce–fir forests varies considerably with elevation. At mid-elevations of 10,000 to 11,000 ft (3050 to 3350 m), these forests are frequently pure spruce in the overstory with fir predominating in the understory. In the central Rocky Mountains, for example, spruce commonly makes up 70 percent or more of the overstory basal area, and fir from two-thirds to three-fourths of the understory and advance reproduction. This structure has developed under natural conditions because spruce is more exacting in its seedbed requirements and less able to compete with fir under low light intensities common to dense forests. Once established, however, spruce lives longer than fir and is less susceptible to disease. At higher elevations, spruce may form essentially pure stands; but at lower elevations, where sites are usually drier, the density of spruce relative to fir may be low.

Western larch is shade intolerant. It is always a seral species that is favored by wildfire. In the absence of disturbance, more shade-tolerant species—Douglas-fir on dry sites; grand fir on warm, moist sites; or subalpine fir on cool, moist sites—will succeed western larch (Shearer 1980b).

4.2.6 Phenology of Reproduction[1]

Calendar date for phenological events differs for all of the host species with latitude, elevation, individual trees in a given locality, and by position within individual tree crowns. Timing will also differ from year to year, depending on weather. Phenological observations on host species of the budworm in the northern U.S. Rocky Mountains are summarized by Schmidt and Lotan (1980).

In all six species, reproductive buds begin to develop the year before flowering. Male and female strobili are borne separately on the same tree, and fruits are mature in the fall of the year when trees flower.

In the interior variety of Douglas-fir, early flowering occurs in mid-April to early May in Colorado and as late as early May to the end of June in northern Idaho and central Oregon. Cone ripening varies from late July at lower elevations in Montana to mid-August in northern Idaho. Seed dispersal begins in mid-August in central Oregon and occurs as late as mid-September at higher elevations in Montana.

The phenology of flowering is similar for the coastal variety of Douglas-fir. Flowering may occur as early as mid-March in the warmer parts of its range and as late as early June in colder areas. At low and middle elevations, cones mature and seeds ripen from mid-August in the southern to mid-September in the northern part of the range. Seed fall occurs soon after cone maturity with, generally, two-thirds of the total crop on the ground by the end of September.

Grand fir starts flowering as early as late March at low elevations in California and as late as mid-June at higher elevations in Oregon and northern Idaho. Seed dispersal generally starts from late August to mid-September at low elevations in western Washington and Oregon, and as late as early October at higher elevations. In the interior part of the range, dissemination begins in early September and often extends well into winter.

White fir generally flowers in May or June. Pollen is disseminated during the last half of May. Cones begin to disintegrate and shed seeds in late September or early October.

Subalpine fir flowers late, from late June to early July in northern Idaho and in early to mid-July in eastern Montana. In the Oregon Cascades, flowering may be as early as the end of May and as late as early July. Cones ripen in mid and late August and start shedding seeds in September.

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[1]Unless otherwise indicated, material in sections 4.2.6 and 4.2.7 is drawn from "Seeds of Woody Plants in the United States," Agriculture Handbook No. 450: U.S. Department of Agriculture, Forest Service, Washington, DC, 1974. 883 p.

Male flowers of Engelmann spruce ripen and pollen flight occurs in June at lower elevations and in July at higher elevations. Cones mature during August and September, and seed dispersal begins near the end of September or in early October. Most of the seed is shed by the end of October, although some seeds continue to fall throughout the winter.

Depending on elevation, flowering of western larch occurs from April to June. Cones ripen by the end of August or in early September. Shedding of seeds begins in mid-September or early October. About 90 percent of the sound seed is disseminated by the end of October.

4.2.7 Cone Crops and Seed Production

Seed production in each of the host species may be reduced by adverse climatic conditions and biological factors. Budworm can have an adverse impact on cone production directly through larval feeding and indirectly through defoliation. Damage to cone crops through feeding of budworm larvae on developing and immature cones has been reported for Douglas-fir (Dewey 1970), grand fir, white fir, subalpine fir, Engelmann spruce, and western larch (Fellin and Shearer 1968). Budworm may also hinder seed production of western larch by severing cone-bearing twigs (Fellin and Schmidt 1967). Results of a study by Chrisman and others (1983) show that budworm infestations reduced cone production in Douglas-fir stands in western Montana. Limitations of the sampling method, however, did not permit distinction between losses from failure of reproductive bud differentiation caused by stress produced by defoliation and losses from budworm feeding during the early stages of budburst and flower development.

Douglas-fir commonly begins to produce strobili at 12 to 15 years. Cone crops are irregular—one heavy and one medium crop every 7 years on the average. Even during heavy seed years, only about 25 percent of the trees produce an appreciable number of cones. Trees 200 to 300 years old produce the greatest number of cones. A stand of old-growth Douglas-fir may produce 20 to 30 times the number of cones per hectare that a second-growth stand 50 to 100 years old produces.

Grand fir begins to bear seed at about age 20. In general, large seed crops occur at 2- to 3-year intervals. In the northern U.S. Rocky Mountains, however, grand fir has been reported to be a poor cone producer, bearing only two fair cone crops over an 8-year period.

The earliest seed-bearing age for white fir is considered to be 40 years, and the optimal cone-producing age is from 50 to 100 years. Tree size influences cone production; trees from 12 to 36 inches (30 to 90 cm) d.b.h. are the best cone producers. In the western part of its range, white fir produces heavy cone crops at 3- to 9-year intervals. In the Rocky Mountains, good seed crops are produced at irregular intervals of 2 to 4 years.

Cone production of subalpine fir starts at about age 20 and reaches a peak in 150- to 200-year-old dominant trees. Good seed crops are borne on an average of every 3 years. A 28-year record of cone crops in northeastern Utah indicates that the average interval between good or better cone crops is 5.75 years (Henderson 1982).

Common to these true fir species is the high percentage of empty or sterile seeds—as high as 75 percent.

Engelmann spruce begins bearing cones between 16 and 25 years of age. The largest amount of seed is produced by dominant trees of 18 to 20 inches (45 to 50 cm) d.b.h. and between 200 and 250 years of age. The interval between large seed crops is 2 to 3 years.

Western larch reaches cone-bearing age at about 25 years. It bears cones abundantly from age 40 to 50 and continues to bear for 300 to 400 years. Because western larch bears cones throughout the crown, seed production is generally proportional to the size of the crown. Therefore, only dominant and codominant trees are effective producers of seed. The species produces good seed crops at intervals ranging from 1 to 10 years. The percentage of soundness of seed is low with poor seed crops and increases with size of crop.

4.2.8 Phenology of Vegetative Growth

Time of flushing of vegetative buds, a key component in the population dynamics of many species of defoliating insects (Thomson 1979), is influenced both by environmental and genetic factors (White and others 1979).

In coastal Douglas-fir, flushing appears to be under multifactorial genetic control (Irgens-Moller 1967). Silen (1962) attributes 96 percent of variation of bud flush among trees within 1 year to genetic makeup. His view is supported by observations that the same trees flush earliest or latest each year, although the dates may change markedly (Griffith 1968, Morris and others 1957). Time of budburst is also age-dependent, with younger plants flushing earlier (Irgens-Moller 1967). In young trees, lateral buds generally flush before terminals (Sweet 1965, Walters and Soos 1963). Among the laterals, in young trees, buds on the south side and close to the ground flush first (Irgens-Moller 1967), suggesting a microclimatic effect on the sequence of flushing.

Provenances from low elevations and lower latitudes tend to have an earlier budburst than those from high altitudes and higher latitudes. An average delay in budburst of 5 days per 400 ft (122 m) in elevation of seed source, and of 4 days per degree of latitude, may generally be expected for coastal provenances (Campbell 1974). Certain topographic features may result in deviations from these general patterns. For instance, budburst of races from the floor of narrow valleys characterized by cold-air drainages is later than for races from broad valleys (Morris and others 1957). Abrupt climatic changes in mountainous terrain, as is common in parts of the northern U.S. Rocky Mountains, for example, are reflected by considerable variation in date of budburst over relatively short distances (Rehfeldt 1978). The effect of topographic features on timing of budburst may reflect not only differences in air temperature but also differences in soil temperature (Sorensen and Campbell 1978).

Thomson and Moncrieff (1982) developed a procedure for prediction of budburst in Douglas-fir based on degree-day accumulation. The values they obtained are an empirical fit to observations on 154 trees over a 10-year period. The relation of these values to physiological characteristics, differences among provenances, and between young and mature trees still need to be determined. In spite of these limitations, their method appears to have high predictive power from relatively few observations.

Information is scarce on pattern of budburst in the other host species. Wickman (1976a) found budburst of grand fir and Douglas-fir in northeastern Oregon to be closely related to accumulated degree-days. Budburst was earliest at lower elevations where heat-unit accumulation was fastest. Budburst often occurred first on the most open-grown trees, the upper crown of large trees, and sometimes on the south side of trees. In general, budburst of Douglas-fir lagged several days behind that of grand fir, which may indicate that Douglas-fir needs more degree-days for flushing.

In a study of progression of phenological development of white fir by elevational gradient in northern California, Wickman (1976b) found budburst started between 290 and 356 degree-days and was 90 percent completed between 474 and 535 degree-days. Heat units are accumulated as sums of daily averages, expressed as degree-days. One degree of the mean daily temperature above a 42 °F (5.6 °C) threshold is defined as a degree-day. Speed of development of buds was also related to size and location on the tree, budburst frequently being earliest on the larger trees and on the south and west side of trees. Observations of white fir in southern Oregon from 1976 through 1980 showed that budburst occurred about May 25 to 31 at 342 to 370 degree-days (Wickman 1981).

Considerable difference in time of budburst was noted in two consecutive years for subalpine fir. In the Mt. Hood area of Oregon, budburst was 29 days later in 1964 than in 1963 (Williams 1968).

Time of budburst in Engelmann and white spruce has been shown to be under strong genetic control (Nienstaedt and Teich 1971). Roche (1969) and Dietrichson (1971) observed that populations of Engelmann spruce from high elevations had the earliest budburst. Dietrichson (1971) also demonstrated a close relation between total nitrogen content of needles at a given date in fall and the date of flushing the following spring. Engelmann spruce populations from high elevations that had the greatest nitrogen content in fall were the first to flush the next spring.

Differences in time of budburst from year to year for both families and individual trees are almost entirely functions of early spring temperature (Wilkinson 1977). Date of budburst also becomes progressively later with advancing age (Nienstaedt and King 1969).

The host species have vegetative buds containing preformed shoots. Much of the growth potential of these shoots is already determined during the year of bud formation. Shoots start elongating in spring, using carbohydrate reserves from the preceding season. Because shoot growth depends on carbohydrate reserves, it frequently shows closer correlation with weather of the year of bud formation than the year of shoot elongation (Koslowski and Keller 1966).

4.2.9 Growth

Growth habits of the host species differ. In general, growth in the Pacific coast region is more rapid and accumulation of biomass larger than in the interior. Ages and dimensions typically attained by hosts are listed in table 4-4.

4.2.9.1 Height Growth—Annual height increment of coastal Douglas-fir is relatively slow the first 5 years but then begins to accelerate, attaining the largest height increments between ages 20 and 30. The tree maintains a fairly rapid rate of height growth over a long period; on high sites, an average of 24 inches (61 cm) a year can be sustained for the first century.

Early height growth of coastal grand fir, up to 3 ft (0.9 m) a year, nearly equals that of coastal Douglas-fir. By contrast, white fir in the western part of its range grows slowly to about age 25 to 30; then growth usually speeds up markedly. Interior white fir grows much slower.

Of the species growing in the interior, western larch has the most rapid juvenile height growth. Trees may be nearly 19 ft (5.8 m) tall at age 15. Early height growth of interior Douglas-fir is about half, and of Engelmann spruce about one-fourth, that of larch.

Table 4-4—Ages and dimensions attained by principal host species.[1] (Data are from various sources, but mostly from Fowells 1965.)

Species		Age	Diameter at breast height	Height
		Yr	Inches	Ft
Douglas-fir	(coast)	750+	60–88 (150–220 cm)	230–262 (70–80 m)
	(interior)	400+	20–50 (51–127 cm)	130–180 (40–55 m)
Grand fir		300+	30–50 (75–125 cm)	130–197 (40–60 m)
White fir	(coast)	300+	40–60 (100–150 cm)	140–180 (40–55 m)
	(interior)			92–125 (28–38 m)
Subalpine fir		250+	18–24 (45–60 cm)	59–98 (18–30 m)
Engelmann spruce		500+	18–40 (45–100 cm)	148–164 (45–50 m)
Western larch		700+	34–60 (14–24 cm)	30–55 (100–180 m)

[1]Maximum ages and sizes for species are generally much greater than those shown here.

Dominant and codominant larch trees grow about 16 ft (4.9 m) between ages 20 and 30 on average sites (site index 50 to 60); they attain about 78 percent of their 200-year height in the first 100 years (Schmidt and others 1976).

Initial height growth of interior grand fir is slow. A comparison of rate of height growth with larch and interior Douglas-fir (Deitschman and Green 1965) on the same site indicates that, at age 50, grand fir attains the same average height—50 ft (15.2 m)—as Douglas-fir but less than larch, which reaches about 57 ft (17.4 m). At age 100, grand fir, with an average height of 97 ft (29.6 m), surpasses Douglas-fir—88 ft (26.8 m)—but does not catch up with larch, which has reached 103 ft (31.4 m). Both white fir and subalpine fir grow very slowly, but quantitative data are apparently not available.

Early growth of Engelmann spruce in the central Rocky Mountains is very slow. The species commonly takes 20 to 40 years to reach 4 to 5 ft (1.2 to 1.5 m), even under favorable conditions. Under a dense canopy, spruces 4 to 6 ft (1.2 to 1.8 m) tall may be 75 or more years old (Alexander 1974). In the northern Rocky Mountains, however, Engelmann spruce grows substantially faster than in the central Rocky Mountains (McCaughey and Schmidt 1982).

Advance regeneration of most host species will respond well to release. The true firs (Hall 1982, Henderson 1982) and Engelmann spruce (Alexander 1974) will respond even after 40 to 70 years of suppression and make acceptable growth. Data are lacking for Douglas-fir. Interior Douglas-fir appears capable of response to release for a long time, but coastal Douglas-fir does not.

4.2.9.2 Volume Production—Total yield of coastal Douglas-fir in unmanaged stands on best sites (site index 210) at age 100 is indicated as 19,820 ft^3/ acre (1386.8 m^3/ha) by McArdle and others (1949). Information is still lacking on yields of coastal Douglas-fir under intensive management for an entire rotation. Presumably, managed stands can produce mean annual increments of 100 ft^3/acre (7.0 m^3/ha) on poor sites and exceed 400 ft^3/acre (28.0 m^3/ha) on the highest sites under rotations between 50 and 80 yr (Scott 1980).

Yields of interior Douglas-fir are generally lower than those of coastal Douglas-fir. Cochran (1979) indicates mean annual increment for interior Douglas-fir (site index 90) of 155 ft^3/acre (10.8 m^3/ha) compared to 200 ft^3/acre (14 m^3/ha) of coastal Douglas-fir (Reukema 1979). In the northern Rocky Mountains, estimates of annual yield capabilities of habitat types, where Douglas-fir is climax, range from about 20 to 100 ft^3/acre (1.4 to 7 m^3/ha). On some of the moister habitat types, where Douglas-fir is seral, annual yields were estimated up to more than 140 feet^3/acre (9.8 m^3/ha) (Pfister and others 1977). Information is scant on annual yields of Douglas-fir in the southern Rocky Mountain region. Growth rates from 27 to 56 ft^3/acre (1.9 to 3.9 m^3/ha) after partial cutting have been reported in New Mexico (Daniel 1980).

White fir is capable of exceedingly high production. It ranges from 15,000 fbm/acre (191 m^3/ha) east of the crest of the Cascades to almost 60,000 fbm/acre (763 m^3/ha) on the west side (Hopkins 1982). Interior white fir does not have the productive capacity of coastal white fir.

Information is lacking on yield of coastal grand fir. The yield tables of Cochran (1979) for grand fir in eastern Oregon and Washington show volumes of 4,690 ft^3/acre (328.2 m^3/ha) for the lowest and 10,839 ft^3/acre (758.4 m^3/ha) for the highest sites at age 100. Mean annual increments of grand fir may differ at the same site index on different sites, however. For site index 50 (15.2), these values were reported: 175 ft^3/acre (12.2 m^3/ha) in Idaho (Stage 1969), 145 ft^3/acre (10.1 m^3/ha) in eastern Oregon (Cochran 1979), 115 and 79 ft^3/acre (8.0 and 5.5 m^3/ha) in the Blue Mountains (Hall 1982), and 64 to 143 ft^3/acre (4.5 to 10.0 m^3/ha) in Montana (Pfister and others 1977). A study of biomass production of grand fir in Idaho (Hanley 1976) indicated a periodic annual productivity of 15,691 lb/acre (17 624 kg/ha).

Subalpine fir usually grows in mixed stands and comprises only a minor part of the volume. In old-growth spruce–fir forests, subalpine fir usually makes up less than 25 percent of the sawlog volume, which may run from 5,000 to 40,000 fbm/acre (63.6 to 509 m^3/ha) (Henderson 1982).

Volume of Engelmann spruce differs considerably depending on site. Average volume ranges on poor sites from 5,000 to 15,000 fbm/acre (63.6 to 191 m^3/ha), on better sites from 25,000 to 40,000 fbm/acre (318 to 509 m^3/ha), and on best sites from 80,000 to 100,000 fbm/acre (1120 to 1400 m^3/ha) (Fowells 1965).

Total volume of western larch at age 140 ranges from 3,623 ft^3/acre (253.5 m^3/ha) to 14,264 ft^3/acre (998.1 m^3/ha), depending on site (Schmidt and others 1976).

Chapter 5

Host Responses
G. A. Van Sickle

5.1 Introduction

Accurate forecasts of forest growth and wood production are necessary to manage forests prudently for multiple use and to allocate harvesting for a sustained yield. The accuracy of the predictions, which are influenced by many factors, including forest pests such as budworm, is increasingly important as short supply of the forest resource is forecast. In this chapter, the effects of budworm infestations on radial and height growth, top-kill, tree defect, mortality, host vigor, and seed production of trees and stands are described.

Until the last decade, relatively little quantitative information was obtained on damage and losses from western budworm. Most information has been collected for Douglas-fir and true fir in natural stands, although damage to other species may be significant and has sometimes been studied. Growth recovery—particularly after severe feeding—is usually slow to be expressed and completed, so study results will continue to be observed and reported after this book is published.

5.2 Physiological Changes

5.2.1 Tree Energy Reserves

The amount of food reserves in trees probably accounts for the commonly observed lag of one or more years between the onset of defoliation and reduction of radial growth. Starch is the principal component of the energy reserve in a tree and a precursor for secondary compounds that resist insects (Hanover 1975). In both Douglas-fir and white fir, starch in twigs at the time of budburst was reduced after defoliation by tussock moth (Webb 1981). Consequently, starch levels may indicate the degree of tree stress and susceptibility to secondary attack by insects. Webb found that defoliated trees without detectable starch content did not recover, and surviving trees with low starch content had fewer needles per shoot than trees with high starch content. Foliage recovery also depended on weather, however, especially in water-stressed sites. Similar studies have not been conducted with budworm-defoliated trees, but a reduction of food reserves could be expected after defoliation from any source.

5.2.2 Growth Responses

Defoliation and canopy discoloration are the most obvious effects of bud-mining and consumption of needles. Although the subsequent effects on tree survival, growth increment, and top-kill can be substantial, foliage recovery is often dramatic. Within a few years of the cessation of feeding, tree crowns may appear almost normal, although the volume of the live crown may have been altered. Some grand fir trees severely defoliated by tussock moth exhibited dramatic foliage recovery after the outbreak ended (Wickman 1978b), and Douglas-fir defoliated by tussock moth or budworm have also demonstrated a surprising resilience and recuperative ability (Silver 1960). Stimulation of adventitious buds and epicormic branching (Bryan and Lanner 1981, Johnson and Denton 1975) may be largely responsible for maintaining or recovering a functional crown during and after periods of defoliation. Epicormic branches appear on the bole long after normal first-order laterals have elongated; they originate from preformed buds that may have been suppressed for up to 14 years (Bryan and Lanner 1981). Adventitious shoots arise from buds produced by conversion of mature tissue into meristematic tissue.

In British Columbia, Silver (1960) reported many adventitious buds were produced in 1955 after heavy defoliation and bud-mining in 1954. By 1959, tree crowns had almost returned to normal, although narrow bushy branches and crowns from the adventitious growth were still evident. I have made annual observations of defoliation of 45 Douglas-fir branches since 1971. In the fall of 1972, only 11 percent of the buds had produced foliage and shoot growth, and the average defoliation per shoot culminated at 97 percent in 1973. The next year, 88 percent of the current growth came from adventitious buds and by 1975, with foliage recovery well advanced, most of the twig and shoot growth stemmed from adventitious growth.

Another response to defoliation may be longer than normal retention of older Douglas-fir needles, at least until new foliage is retained after the outbreak declines, and then a heavy drop of old needles may occur (Ross and others 1978 unpubl.). This, presumably, is a response to the altered production of growth regulators. As a result of increased photosynthesis of previously shaded foliage, decreased demand for carbon, and altered water and mineral status, the photosynthetic capacity of the tree is not diminished proportional to the intensity of defoliation (Webb 1978).

5.2.3 Changes in Foliage Chemistry

Considerable recent literature concerns the effects of natural and fertilizer-influenced variations in host chemistry on the selective feeding patterns of budworm and subsequent population developments (for example, Cates and others 1983; Schmidt and Fellin 1983a; Shaw and others 1978). Some are contradictory, however, and little knowledge exists yet of changes in host-foliage chemistry brought about by an extended period of defoliation.

Carbohydrates are the direct products of photosynthesis; thus, reduction in photosynthesis will reduce carbohydrate production and storage. Hormone production is likewise affected because most hormones are produced in 1-year-old foliage, expanding buds, and currently forming buds (Cuddy 1982). Even hormones produced at other sites may be affected if they depend on precursors produced in the crown. Foliage nutrients may also be altered by defoliation. Cook and others (1978) found that new buds of white spruce heavily defoliated by sawflies had higher concentrations of nitrogen, potassium, phosphorus, and magnesium than buds from lightly defoliated trees.

5.2.4 Stress and Predisposition to Other Pests

Mortality of defoliated trees is presumed to increase when associated with root rots, drought stress, dwarf mistletoes, and bark beetles, but only the last is reasonably well documented. Population increases of the fir engraver beetle (*Scolytus ventralis* Le Conte) and Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) were closely associated with tussock moth outbreaks (Berryman and Wright 1978, Shepherd and others 1980). Observations in British Columbia, however, showed that beetle populations did not build up in budworm-defoliated trees (Shepherd and others 1977). Although the Douglas-fir beetle occurred in some defoliated stands, it was generally absent. Little evidence was found of an association between defoliation and the beetle; brood productivity was low, and the attacks eventually subsided. In one severely defoliated stand, bark beetle attacks began in 1975 and by 1976, 17 percent of the trees were attacked. By 1980, however, only 2 percent of the trees had died, some of which would have died even without beetle attack (Alfaro and others 1982).

Along the Madison River in Montana, Douglas-fir bark beetle has increased in mature stands top-killed by budworm feeding since 1971 (McGregor and others 1983). They also reported the beetle's preference, in decreasing order, for windthrown and windbroken trees, larger diameter logging debris, trees damaged by ice and snow, and defoliated trees.

5.3 Physical Changes

5.3.1 Height Growth

Budworm affects height growth in at least three ways. A completely mined or destroyed terminal bud will not produce an annual internode. Consecutive severe defoliations can cause top-kill of one or more internodes grown in previous years, or if the terminal is not killed, growth may be reduced during periods of lighter defoliation or during recovery after feeding stops. Height loss from destruction of the terminal bud probably occurs more frequently than is reported because of the difficulty in sampling tall trees. Severely defoliated Douglas-fir, in one stand in British Columbia defoliated for 5 years, produced no height growth from 1970 to 1976, and about three internodes predating the outbreak were killed as a result of defoliation, for a total loss of 10 years of height growth (Shepherd and others 1977). In another stand where defoliation started in 1975, none of the 20 severely defoliated trees examined had a 1976 or 1977 terminal internode, most lacked or had only a partial 1975 internode, and the 1974 internode had been killed on six trees (Collis and Van Sickle 1978). Missing internodes could only be detected by cross-referencing precise ring and internode counts. In Washington, with lighter defoliation, few instances were found in which a lateral did not quickly achieve dominance, and the proportional loss of height growth was similar to or less than that of diameter growth (Scott and Nichols 1983, unpubl.).

Top-kill, severe enough to be observed during stand cruises, affected up to 63 percent of the Douglas-fir in individual stands and averaged 16 percent in the previously defoliated stands surveyed in British Columbia (Fiddick and Van Sickle 1979). In Idaho, 2 to 47 percent of the trees examined were top-killed; top-kill was most frequent on grand fir and less common on subalpine fir and Douglas-fir (Beveridge and Cahill 1984, Bousfield 1980, Bousfield and Franc 1979, Bousfield and others 1975, Ciesla and others 1973). In eastern Oregon, Williams (1966) reported no dead tops on lightly damaged Douglas-fir during an 8- to 12-year infestation, but found 1 to 6 m of top-kill on grand fir. Mika and Twardus (1983 unpubl.) found 26.9 percent of the subalpine fir, 10.9 percent of the grand fir, and 7.1 percent of the Douglas-fir top-killed. Similar values were reported by Gregg and others (1979 unpubl.), who also noted that all the damage was clustered in 34 percent of the plots. Most of these surveys recognized only the top-kill form of height loss. Surveys during outbreaks may overestimate the frequency of top-kill because of the difficulty in distinguishing trees with living defoliated tops from those with dead tops. After recovery, top-kill may be underestimated because smaller dead tops are hidden within the crown and not visible from the ground (Van Sickle and others 1983).

In Idaho, 12.7 percent of the young, defoliated trees did not increase in height during a 5-year study, and subalpine fir were more frequently affected than grand fir, Douglas-fir, or Engelmann spruce (Ferguson and Stage 1983 unpubl.). The probability of loss increased with increasing defoliation and with height of the tree, but was less in trees having the greatest crown ratios at the beginning of the study. Height growth of the balance of the trees decreased proportionally, with defoliation averages greater than 10 percent. Changes in crown ratio were influenced both by top-kill and by changes in the base of the live crown. The base of the live crown usually increased in height, but sometimes it dropped because a dormant bud sprouted on the main stem. Similar changes in the position of the base of the live crown were recognized in a mature stand in British Columbia when I observed that branch stubs remaining after lower crown branches were sampled in 1971 were, by 1975, no longer within the live-crown portion of the defoliated trees.

By severing the stems of current-year shoots, budworm may also affect height growth and form of young western larch (Schmidt and Fellin 1973). Severance of terminal shoots ranged from 24 to 78 percent during their 5-year study in Montana. The net annual height growth of trees with severed terminals averaged 27 percent less than that of unaffected trees.

Patterns of height and radial growth (see section 5.3.2), based on Douglas-fir affected by four budworm infestations near Pemberton, BC (Van Sickle and others 1983), are compared in figure 5-1. Radial growth typically continued to decrease during the period of active feeding and then gradually recovered. Height growth, at least with moderate and severe defoliation, dropped abruptly during the outbreak, and top-kill destroyed internodes that were formed before the outbreak began. Dissected trees lost an average of 7.3 internodes in each infestation, of which 4.2 were destroyed or failed to grow during the budworm feeding and recovery periods and 3.1 were existing internodes lost. Height-growth recovery after the outbreak was variable, depending on the severity and duration of feeding and on the manner in which terminal dominance was reestablished (see section 5.3.4). Height losses during the period of rapid juvenile growth most seriously affect tree volume and form (see sections 5.3.3 and 5.3.4), but trees that are semimature or mature when damaged may be harvested with the damaged portion still in the unused portion of the tree.

5.3.2 Radial Growth

Insect defoliation has frequently been shown to cause marked reduction in radial growth (Kulman 1971), but in only relatively few studies have the losses been quantified or correlated with the severity and duration of defoliation. Periods of budworm activity have been dated by incremental analyses (Blais 1962, Turner 1952, Williams 1967). In the West, trees have sustained up to five budworm outbreaks since 1900 (Alfaro and others 1982, Johnson and Denton 1975, Shepherd and others 1977). Numerous studies have shown that radial-growth reduction usually lags behind foliage removal by 1 to 3 years (for example, Alfaro and others 1982, Crimp 1982). Similarly, growth recovery lags behind refoliation. Variation in vertical distribution of radial growth is widely recognized, the earliest and greatest reduction from defoliation occurring in the bole within the defoliated crown. The effect of budworm defoliation is generally believed to be observable on the lower bole (fig. 5-2).
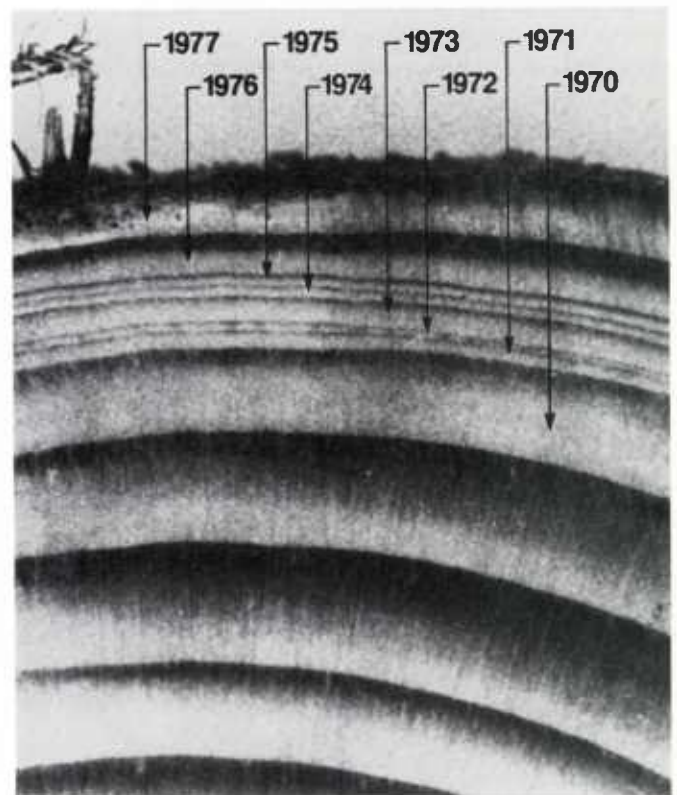
Figure 5-2—Effect of severe budworm feeding, 1970 to 1974, on annual-ring growth of Douglas-fir.

Figure 5-1—Pattern of annual height and radial growth in Douglas-fir affected by four budworm infestations. The zero height growth before each infestation results from top-kill.

In Montana, 38 of 46 randomly selected stands had evidence of past infestations (Carlson and McCaughey 1982). In British Columbia, trees I examined in 108 stands throughout the area infested during the 1970's also indicated up to four previous infestations, although considerable variation occurred in apparent intensity and duration among stands and trees within stands. Carlson and McCaughey (1982) used the magnitude of growth reduction to calculate a severity index of previous budworm activity.

Swetnam (1983 unpubl.) compared increment cores of Douglas-fir and ponderosa pine (nonhost) from budworm-infested forests in New Mexico; the comparison allowed removal of the effects of weather from host chronologies. Corrected host-tree growth indexes were used to assess growth loss during known outbreaks. Average growth loss for 5-year periods during outbreaks was 30 to 40 percent.

Many radial measurements are taken during infestations, and any reduction is expressed relative to preoutbreak growth rates. Only part of the total loss is recorded, however, because any reduced growth during recovery after the infestation (fig. 5-1) is not included. Annual increments in Douglas-fir during earlier infestations were reduced by 40 to 80 percent compared to preoutbreak averages (Shepherd and others 1977, Williams 1967). A method of estimating and expressing loss as a proportion of potential growth was described by Thomson and Van Sickle (1980). During four outbreaks, the average radial loss per outbreak ranged from about 1¼ to 4⅜ inches (3.28 to 11.02 mm), which altogether represented a 12-percent reduction in diameter or a basal-area reduction of 22 percent, based on the size that the average tree should have reached by 1980 (Alfaro and others 1982). For one stand, they also related graphically the proportional reduction in increment to the defoliation for each year of a 5-year outbreak (fig. 5-3). In the most recent infestation, Gregg and others (1979 unpubl.) found the reduction in mean annual increment relative to predicted growth, during the fifth year of consecutive defoliation, reached 12.2 percent in Douglas-fir and 27.3 percent in true firs.
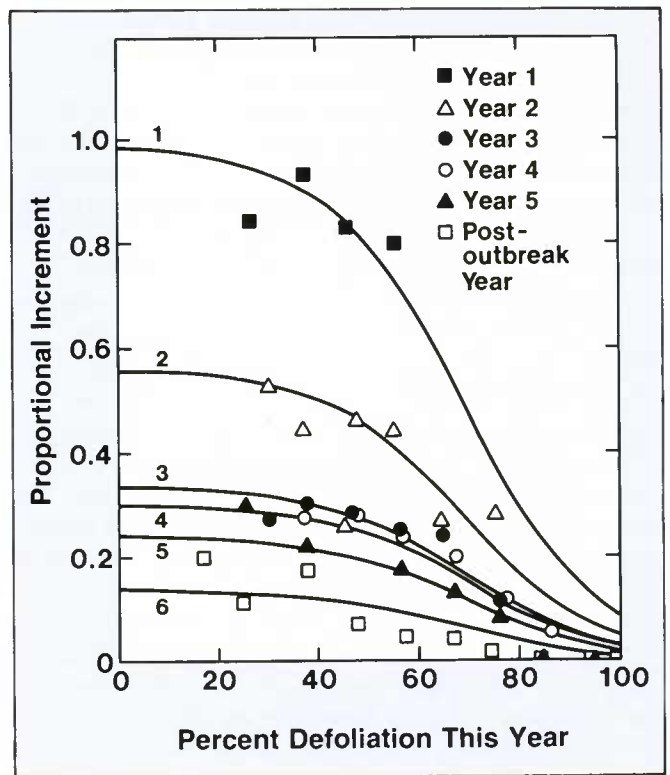
Figure 5-3—Proportional increment in trees with varying defoliation during each year of a 5-year outbreak and 1 year of recovery in a selected Douglas-fir stand (from Alfaro and others 1982).

In central Idaho, the Prognosis Model was used with site-specific equations to estimate the growth of sampled trees without the defoliation effects that had persisted for the last decade (Beveridge and Cahill 1984). Annual radial growth of grand fir was reduced 20 percent shortly after the outbreak began, reaching 30 percent after 4 to 6 years of defoliation. Growth of subalpine fir decreased 40 percent; and Douglas-fir, which escaped heavy defoliation, averaged 15 percent reduction after 6 years.

Significantly more radial-growth depression was caused by budworm in grand fir than in Douglas-fir. The greatest 1-year growth loss of grand fir was nearly three times that of Douglas-fir in a stand that was 50 to 75 percent defoliated in 1952 (Brubaker and Greene 1979). This agrees with other studies (Carolin and Coulter 1975, Gregg and others 1979 unpubl., Williams 1967), although it may reflect the usually greater defoliation of grand fir because Crimp (1982) found growth loss to be similar in both species for a given defoliation level and duration of attack. The basal-area growth loss, after a 10-year outbreak, was 3.8 percent for Douglas-fir and about double for grand fir and subalpine fir (Mika and Twardus 1983 unpubl.).

Occasional sources of error in radial-growth analysis are partial or absent growth rings because of severe defoliation (fig. 5-4). Failure of defoliated trees to produce one or more annual rings, particularly near the stump, has been reported to be caused by other insects (Evenden 1940, O'Neil 1963). The frequency of missing rings, even in nondefoliated trees, increases with age and varies with position in the stem (Fritts 1976).

In 85-year-old Douglas-fir that survived heavy feeding by budworm from 1970 through 1974, I found that 27 of 31 trees had partial or missing rings. Based on examination of two radii from each of 11 discs cut throughout the length of the tree, 22 percent of the expected rings were absent during a 5-year period. Reexamination of the entire circumference for rings designated as missing on the two radial sections indicated three-quarters were absent around the entire circumference, and less than one-tenth formed partial rings that included more than 80 percent of the circumference. The frequency of missing rings increased with defoliation severity but did occur occasionally in trees less than 50 percent defoliated. The frequency of missing rings was highest near the top of the tree and was highly variable lower in the stem. Few rings were absent at breast height, but the rings were very fine and easily confused or miscounted. The annual ring most frequently absent was that of 1974, the year active feeding culminated, followed by those of 1975, 1973, 1972, and 1976. In a less severely defoliated stand, annual rings were missing in less than 2 percent of the samples.
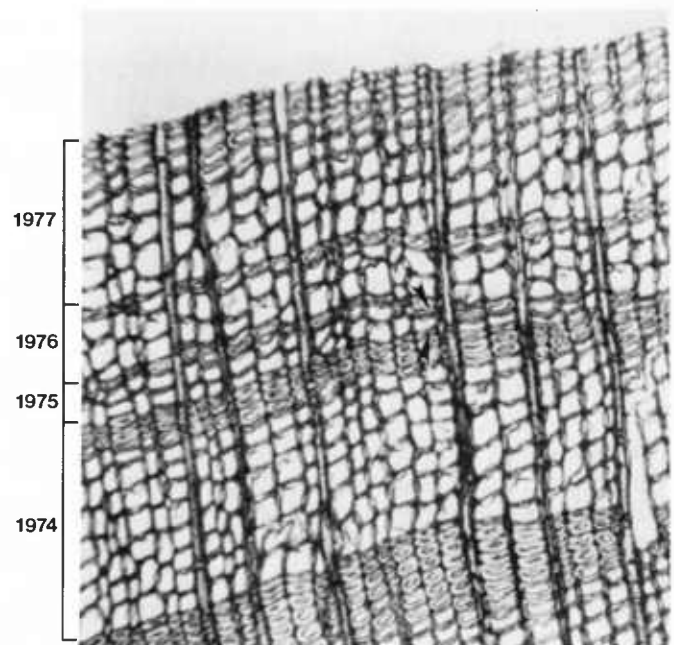
Figure 5-4—Small, incomplete annual ring only a few cells wide at stump height in a Douglas-fir defoliated by budworm. Obviously, depending on their position, measurements can be in error.

Similarly, in eastern Washington, annual rings were missing at breast height in only 4 of 194 trees examined, and partial rings were observed in 10 of the trees (Scott and Nichols 1983 unpubl.). The main indicators of missing rings were asynchrony of ring patterns in and among trees and fine rings near wounds or at branch whorls that were not continuous into the internodes.

5.3.3 Volume Growth

The effect of budworm in reducing growth in both height and diameter is combined in the calculations of tree and stand volumes. The difference between measured volume and a predicted volume is an estimated loss (fig. 5-5). Budworm-caused volume losses have been measured in relatively few forest surveys and require careful interpretation. Unattacked stands truly comparable in climatic or site characteristics seldom exist, repeated outbreaks complicate site definition, and nonhost trees may respond with greater than average growth.

For Douglas-fir and grand fir stands in eastern Washington, the average stand-volume loss was 5.9 percent of the predicted growth over a 10-year period (Mika and Twardus 1983 unpubl.). In north-central Washington, stand-volume losses reached 1.0 percent in Douglas-fir and 2.8 percent in grand fir with five consecutive years of defoliation (Gregg and others 1979 unpubl.).

In Idaho, losses, which averaged 1 percent, were more significant in subalpine fir and grand fir than in other host trees (Bousfield and others 1975). In central Idaho in two selected areas with a history of three infestations, volume loss in grand fir averaged 10 percent, when increment reduction and associated cull resulting from deformities were combined (Ferrell and Scharpf 1982). The loss per infestation in individual trees ranged from 0 to 93.3 percent.

Direct measurement of height and radial growth can be made only on surviving trees, and potential growth in the absence of budworm can only be estimated. Because a multitude of variations in weather, severity and duration of feeding, stand density, and site factors can influence estimates of growth, different approaches in computer modeling have been developed. A method of manipulating and projecting a data set collected during and after an infestation was described by Thomson and Van Sickle (1980). Baskerville and Kleinschmidt (1981) modeled physiological processes in balsam fir to forecast growth loss from defoliation. The CANUSA-West model that combines budworm and host dynamics is described in chapter 8.
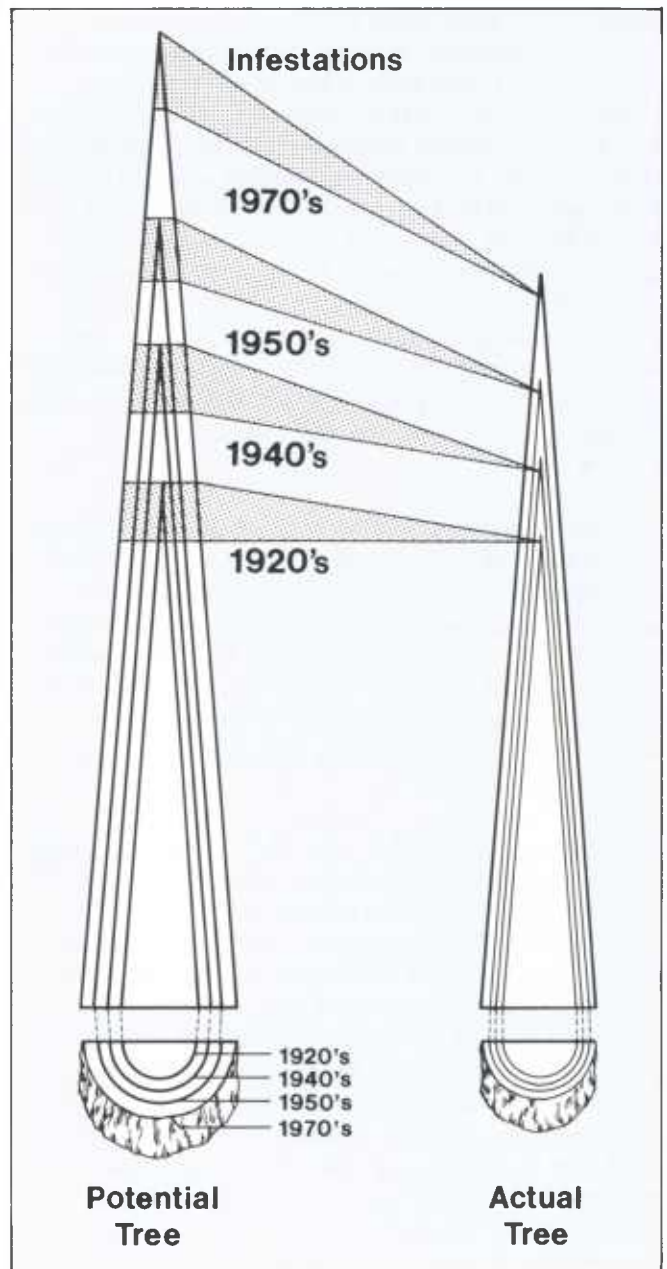
Figure 5-5—Radial and height growth of a Douglas-fir after four budworm infestations compared schematically to the tree's potential size.

With detailed measurements of height and radial increments and records during and after five consecutive years of severe defoliation in one Douglas-fir stand in British Columbia, volume losses were calculated according to the method described by Thomson and Van Sickle (1980). Average volume losses were 19.0, 16.7, 8.6, and 13.7 percent of the potential volumes after infestations in the 1920's, 1940's, 1950's, and 1970's, respectively (Alfaro and others, in press). The volume loss of the four infestations was 45.7 percent of the potential cumulative volume. Annual defoliation estimates for individual trees were available only during the 1970–74 infestation, when volume losses ranged from 8.7 percent in trees less than 50 percent defoliated to 17.8 percent in the 90- to 100-percent class. Individual losses by trees in one infestation were significantly correlated with losses in previous infestations—that is, individual trees lightly defoliated in the most recent infestation were also most likely to have been lightly defoliated in earlier infestations. Differences in susceptibility to budworm feeding have been reported in a single infestation (McDonald 1981) and could be associated with differences in bud and foliage phenology (Thomson and Moncrieff 1982). A long-term effect also occurs on the potential volume growth because loss of radial and height growth results in a smaller and shorter volume core for the individual tree on which the subsequent year's growth is added (fig. 5-5).

5.3.4 Top-Kill

Assessing top-kill in standing trees can be difficult until they have recovered, and the frequency of top-kill is highly variable among stands and among the different tree species susceptible to budworm defoliation (see section 5.3.1). The severity of top-kill, as well as its frequency, may influence the resulting losses. Length of top-kill, however, was usually not a reliable measure because of breakage of the dead "spike" top before or after trees are felled. In a study of felled trees selected for obvious top-kills arising from earlier outbreaks, Aho (1982 unpubl.) found the average diameter at the base of the dead top was about one-half of an inch (1.3 cm) in Douglas-fir and about seven-eighths of an inch (2.3 cm) for true fir. Both averaged about 5 years of growth. In similar studies on Douglas-fir in British Columbia, I found that the average diameter of the dead top was about 1¾ inches (4.4 cm) (range 0.6 to 6 cm) and represented up to 12 years' growth.

Distortion of tree form is more often related to the method of recovery than to the severity of top-kill. Large-diameter kills often result in more severe tree deformity and smaller kills may be overgrown, but even a slightly damaged top may fork if two or more branches or new terminals compete for dominance (Collis and Van Sickle 1978).

Little height growth was lost when only the last year or two of the tops of Douglas-fir or true firs were killed because a lateral branch quickly assumed dominance and formed a new top. If defoliation caused several years of top-kill, however, the loss was more severe because laterals lower in the crown were less likely or slower to express dominance (Aho 1982 unpubl., Thomson and others 1982). A new top may also develop from adventitious or epicormic branching (see section 5.2.2), and the severity of distortion depends on the point of origin of the new top.

In white firs defoliated during relatively short Modoc budworm outbreaks in northeastern California, top-kill was usually limited to a single year's growth; consequently, height-growth deficits were slight, and only a slight crook—and no decay—occurred in the stem in later years (Ferrell 1980).

Stem deformities (fig. 5-6) that develop after top-kill may eventually be evident as forks and crooks, either of which may have a remnant of the original top as a spike, or as a crease—which may result if the dead top is overgrown (Collis and Van Sickle 1978). Because storms and other injuries may also cause terminal breakage resulting in bole deformities, budworm should not be assumed to be the cause. Often budworm-caused top-kill may be less than that from other causes (Ferrell 1980, Gregg and others 1979 unpubl.). Frequency and severity of stem deformities from all causes are highly variable among stands.
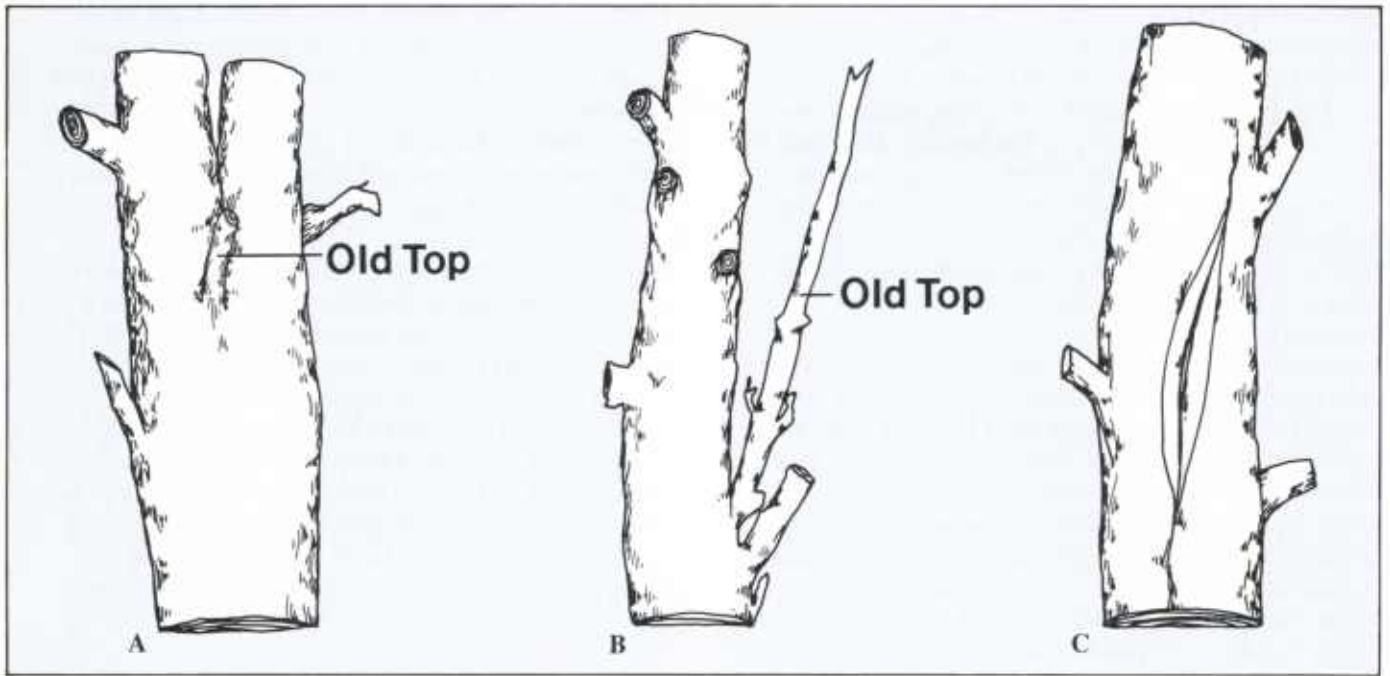
Figure 5-6—Types of tree recovery in Douglas-fir after top-kill by budworm defoliation. A = forked top produced by terminal leader kill and two or more branches seeking dominance. B = crook, terminal leader killed and offset by development of a new top; the crook may be slight, or, if an older branch becomes dominant, extreme. C = crease, dead top replaced and healed over.

Forks, crooks, and creases caused by up to three previous infestations were found on 11 percent of the standing Douglas-fir surveyed in British Columbia, but ranged from 0 to 70 percent in individual stands (Collis and Van Sickle 1978, Shepherd and others 1977). In Idaho, 70 and 20 percent of the grand fir in two selected stands had evident damage from outbreaks in 1922–30 and 1952–55, respectively (Ferrell and Scharpf 1982). Forks in western larch resulting from budworm severance of the terminals did not persist beyond 5 years because of the strong apical characteristics of larch (Schmidt and Fellin 1973). Furthermore, the rate of recovery was slower in the denser stands (Schmidt 1980).

Stem injuries from budworm in Douglas-fir are seldom decayed, unlike those of balsam fir defoliated by eastern budworm or white fir after tussock moth outbreaks. All balsam fir with forked tops or marked crooks resulting from eastern budworm attack 35 years earlier contained decay that had entered through injured tops killed back to a diameter greater than about one-half of an inch (1.3 cm), and older than 5 years (Stillwell 1956). Decay losses associated with tops killed by tussock moth up to 35 years earlier were not economically serious in white fir in eastern California (Wickman and Scharpf 1972). Losses to decay in grand fir in eastern Washington averaged 4.8 percent of the gross volume in selected damaged trees (Aho and others 1979).

Similar studies of more than 200 budworm-caused injuries in Washington found only limited decay in one Douglas-fir and two grand fir trees. In British Columbia, none of the many previous or current top-kills in Douglas-fir contained decay attributable to the dead tops serving as entry courts (Shepherd and others 1977). In Idaho, however, 19 of 40 selected grand fir trees severely top-killed 60 years earlier had decay columns averaging about 15.4 ft (4.7 m) long (Ferrell and Scharpf 1982).

5.3.5 Tree Mortality

Budworm-caused tree mortality, even after several consecutive years of defoliation, is usually light and frequently concentrated among the smaller, suppressed trees. Individual stands may be more severely affected, however. Douglas-fir mortality caused by up to 7 years of moderate or severe budworm defoliation averaged less than 1 percent of the trees in most stands in British Columbia, but individual stand extremes reached 39 to 53 percent (Alfaro and others 1982, Collis and Van Sickle 1978). Comparable averages in Washington and Oregon after 5 years of defoliation were 1.3 percent for Douglas-fir and 3.0 percent for grand fir (Gregg and others 1979 unpubl.); Mika and Twardus (1983 unpubl.) reported 3.8 percent for Douglas-fir, 4.9 percent for grand fir, and 1.6 percent for subalpine fir after the 10th year of the outbreak. Tree mortality was highly variable among stands and was clustered in only 9 percent of the plots surveyed (Gregg and others 1979 unpubl.). In Idaho, after 9 years of variable defoliation, average percentages were 1.8 for Douglas-fir, 0.7 for grand fir, and 18 for subalpine fir (Bousfield and others 1975).

5.3.6 Root Growth

Rootlet mortality has been shown to occur with severe, prolonged feeding by eastern budworm on balsam fir (Craighead 1924, Redmond 1959), but no comparable studies have been made with tree species affected by western budworm. Redmond (1959) confirmed that rootlets less than 0.08 of an inch (2 mm) in diameter had died on severely defoliated balsam fir; defoliation of 70 percent caused more than 30-percent rootlet mortality, and although young trees were able to produce new rootlets after defoliation, mature and overmature trees were not. Rootlet recovery lagged behind foliage recovery by 3 years (Stillwell 1960).

5.3.7 Cone and Seed Production

Budworm feeding can reduce cone and seed production of host conifers directly by larval feeding on the male and female flowers or in the cones (Hedlin and others 1980) and probably contributes to long-term reductions by reducing food reserves and weakening the trees. Although not documented, budworm-caused top-kill (see section 5.3.4) and defoliation also probably affect cone production, especially in true firs and spruce in which cone production is concentrated in the upper crown.

In the West, feeding by budworm on cones was believed to be atypical and feeding on staminate flowers of pine occasional (Fellin and Shearer 1968). Many western larch cones were superficially mined and a few had the central axis destroyed, however. Even when foliage feeding was light, Dewey (1970) found 9 to 71 percent of the Douglas-fir cones infested in 13 stands in Montana. Many of the small conelets attacked in early June shriveled and died.

In seed-production areas, budworm was found to be the principal insect damaging cones of Douglas-fir, grand fir, and western larch (Dewey and Jenkins 1979). In Montana, budworm killed conelets of Douglas-fir and larch soon after the ovulate buds opened and then consumed Douglas-fir seed while feeding within developing cones (Shearer 1982 unpubl., Shearer and Tiernan 1981 unpubl.). Other insects, frost injury, and—to a lesser degree—budworm reduced the 1980 seed crop to about one-quarter of its potential.

At 12 western Montana study sites, budworm feeding on Douglas-fir included the developing conelets and reduced the photosynthetic capacity of foliage needed for reproductive bud development (Chrisman and others 1983). Average cone production was lower in heavily defoliated stands, but losses could not be quantified because of variation in defoliation and cone production among trees and sites.

The emphasis in the balance of this chapter is on observed effects of budworm on the structure, composition, volume recovery, and regeneration of forest stands. The physiological and mathematical relations of the insect–host interactions are discussed in chapters 7 and 8. Because most budworm-influenced changes in stands are gradual and are stable and measurable only considerably after outbreaks subside, few observations from recent and, in many areas, continuing infestations have yet been reported.

5.4.1 Stand Structure and Composition

Tree mortality from budworm in western forests tends to increase average diameter of trees in the stand because most of the mortality is of the smaller, suppressed trees. Even in a severely defoliated Douglas-fir stand, less than 5 percent of the dominant trees were killed, compared to 78 percent of the suppressed trees (Alfaro and others 1982); reductions in basal area for these two crown classes were 2.7 and 64.9 percent, respectively. Bousfield and Chase (1982) reported most tree mortality was in trees of smaller diameter in Montana, as was also reported for the previous infestation (Johnson and Denton 1975). Such a shift in the crown-class structure of stands towards a larger proportion of dominant and codominant trees was also reported after defoliation by eastern budworm (Baskerville and MacLean 1979).

Although not documented, some dominant and codominant trees may lose their competitive position in the canopy through top-kill and lack of height growth. Sometimes several meters of a tree may be lost. Furthermore, if multiple or no new leaders develop, individual trees may not grow any commercially useful material above the point of injury. The frequency of top-kill has not been related to tree diameter or crown class, although in one survey it was most pronounced in stands with the highest basal area (Bousfield and Chase 1982).

With the greater chance of mortality of true firs, stand composition in mixed stands may shift in favor of Douglas-fir, larch, and any nonhost species. Also, an acceleration of growth in nonhost trees in defoliated stands may, in part, compensate for growth loss in host trees (see section 5.4.3). In British Columbia, where infestations to date have been concentrated in mostly pure Douglas-fir types, shifts in species mixtures are not as common as in the adjacent States where the true fir component is much greater.

5.4.2 Regeneration

Cone and seed production can be largely destroyed by even relatively light budworm feeding, which may profoundly affect seedling establishment over a prolonged period and may be particularly serious if competitive vegetation becomes established. In addition, direct feeding on established understory regeneration can be severe. In the past, clearcut harvesting followed by planting has been a common practice in many Douglas-fir stands, and loss of natural regeneration has not been considered serious.

On drier sites with shelterwood management, natural regeneration is of greater importance. Understory stocking decreased with the years of budworm defoliation, reaching an average loss of 6.9 percent after five consecutive years of defoliation (Gregg and others 1979 unpubl.). Ferguson and Stage (1983 unpubl.) also observed a lower stocking of advance host regeneration in defoliated than in nondefoliated areas in Idaho. The probability of any stocking by host regeneration subsequent to harvest decreased as defoliation increased, as did the number of trees per stocking unit. Stocking probability was also significantly reduced in Douglas-fir habitats in Montana (Carlson and others 1982 unpubl.).

5.4.3 Long-Term Effects on Volume

Despite considerable short-term reduction in growth caused by budworm (see section 5.3.3), long-term effects may not be as serious as first indicated. If a commercial nonhost species comprises a large enough proportion of the stand, and if growth is accelerated by the thinning and reduced competition resulting from defoliation, growth loss will be at least partially compensated. Even if the stand is primarily of host species, if sufficient trees survive for optimum spacing, and if the stand is near enough to harvest that any top-kill occurs mostly above the minimum usable top diameter (see section 5.3.1), subsequent growth will be concentrated on the larger, crop trees.

Unfortunately few growth studies have been long term enough to measure the insect–stand dynamics during and long after infestations. From stem analyses of trees in a pure 80-year-old Douglas-fir stand, radial growth greater than normal was not observed after any of the four periods of budworm feeding (Alfaro and others 1982, Thomson and Van Sickle 1980). Stand age and degree of change in stocking density may affect the response, however. In Montana, in 17 of 38 mixed stands with a probable budworm history, nonhost trees, such as ponderosa pine, had accelerated radial growth relative to expected growth (Carlson and McCaughey 1982).

In a white fir stand in California defoliated by tussock moth, stocking had been reduced 27 percent and volume 16 percent, but radial-growth increments had recovered to preoutbreak rates within 5 years and surpassed them after 10 years (Wickman 1978a). For 36 years after the outbreak, radial growth was significantly greater than that of nearby nondefoliated trees (Wickman 1980). As in the other studies, a measure of the long-term net damage from the outbreaks in terms of stand volume would be more meaningful. Only further monitoring will determine if the positive effects will eventually compensate for the growth loss and mortality caused by defoliation.

In the only long-term observation of stand recovery after eastern budworm, Baskerville and Maclean (1979) observed diameter growth substantially increased beyond predefoliation levels; but because stand density was reduced, the recovery in terms of volume per hectare was poor. Only 1 of 10 plots had regained its predefoliation volume 15 years after defoliation ceased. In simulating stand volumes over 20 years and a range of defoliation histories, Baskerville and Kleinschmidt (1981) showed, for balsam fir defoliated by eastern budworm, that although volume increment recovers, the stand volume does not reach that projected for healthy stands.

Chapter 6

Population Dynamics

71-88

6.1 Introduction
Robert W. Campbell

6.1.1 Likelihood and Persistence of Outbreaks

Throughout its range, detectable populations of the western budworm appear to persist indefinitely in stands that contain a substantial proportion of suitable hosts. Populations in these stands have exhibited one of three numerical patterns. The first pattern, chronically high populations, occurs in many stands, particularly in Montana and Idaho. In one extreme case, visible defoliation was recorded for 29 successive years in the same stand. Thirteen of 91 documented outbreaks (14 percent) persisted without a break for at least 9 years; 32 of 91 (35 percent) persisted for at least 4 years (Johnson and Denton 1975). In the second pattern, outbreaks may last only 1 or 2 years. Even in the northern Rocky Mountain area reported by Johnson and Denton (1975), 44 of 91 outbreaks (48 percent) persisted for only 1 or 2 years.

Persistence at sparse densities is the third numerical pattern exhibited by the budworm. Unfortunately, only a few records document this sparse pattern. Unlike outbreaks, which are obvious, sparse populations are only detectable by sampling.

6.1.2 Outbreaks and Weather

Several investigators have found correlations between warm, dry periods and subsequent outbreaks in both the eastern and western budworms. Hard and others (1980) examined records from northwest Montana and northern Idaho. They found that defoliation varied with weather during May, June, and July of the previous year—directly with mean maximum temperature and inversely with the frequency of days with measurable precipitation. Similarly, Twardus (1980 unpubl.) found in north-central Washington that warm, dry periods often preceded outbreaks. In British Columbia, Thomson and others (1984) found that synchrony of larval emergence and budburst—also dependent on weather factors—was associated with the weather of the preceding year. The collapse of two of the five outbreaks studied was clearly associated with extreme high temperatures after moth flights.

Blais (1957, 1968) associated eastern budworm infestations with dry summers and suitable densities of host species.

From defoliation records, Kemp and others (1983 unpubl.) defined three broad classes of outbreak frequency in the forested areas of four States (fig. 6-1, bottom). They examined several climatic features in Washington, Oregon, Idaho, and Montana to determine their association with budworm outbreaks. They concluded that outbreaks were associated with drier climates and occurred most often in a fairly limited range of mean temperatures in January and July. In general, outbreaks occurred where annual precipitation was between 9 and 36 inches (23 and 91 cm). Outbreaks were also associated with January and July temperatures:

	Mean minimum		Mean maximum	
	°F	°C	°F	°C
January	3 to 23	−16 to −5	26 to 38	−3 to 3
July	40 to 53	4 to 12	75 to 90	24 to 32

Links between climatic trends and defoliation frequency remain somewhat obscure. Kemp and others speculated that this linkage may be through increased host-plant stress and increased insect survival. They did not analyze weather trends that might be associated with the end of an outbreak. Once a population is released, adverse physical factors—such as cold, wet summers—may not bring either the eastern or western budworm under control (Greenbank 1956, Thomson and others 1983 unpubl.).

Using procedures similar to Kemp's, Van Sickle (personal communication) provided an outbreak frequency map of British Columbia (fig. 6-1, top). Note that the zones of outbreak frequency are defined differently in the two areas; in British Columbia, outbreaks were shorter, fewer, or both.

Figure 6-1—Frequency of budworm outbreaks = $\dfrac{\text{years of defoliation at a location}}{\text{total years considered}}$ in forested areas:
top, British Columbia (Van Sickle, personal communication); bottom, Idaho, Montana, Oregon, and Washington (after Kemp and others 1983 unpubl.). The classes of outbreak frequency (1947–78) in the lower map are: high, 1; medium, 2; low, 3; and none, 0.

Fellin and others (1983) summarized the history of the western budworm in the northern Rocky Mountains as follows:

> Two infestations were reported near Priest Lake in northern Idaho [in 1922]. Over the next 30 years, only scattered and insignificant infestations were reported. . . . The first significant outbreak . . . began about 1948 and has persisted until now [1983].

Over western North America, budworm densities may range over five orders of magnitude. Populations are usually either at densities where they are barely discernible by standard sampling techniques, or at densities so high that defoliation is obvious. Populations of intermediate density are in transition—either increasing to outbreak or decreasing to sparse. The significance of this pattern is that it focuses attention on the two major population modes (outbreak and sparse) and two transient phases (release and decline) where we must have information for evaluating and understanding numerical changes. Processes that appear to dominate each mode or phase of this life system (sparse, release, outbreak, and decline) are summarized below.

6.2.1 Sparse Mode

Populations may be considered sparse if their average density is <1 egg mass (2 to 5 eggs)/ft^2 (20 to 50 eggs/m^2) of foliage. Poor survival is characteristic from fourth instar to residual pupae (pupae remaining after predation) among sparse, stable populations (6.6.1). At least in the Northwestern United States, this low survival is established largely through predation by birds and ants (6.6.3). Unless unusually high survival or inward migration occurs during other stages, this predation appears adequate to maintain populations at sparse densities indefinitely.

6.2.2 Release Phase

Two major events, either singly or together, are sufficient to enable a sparse population to increase to an outbreak: high survival during dispersal (fall and spring) of small larvae (6.4.5), and redistribution of egg masses by gravid females (6.7).

High survival during larval dispersal is associated with abundant host foliage, multistoried stands, and a particularly favorable conjunction between spring budburst and emergence of the larvae from hibernation. Relatively little is known about the redistribution of eggs by adult females, but the adult insects appear particularly likely to lay their eggs in the tops of older trees (Campbell and others 1984b).

6.2.3 Outbreak Mode

Once an outbreak starts, declining survival among young larvae (probably primarily caused by competition for feeding sites during spring dispersal) appears to be important in maintaining the outbreak from one year to the next. During outbreaks, this survival rate appears to decrease as density increases (6.4.1). This phenomenon undoubtedly reduces the chance that later instars will exhaust the foliage and starve (6.4.5, 6.6.1).

6.2.4 Decline Phase

Outbreaks may decline through any combination of processes that can operate against dispersing small larvae, larger larvae, residual pupae, or adult moths. Exceptionally low survival of the small larvae could be caused by differences in timing between larval emergence from hibernation and budburst (6.4.2), late frosts that destroy both the new foliage and the budworm, or foliage depletion through previous defoliations. Survival of the larger larvae is also at risk where most of the foliage has already been destroyed.

Parasitism among the residual pupae, which tends to be highest in places where mortality during earlier stages had already been high, may accelerate the collapse of an outbreak (6.6.2). Adult moths are also likely to disperse if they emerge in sites with little foliage suitable for laying eggs.

Historically forest managers have been most interested in forest pests after they reach high densities and threaten forest productivity or value (Mason 1978). Obtaining knowledge on how potentially damaging pest populations behave at sparse densities has been secondary. Currently, interest in the western budworm has shifted toward preventing possible future outbreaks through judicious management. To design appropriate preventive practices, managers need to know a great deal about both the processes that maintain populations at sparse densities, and the processes that upset this stability and lead to outbreaks.

Life tables represent an important tool for studies on population dynamics. One table can summarize much biologically rational information about a sequence of densities, mortality-causing factors, and fecundity in one place and in one budworm generation. Although life tables for forest insects go back at least as far as Tothill's work (1922), their usefulness was not recognized by many investigators until the classic paper by Morris and Miller (1954) on the development of life tables for the eastern budworm. Morris (1955) also described a pattern for developing sampling methods for the eastern budworm that has been adapted by other workers. With these methods, investigators can estimate densities per unit of foliage area with specified confidence.

McKnight (1971) adapted Morris's methods to develop budworm life tables in Colorado. Carolin and Coulter (1972) also adapted these methods to develop sampling procedures for budworm in eastern Oregon. More recently, Waters and Volney adapted these methods for use in New Mexico and southwestern Oregon. Campbell and others (1983a) used or adapted these methods to develop life tables for budworm in the Pacific Northwest.

Successive average densities, derived from life-table studies, are shown in figure 6-2 for both the populations that increased and those that decreased. For almost every successive age interval, average survival was higher among populations that increased. Processes operating during each of these age intervals are discussed in following sections.
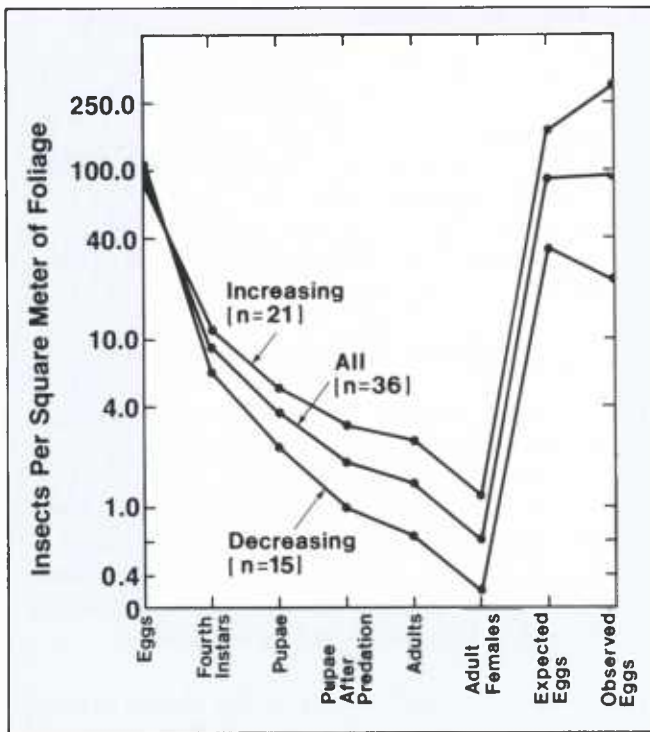
Figure 6-2—Successive average densities among western budworm populations. Data from populations studied in the Pacific Northwest (1978–82).
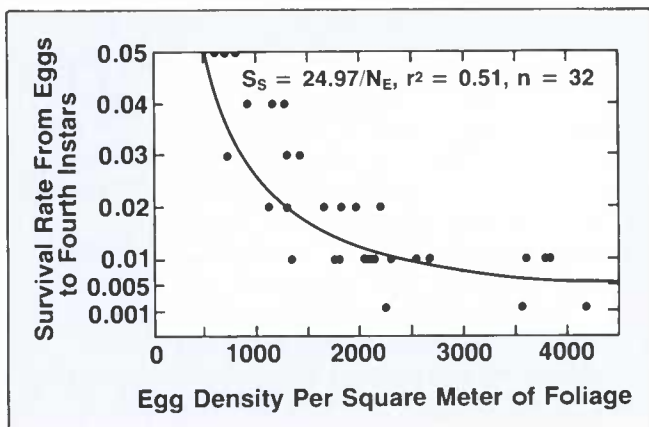
Figure 6-3—Egg density versus subsequent survival from eggs to fourth instar (early survival). Data from northern New Mexico (1978–81). Several assumptions had to be made to estimate egg densities and survival rates from the original data (adapted from Stein and McDonnell 1982 unpubl.).

Among the Northwest populations studied between 1978 and 1982, survival from eggs to fourth instars (early survival) ranged from about 30 percent down to about 2 percent. Carolin (personal communication) estimated that survival from egg hatch to fourth instar was 43 percent in one plot, 7 percent in a second, and 6 percent in a third. Carolin later judged 6- to 7-percent survival to be more typical (Carolin, personal communication). Volney and Waters (1983 unpubl.) noted that survival at this stage was high (37.1 percent) in a New Mexico population that increased 8.36-fold in a single generation. McKnight (1971) described average early survival of 64.9 percent for the populations he studied in Colorado between 1964 and 1966. The survival rates calculated by McKnight, however, use uncorrected estimates of density on midcrown branch tips. When these data were corrected to represent the whole plot, average early survival in these populations was estimated to be 18.8 percent (Srivastava and others 1984)—within the range found by others.

6.4.1 Density Versus Early Survival

Egg densities ranged from about 0.28 to 93 eggs/ft^2 (3 to 1,000 eggs/m^2) among the Northwest populations studied between 1978 and 1982. Across this range, almost no correlation was found between egg density and early survival (r^2 = 0.08).

Some populations studied recently in northern New Mexico (Stein and McDonnell 1982 unpubl.) were commonly much denser than any of the Northwest populations. Among these New Mexico populations, early survival declined from 5 percent in places and years where egg density was lowest to only about 0.1 percent where it was highest (fig. 6-3). Thus, early survival became a function of density above a threshold somewhere between 46 and 93 eggs/ft^2 (500 and 1,000 eggs/m^2). Other New Mexico populations within this density range studied by Volney and Waters (1983 unpubl.), which were either increasing or stable, showed a similar correlation between density and early survival. Survivorship ranged from 41.1 to 1.0 percent in these populations, however. Some likely consequences of this relation are discussed in sections 6.4.5 and 6.6.1.

6.4.2 Egg Survival

The incubation period is brief; hatching occurs about 10 days after the eggs are laid (Carolin and Coulter 1972). During this interval, the eggs are in danger from parasites and predators and may fail to hatch from other causes.

Average hatch was 93 percent among populations studied recently in the Pacific Northwest. Parasitism was generally extremely low, averaging only 1.2 percent (Torgersen and others 1984). Average mortality from all other factors was 5.4 percent. Carolin (personal communication) also found high survival among eggs.

6.4.3 Fall Dispersal

Only a few estimates of fall dispersal have been made for western populations. After intensive study in two sites in north-central Washington, Eldridge and Egan (1983a unpubl.) found that survival during this interval was 39 percent in one site and 77 percent in the other.

Dispersal from the egg mass is initiated as soon as the larvae hatch. Eastern budworm larvae on silk threads can be carried long distances by the wind (Henson 1950), but the larvae generally hibernate within a few hours of hatch (Morris and others 1958a). During this brief interval, the larvae are at risk from spiders and other predators. Most of their mortality, however, can be attributed to dispersal.

Dispersal losses of eastern budworm increase as the density of host trees decreases and as the host stand becomes more isolated (Morris and Mott 1963). Miller (1958) characterized survival during this interval as more variable than survival among either eggs or larvae in hibernacula.

6.4.4 Hibernation Survival

Survival across this interval is both high and relatively invariant. In two populations in north-central Washington, Eldridge and Egan (1983a unpubl.) found survivals of 79 and 87 percent. Miller (1958) found remarkably similar survival (78 to 91 percent) in New Brunswick, and Terrell (1959) reported generally high and invariant survival in the northern U.S. Rocky Mountains.

6.4.5 Spring Dispersal

Most of the variability in survival during the spring appears to be a consequence of variable losses from dispersal. Multiple dispersal episodes may be common, at least under some stand conditions. For example, Beckwith and Burnell (1982) found that dispersal of third and fourth instars represented about 38 percent of the larvae caught in dispersal traps in a mixed stand of Douglas-fir and western larch.

Spring dispersal begins as soon as the second instars emerge from hibernation. In northern New Brunswick, birds do not feed on young larvae of the eastern budworm (Cheshire 1959 unpubl.), but the larvae are again subject to predation by spiders and insects as they are during fall dispersal (Mott 1963a).

Whether dispersing eastern budworm larvae live or die is largely a question of finding hospitable sites (Mott 1963a). As in the fall, spring survival is directly related to the density of host trees and inversely to the degree of isolation of the host stand (Morris and Mott 1963). Western silvicultural recommendations are based partly on relations between the amount and placement of host foliage and the dispersal requirements of the larvae (Carlson and others 1983, Schmidt and others 1983, Wulf 1982 unpubl.).

In addition to problems with movement between hibernation site and suitable foliage, insects emerging from hibernation must also deal with possible asynchrony between their emergence and the availability of suitable food. Emergence of the population from hibernacula is prolonged, but most larvae hatch at about the same time (Volney and others 1983b). Thus, at least some larvae will find suitable feeding sites regardless of host phenology, but the rate of survival of the population depends on the degree of synchrony between budburst and the peak of second-instar emergence.

Losses during spring dispersal may reflect the probability that the larvae will find suitable food before their energy reserves are depleted. For example, an extended period of warm fall weather may critically deplete these reserves among eastern budworm larvae that will have to find suitable feeding sites after they emerge from hibernation (McMorran 1973).

Thomson and others (1984) recently analyzed relations between budworm outbreaks and long-term weather in British Columbia. They concluded that outbreaks were triggered by warm, dry summers in conjunction with optimal timing between larval emergence and the flush of Douglas-fir buds. All five outbreaks recorded among the records analyzed by Thomson and his colleagues "were associated with warm dry summers in conjunction with synchrony of larval emergence and bud flush."

As reported before (6.4.1), early survival was inversely related to density, at least among dense populations in northern New Mexico. In all probability, this inverse relation reflects some sort of intraspecific competition among the larvae. Such competition seems most likely either in the fall—for places to hibernate—or during the following spring—for suitable needles and buds. If this inverse relation between density and early survival proves generally true, it will probably also constitute a potent process in the population dynamics of the pest. Specifically such a process would thin overly dense egg populations to densities that would minimize the chance of exhausting the host foliage and subsequent mass starvation. Such a process would tend to ensure that ongoing outbreaks will persist.

6.5.1 Density Versus Late Survival

Fourth-instar densities ranged from about 0.03 to 7.4 larvae/ft^2 (0.3 to 80 larvae/m^2) among the populations studied recently in the Northwest. Among these populations, survival from fourth instar to adult females (late survival), like early survival, ranged from about 30 percent down to 2 percent. Late survival was uniformly low among populations where density of fourth instars was below about 3/m^2. Above this density, no clear relation appeared between density and survival.

6.5.2 Late Larval–Early Pupal Survival

Late survival is defined as survival from fourth instar to pupae remaining after predation (residual pupae) (fig. 6-4). Late larval and early pupal survival ranged across about 15-fold, and they varied together (r^2 = 0.85). Similarly, Morris (1963a) found a particularly close correlation in populations of eastern budworm between survival during fourth through sixth instars and generation survival.
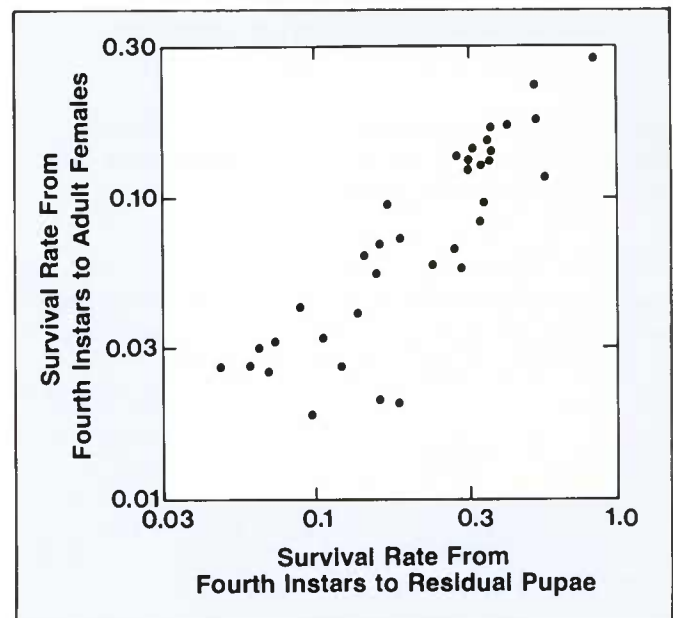
Figure 6-4—Survival from fourth instar to residual pupae (late larval–early pupal survival) versus survival from fourth instar to adult females (late survival). Data from populations studied in the Pacific Northwest (1978–82).

Much research has been devoted to events that occur during the late larval–early pupal interval. For this reason, description and discussion of the principal mortality-causing processes that operate during this interval are presented in a separate section (6.6).

6.5.3 Survival of Residual Pupae

Among the populations studied in the Pacific Northwest, survival of residual pupae ranged from about 25 to 100 percent. Except for two populations in north-central Washington, however, the lowest survival observed was about 50 percent. In general, survival of residual pupae was lower in north-central Washington than in the other areas.

Most of the variability in survival of residual pupae was induced by mortality from parasites (Campbell and others 1983a; Torgersen and others 1984). Among those populations, pupal parasitism ranged from a trace to 51 percent (Torgersen and others 1984). Parasites also appear to be a principal cause of mortality during this interval in other areas. For example, pupal parasitism accounted for 43 percent pupal mortality among the Colorado populations studied by McKnight (1971). See also table 6-1.

Variation in the survival of residual pupae played a generally minor role among western populations that have been intensively studied.

Table 6-1—Percentage contributions of larval and pupal parasitism to total killing power during the budworm generation, and during the interval from fourth instar to adults (after Torgersen and others 1984)

Location	Population trend	Number of sites	Average percent contributed to:	
			Generation	Interval
			Larval parasitism	
Washington	Decreasing	5	5.7	18.0
Idaho	Decreasing	4	2.7	9.5
Montana	Increasing	4	4.5	8.2
Oregon	Increasing	2	3.5	6.5
			Pupal parasitism	
Washington	Decreasing	5	13.2	30.2
Idaho	Decreasing	4	1.3	4.5
Montana	Increasing	4	4.5	9.7
Oregon	Increasing	2	1.0	2.0

6.5.4 Proportion of Females

In 22 of 24 Pacific Northwest populations, the sex ratio among pupae was 1 to 1. In 21 of these populations, the sex ratio among adults was also 1 to 1. In all populations, differences between survival of male and female pupae were attributed to chance. The proportion of females among pupae did not differ on Douglas-fir and grand fir, was slightly but significantly higher in the midcrown than in the lower crown, and was significantly higher in the one site studied where average defoliation of current-year shoots was greater than 50 percent (Campbell and others 1984b).

Other investigators have also noted only minor departures from 1 to 1 in the adult sex ratio in populations of both eastern and western budworms. In New Brunswick, Miller (1963b) reported that the proportion of females ranged from 0.33 to 0.54. Miller concluded that ". . . this proportion did not differ markedly from the expected value of 0.50 during the outbreak, and changes that did occur had a negligible effect on generation survival and population trend." For these same data, Morris (1963a) found almost no correlation between the proportion of females and generation survival ($r^2 = 0.01$).

In Colorado, McKnight (1971) found that 30 to 62 percent of the adults were female. McKnight thought that differential mortality among subadult males and females was probably because the males tend to pupate sooner, which would make them more susceptible to predation by both spruce coneworm larvae and female larvae of their own species.

In five of six sparse populations in southwestern Oregon (densities ranged from 0.08 to 1.1 eggs/ft^2 of foliage (0.87 to 12 eggs/m^2), the sex ratio was skewed in favor of males, and the proportion of females was positively associated with density (Volney and Waters 1983 unpubl.).

Variation in the proportion of females among adults appears to have had a negligible effect on populations that have thus far been studied.

6.6 Survival of Late Larvae and Early Pupae

6.6.1 Density Versus Survival of Late Larvae and Early Pupae

Survival of late larvae and early pupae is shown as a function of fourth-instar density in figure 6-5. Up to about 2.8 insects/ft² (30 insects/m²), these data show an inverse relation between density and late larval–early pupal survival. Above that density, the data are too sparse to discern any underlying relation.

For western budworm, our highest recorded densities were 15 fourth-instar insects/ft² (160/m²). For eastern budworm, Watt (1963) showed that late larval survival continued to increase slightly to about 13 fourth instars/ft² (140/m²). Ultimately, as densities increased beyond that point, average survival decreased.

Obviously fourth-instar density commonly exceeds 7.5/ft² (80/m²) among populations of the eastern budworm. Conversely, fourth-instar densities of western budworm greater than about 9.3/ft² (100/m²) were rarely found in either the Pacific Northwest or in northern New Mexico by either Stein and McDonnell (1982 unpubl.) or Volney and Waters (1983 unpubl.).

As described earlier (6.4.5), the apparent upper limit on fourth-instar densities in the northern New Mexico populations was induced by an inverse relation between egg density and early survival (fig. 6-3). No similar relation has been suggested for the eastern budworm. If this major apparent difference between the numerical behavior of the two budworm species proves to be general, it should provide much of the basis for understanding both the relatively indeterminate duration of outbreaks by the western species and the relatively mild biological effects of those outbreaks, compared to those by eastern budworm.
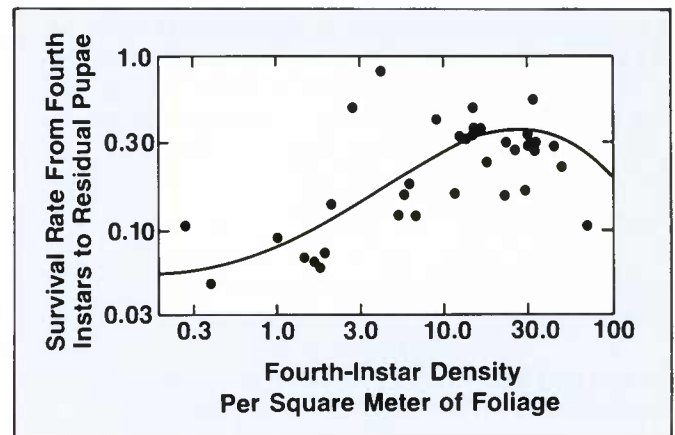
Figure 6-5—Fourth-instar density versus subsequent survival from fourth instar to residual pupae (late larval–early pupal survival). Data from populations studied in the Pacific Northwest (1978–82).

6.6.2 Role of Parasites

The bulk of our information about natural enemies of both the eastern and western budworms has been obtained during outbreaks, and to some extent during the decline phase of these outbreaks. Varty (1974) indicated that about 150 species of arthropods attack the budworms, and that about a third of these are predators.

Fourteen species of parasites were consistently represented in rearings from populations of the budworm studied recently in the Northwest. Torgersen and others (1984) listed the species as follows, in approximate order of decreasing dominance:

> *Apanteles fumiferanae* Viereck, *Glypta fumiferanae* (Viereck), *Charmon gracile* (Provancher), *Enytus montanus* (Ashmead), and *Mesochorus tachypus* Holmgren—a secondary parasite; all from larvae. Species reared from pupae were: *Agria housei* Shewell, *Madremyia saundersii* (Williston), *Ceromasia auricaudata* Townsend, *Phaeogenes maculicornis hariolus* (Cresson), *Itoplectis quadricingulata* (Provancher), *Ephialtes ontario* (Cresson), *Phorocera incrassata* Smith, and *Timavia fumiferanae* (Tothill). *Trichogramma minutum* (Riley) was the only parasite reared from budworm eggs.

The percentage contribution of parasitism to total killing power (equivalent to the killing power defined by Varley and Gradwell 1960) was lowest among the populations in Idaho and Oregon, intermediate in Montana, and highest in Washington (table 6-1). Because the contribution of parasites was highest in Washington, where the populations had been decreasing for several years, parasites may be reinforcing the decline of these populations (Torgersen and others 1984).

Several investigators have concluded that parasites play a substantial part in regulation of eastern budworm at sparse densities, but that their potential for rapid numerical response cannot curtail host numbers once release has begun (Blais 1960, Dowden and others 1948, Graham and Orr 1940, Miller 1963b, Tothill 1923). Morris and others (1958a) believed that the pronounced delay in response of parasites was compounded by adult-dispersal behavior of the eastern budworm, which could dilute or destroy developing synchronization between the budworm population and its parasite complex. This same observation could also apply to other natural enemies. Apparent increases in parasitism during a decline of the budworm could simply indicate that the residual population, which has already suffered heavy losses, is immediately subject to pressure from a parasite complex that is still increasing in response to the former density of the host.

6.6.3 Role of Birds and Ants

At the start of the CANUSA program, information about the role of birds in the West was limited to a record attributing the collapse of an outbreak at Lillooet, BC, to the joint effects of birds and parasites (Wilkes 1946). In contrast, a wealth of information was available on the role of birds in the dynamics of budworm populations in the East. They had been identified as playing significant roles in terminating outbreaks of the eastern budworm (Blais and Parks 1964, Dowden and others 1950, Jaynes and Drooz 1952). Dowden and others (1948, 1953) found that about 15 species of resident and nonresident birds fed heavily on the eastern budworm. Shooting-out techniques by Dowden and others (1953) and caging studies by Jaynes and Drooz (1952) demonstrated striking quantitative effects of excluding birds (and parasites) from individual trees and entire plots.

Detailed studies on avian predation on the eastern budworm (Mook 1963, Morris and others 1958a) indicate that predation was greatest during the sixth instar and pupal stage. All bird species, particularly three warblers, showed pronounced, direct numerical responses to budworm density. Graham and Orr (1940) suggested that the scarcity of insectivorous birds brought on by a combination of unfavorable weather and lack of food may have stimulated an eastern budworm outbreak in Minnesota. Most recently, Crawford and others (1983) concluded that birds ate about 87, 23, and 2 percent of the insects in sparse, transition, and dense populations of the eastern budworm.

In 1979, several species of birds were commonly observed preying on the western budworm. Two sites, with single-branch bird exclosures (Campbell and others 1981) had pupal densities on protected branches twice as high as on control branches (Torgersen and Campbell 1982). These results stimulated studies on insectivorous birds (see section 6.4).

Ants were also seen investigating and eating the budworm. In 1980, to cite an extreme example, 96 separate observations were made of ants investigating or eating pupae in 48 hours after 150 pupae were stocked in one site in north-central Washington (Campbell and Torgersen 1982). Between 1979 and 1982, species of ants observed eating budworm pupae included the following: *Camponotus modoc* Wheeler, *C. vicinus* Mayr, *C. laevigatus* (Smith), *Formica haemorrhoidalis* Emery, *F. accreta* Francoeur, *F. podzolica* Francoeur, *F. neorufibarbis* Emery, and *F. lasiodes* Emery (Youngs and Campbell 1984).

Ant predation on both the eastern and western budworms has been observed by other investigators. Mathers (1932) in British Columbia and Thomson (1957) in Ontario considered ants important budworm predators, and both Bain (1974) and Markin (1979a unpubl.) identified ants as predators of the western species.

In 1980, whole-tree exclosures and sticky barriers were used to exclude avian predators, predaceous ants, or both from open-grown trees 29.5 ft (9 m) tall on one site in north-central Washington and four sites in central Idaho. Budworm on these trees were protected from about the fourth instar until they either died or became adults. At the lowest budworm density (0.16 fourth instar/ft^2, 1.7/m^2), 10 to 15 times as many adult moths were produced on trees protected from both birds and ants as on control trees. Even when fourth-instar density was 2.3 insects/ft^2 (25/m^2), adult density continued to be about twice as high on protected trees as on controls. Birds alone or ants alone were usually sufficient to greatly dampen the high survival observed when both groups were excluded (fig. 6-6).

In 1981, the trials initiated in 1980 with whole-tree exclosures and sticky barriers were continued on sites in northwestern Montana and eastern Oregon. Again, the results showed a strong inverse relation between budworm density and the effects of birds and ants. This predation, combined with mortality from all other sources, was consistently adequate to reduce survival across the late larvae to early pupal interval to about 5 percent in populations with fourth-instar density of <0.09 insect/ft^2 (<1/m^2). When these predators were removed, however, average survival increased to about 40 percent (fig. 6-7). Unless other processes upset low-density stability, predation by birds and ants can maintain most budworm populations in the Pacific Northwest at sparse densities indefinitely.

The relative influence of birds versus ants can be greatly influenced by stand age and structure. For example, birds were as effective in destroying pupae on branches in the upper crowns of tall trees as on branches at about breast height; ants, however, were only effective on low branches (Campbell and Torgersen 1983b). In contrast to the dominance of birds on tall trees, the roles of birds and ants tended to be reversed on seedlings (Campbell and others 1984a).
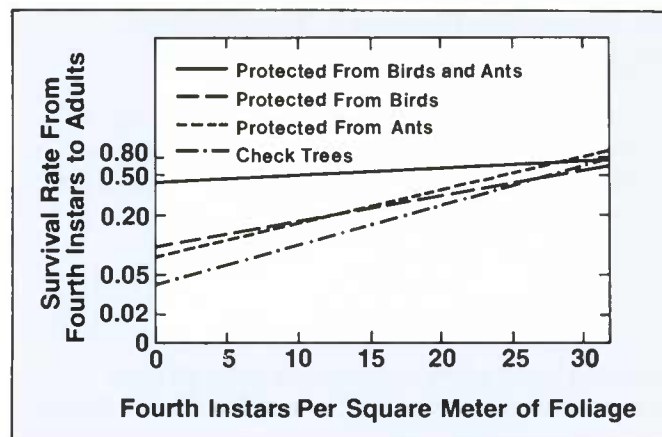
Figure 6-6—Fourth-instar density versus survival on trees protected from birds, ants, and both groups, and on control trees (after Campbell and others, in press).
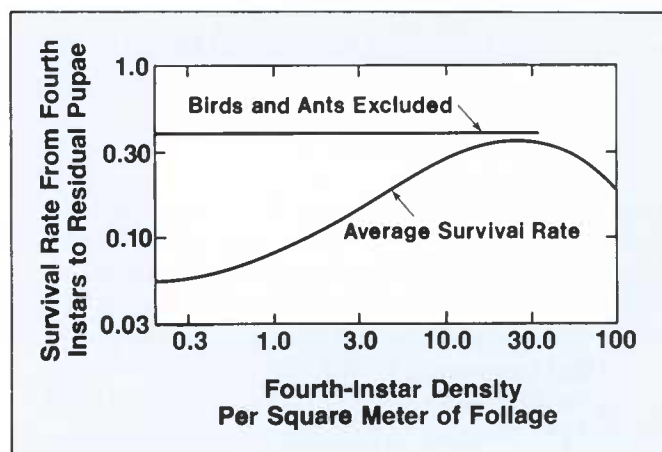
Figure 6-7—Fourth-instar density versus survival from fourth instar to residual pupae, on both trees where birds and ants had been excluded and control trees. Data from populations studied in the Pacific Northwest (1978–82).

6.6.4 Habitat Requirements of Avian Predators

Edward O. Garton

Dramatic increases in budworm populations on trees protected from forest birds (fig. 6-6) has heightened interest in these predators, their habitat requirements, and potential for managing their populations (Takekawa and others 1982). Ecological characteristics of bird species occurring in western forests have been summarized in detail for only two regions (Thomas 1979, Verner and Boss 1980). Potential approaches to managing many of these species were examined in a series of symposia (Smith 1975; DeGraff 1978, 1980).

Bird species known to consume western budworm can be grouped into guilds based on their feeding activities during the spring and summer. The major guilds are flocking, conifer gleaning, shrub gleaning, ground foraging, and flycatching. Birds within each guild show many similarities in feeding behavior, diet, nesting requirements, and taxonomy. The role of the species known to be important in regulating budworm populations and their habitat requirements are summarized, by guild, in this section.

6.6.4.1 Flocking Guild—

In spite of their general classification by ornithologists as seed-eaters (Bent 1968), the members of the flocking guild show the highest rates of consumption of budworm larvae and pupae (table 6-2). These species are unique in the forest bird community in that they are not territorial during the breeding season but forage widely in flocks (Bent 1968). Because of this, their numbers may increase enormously on sites experiencing budworm outbreaks. These species all nest in conifers or deciduous trees (table 6-2); consequently, they breed more commonly in mature and old-growth stands than in early successional stages (table 6-3). Their occurrence in a particular stand is sporadic from year to year and most likely related to insect abundance. The flocks appear to be nomadic during the nonbreeding period, moving from area to area or even region to region in search of seeds of conifers and other trees (Bent 1968). During the late summer and fall, they consume large quantities of berries. Beyond these general statements, little is known about the specific factors influencing the numbers of these species from year to year and stand to stand.

6.6.4.2 Conifer-Gleaning Guild—

Budworm consumption by the large guild of conifer gleaners (table 6-3) ranges from two to over six budworm larvae and pupae per bird per hour (table 6-2). These species are all strongly territorial, with consequent stability in numbers from year to year in any particular stand. They hunt for insects on the foliage and small branches of conifers during the breeding season and play a major role in maintaining sparse budworm populations during intervals between outbreaks. The species resident in fir and mixed-conifer forests during the winter—such as chickadees and kinglets—probably consume large numbers of hibernating larvae. The species in this guild are most diverse in mature and old-growth forests, and the total number of birds in this guild increases with increasing volume of foliage (MacArthur 1958; Garton and Langelier, in press). The guild is most abundant in stands with a multistoried canopy and an abundance of shrubs (Garton and Langelier, in press). The habitat requirements of many of these species are well studied (Bent 1963b, 1964a, 1964b, 1964c, 1965a, 1965b, 1968). Some, such as the yellow-rumped warbler and the western tanager, are adaptable and occur widely. Others—such as the chickadees—have specific nesting requirements, which may limit where they occur (Thomas 1979).

6.6.4.3 Shrub-Gleaning Guild—

Members of the shrub-gleaning guild feed in shrubs predominantly and conifers secondarily. Mean consumption rates varied from 1.7 to 6.0 budworm per bird per hour (table 6-2). These species nest in or under shrubs and are less abundant where shrubs are reduced (Garton and Langelier, in press).

Table 6-2—Budworm consumption, foraging-guild membership, and nesting requirements of 26 bird species that are important predators of budworm[1]

Species	Budworm consumption[1]	Foraging guild	Nesting substrate
Evening grosbeak	36.3	Flocking	Conifers or deciduous trees
Red crossbill	18.3	Flocking	Conifers
American robin	15.0	Ground	Shrubs or low in trees
Pine siskin	12.1	Flocking	Conifers or deciduous trees
Cassin's finch	8.3	Ground	Conifers or deciduous trees
Warbling vireo	6.5	Conifer	Conifers or deciduous trees
Black-capped chickadee	6.1	Conifer	Cavities made by other species
Mountain chickadee	6.1	Conifer	Cavities made by other species
Nashville warbler	6.0	Shrub	Ground
Brown-headed cowbird	5.4	Ground	Parasitic—eggs laid in nest of other species
Chipping sparrow	5.3	Ground	Shrubs or low in trees
Dark-eyed junco	5.1	Ground	Ground
Townsend's warbler	5.0	Conifer	Conifers
Townsend's solitaire	4.0	Conifer	Ground
Yellow warbler	3.7	Shrub	Shrubs, especially riparian willows
Solitary vireo	3.5	Conifer	Conifers or deciduous trees
Yellow-rumped warbler	3.4	Conifer	Conifers
Western tanager	3.1	Conifer	Conifers or deciduous trees
Golden-crowned kinglet	2.9	Conifer	Conifers
Ruby-crowned kinglet	1.9	Conifer	Conifers
MacGillivray's warbler	1.7	Shrub	Shrubs
Swainson's thrush	1.3	Ground	Shrubs or low in trees
Hammond's flycatcher	1.2	Flycatching	Conifers or deciduous trees
Rufous-sided towhee	1.1	Ground	Shrubs
Hermit thrush	1.0	Ground	Ground
Western wood pewee	0.1	Flycatching	Conifers or deciduous trees

[1]Budworm consumption (mean number of large larvae and pupae consumed per hour per bird) was estimated from stomach contents and digestive-rate studies.

Table 6-3—Successional stages and ecotones of fir and mixed-conifer forests used for breeding (B) and feeding only (F) by 26 important avian predators of budworm (after Thomas 1979)

Foraging guild	Species	Successional stages						Ecotones		
		Grass–forb	Shrub–seedling	Pole–sapling	Young	Mature	Old-growth	Grass–shrub	Shrub–forest	Grass–forest
Flocking	Evening grosbeak	F		F	F	B	B		B	B
	Red crossbill				F	B	B		F	F
	Pine siskin	F	F	B	B	B	B	F	B	B
Conifer	Black-capped chickadee			B	B	B	B	F	B	
	Mountain chickadee			B	B	B	B		B	B
	Warbling vireo		F	B	B	B	B	F	F	
	Solitary vireo			B	B	B	B			
	Townsend's solitaire	B	B	B	B	B	B	B	B	
	Townsend's warbler				F	B	B			
	Yellow-rumped warbler			F	B	B	B	F	F	
	Western tanager		F	F	B	B	B		B	B
	Golden-crowned kinglet		F	F	B	B	B			
	Ruby-crowned kinglet			F	F	B	B	F	F	
Shrub	Nashville warbler		B	F	F				B	
	Yellow warbler		B	B	B	B		F	F	
	MacGillivray's warbler		B	B	B	B			F	
Ground	American robin	F	B	B	B	B	B		B	B
	Cassin's finch	F	F	F	B	B	B	F	B	B
	Brown-headed cowbird	B	B	B	B	B	F			
	Chipping sparrow	F	B	B	B	B	B	B	B	
	Dark-eyed junco	B	B	B	B	B	B		B	B
	Swainson's thrush		B	B	B	B	B		B	
	Hermit thrush			F	F	B	B			
	Rufous-sided towhee		B	B	B	B	B	B	B	
Flycatching	Hammond's flycatcher		F	F	F	B	B		B	
	Western wood pewee		F	F	B	B	B		B	B

6.6.4.4 Ground-Foraging Guild—Members of the ground-foraging guild feed on the ground and in the grasses, forbs, shrubs, and lower foliage of trees. Mean budworm consumption varies from 1 to 15 larvae and pupae per bird per hour (table 6-2). These species are territorial and do not show major increases in abundance associated with budworm outbreaks. They apparently shift their foraging locations from the ground and low vegetation to the lower portion of the canopy during outbreaks and apply additional pressure toward suppression of outbreaks during the period of initial buildup. Several of these species nest in shrubs, and most depend on the low vegetation in some way. Even those species nesting on the ground require low vegetation to cover the nest. Members of this guild occur in all successional stages and are particularly associated with ecotones (table 6-3).

6.6.4.5 Flycatching Guild—Only the Hammond's flycatcher in the flycatching guild consumes many budworm larvae and pupae (table 6-2), but the members of this group probably consume many adults. This guild is most abundant in later successional stages (table 6-3) and in diverse stands with an open canopy structure (Bent 1963a).

6.6.4.6 Other Guilds—Some of the other groups of birds occupying forest stands, such as the raptors, are unlikely to play a direct role in budworm population dynamics. Such groups as woodpeckers, however, which feed extensively on tree trunks during winter, and swifts and swallows, which consume large numbers of adult lepidopterans in the air, may be valuable budworm predators. Members of other guilds have been observed to feed on moths. The roles of these groups relative to budworm have not been studied.

6.6.5 Other Mortality-Causing Factors
Robert W. Campbell

Casual observations have shown that insectivorous mammals eat both late instars and pupae. No attempt has been made, however, to quantify the effect of this predation. In the East, Morris (1955) noted that most of the large larvae that drop to the understory are eaten by white-footed mice, *Peromyscus leucopus* Rafinesque. As an influence on eastern budworm population dynamics, however, small mammals have essentially no effect (Morris and others 1958a).

The activity of arthropod predators is seldom reported. Brief mention is made of predation by representatives of several groups, such as a clerid beetle and a snake fly (Carolin 1976), a carabid beetle (Sanders and Frankenhuyzen 1979), and mites (Jaynes and Drooz 1952). But most of the interest in arthropod predators of the budworms has been in spiders (Loughton and others 1963, Turnbull 1956). These authors concluded that spiders take whatever prey is most abundant, and that by sheer weight of numbers they are important in budworm regulation. The web-spinning therediids and the hunting salticids constitute the dominant families known to prey on budworm.

Four groups of microorganisms—microsporidia, viruses, bacteria, and fungi—are known to occur in all budworm stages except the egg. The relevant literature was reviewed by Neilson (1963), who concluded that the diseases affecting the eastern budworm are only mildly infectious and have low epidemiological potential. In populations studied in the Pacific Northwest between 1978 and 1982, only a very few specimens showed symptoms of lethal infectious or noninfectious disease.

At least across the interval from fourth instar to adults, survival of populations in the Northwest consistently approached a high constant on trees that had been protected from birds and ants (figs. 6-6, 6-7). Increased mortality from other sources did not effectively compensate for their absence. In short, other mortality-causing factors played a minor role in regulating late survival, once birds and ants had been excluded (Campbell and Torgersen 1983a).

6.6.6 Foliage Quality

Several investigators have recently examined relations between the natural defensive chemistry of Douglas-fir and success of the western budworm. To explore some of the reasons why populations rarely reach outbreak densities west of the Cascade Range, Perry and Pitman (1983) tested responses of larvae to foliage from seedlings of both west-side Douglas-fir (var. *menziesii*) and interior Douglas-fir (var. *glauca*) grown in the same west-side garden. Surprisingly foliage from the interior Douglas-fir caused a wide range of larval mortality; foliage from the west-side Douglas-fir caused no significant larval mortality. Perry and Pitman concluded that environmental factors east of the Cascades may alter the ability of the trees to produce allelochemics and thus play a key role in regulating interior populations. They concluded that the apparent lack of defensive chemicals in west-side Douglas-fir suggests either that "inducible defenses may play a role" or that predators and parasites may keep budworm populations at low densities in west-side ecosystems.

Studies by Cates and others (1983a, 1983b) indicate that resistance is associated with terpene chemistry, variation in budburst, and tree vigor; the terpene complement associated with resistant trees in Montana was different from that found in New Mexico, however. Agar-diet studies showed that high concentrations of bornyl acetate and beta-pinene—similar to the concentrations in the foliage of resistant trees—increased the duration of the larval stage and decreased dry weight. In apparently vigorous trees in New Mexico, high levels of beta-pinene, myrcene, and an unknown terpene were correlated with reduced fecundity (Redak and Cates 1984).

In the Pacific Northwest, the number of eggs deposited per female pupal case (observed eggs per female), ranged across about 100-fold, from a low of about 10 to a high of about 1,000. The correlation between observed eggs per female and annual trend is $r^2 = 0.25$. As suggested earlier (Campbell and others 1983a), both the range in the number of eggs deposited per female and the correlation between this number and annual trend show that variation in observed eggs per female has an important influence on the dynamics of this life system.

Although many complex processes are involved (Greenbank and others 1980), observed eggs per female moth is the result of both the average fecundity of those moths at the time they emerge, and the net result of all the processes of migration and mortality that influence those moths until they die or finish laying their eggs.

6.7.1 Fecundity

In any population, average fecundity can be estimated by rearing a sample of mated female moths and counting the eggs they produce. Fecundity is affected largely by the quantity and quality of food available to the preceding larvae (Blais 1952, Kirkbride and Wagner 1983a unpubl., Miller 1963a). Other extrinsic factors that may affect fecundity indirectly include weather (Greenbank 1956), the availability of suitable places to lay eggs, and disease (Neilson 1963). In populations of both eastern and western budworms, mean fecundity is closely correlated with size or weight of female pupae (Kirkbride and Wagner 1983a unpubl., Miller 1957).

Average fecundities ranged from about 100 to 200 among populations studied in the Pacific Northwest. Almost no correlation was found between these fecundities and the observed number of eggs per female pupal case ($r^2 = 0.03$). Apparently, variation in average fecundity had almost no effect on the number of eggs actually deposited per female moth.

6.7.2 Index of Adult Dispersal

The net results of moth migration and mortality (index of adult dispersal) can be estimated from the ratio between egg density on the foliage and the innate egg-laying ability of the emerging females. Relations between the index of adult dispersal and observed eggs per female pupal case (fig. 6-8) are very close ($r^2 = 0.92$). Thus, almost all of the variation in observed eggs per female pupal case resulted from variation in adult migration and mortality. Immigration clearly exceeded the combined effects of emigration and mortality where observed eggs per female pupal case were greater than the inherent ability of females to produce eggs (about 200). Significantly, observed eggs per female pupal case were consistently much greater than 200 among the populations we studied in eastern Oregon at the start of the current outbreak. Just as in eastern budworm, redistribution of adult female moths appears to be a major factor in the population dynamics of the western species (Campbell and others 1983b).
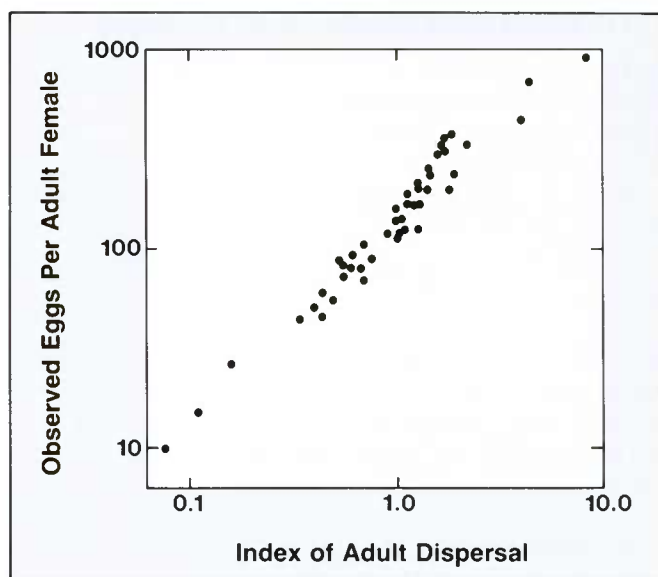
Figure 6-8—Adult-dispersal index versus observed eggs per female. Data from populations studied in the Pacific Northwest (1978–82).

6.7.3 Density of Adult Females Versus Egg Density

Redistribution of adult females clearly seems to be a major factor in western budworm population dynamics. In 1981, the life-table studies were supplemented with data from 10 additional sites: 6 in southwestern Montana and 4 in eastern Oregon. Both adult female densities and subsequent egg densities per square meter were estimated on each of these additional sites.

Egg density in the 46 Northwest populations was examined as a function of both the density of preceding adult females and an index of defoliation. This index, based on average defoliation of current-year shoots, was

No defoliation = 1;
$0 < $ defoliation ≤ 25 percent = 2;
25 percent $<$ defoliation ≤ 50 percent = 3; and
50 percent $<$ defoliation ≤ 75 percent = 4.

Average defoliation of current-year shoots never exceeded 75 percent among the populations studied.

Relations between adult females, defoliation, and subsequent egg density are shown in figure 6-9. Only 15 of the 46 predicted values (33 percent) were within ± 20 percent of their observed values. Seventeen predicted values (36 percent) deviated from observed by more than ± 75 percent.

Perhaps much of the variation in the density of eggs not associated with either the density of adult females or defoliation will prove to be a function of identifiable characteristics of sites and stands. Only further studies can provide an answer.

$$N_{E(n+1)} = [(76.01) \cdot (N_{\female A})^{0.797}] \cdot [DEF^{0.844}]$$
(On a logarithmic scale, $R^2 = 0.81$)
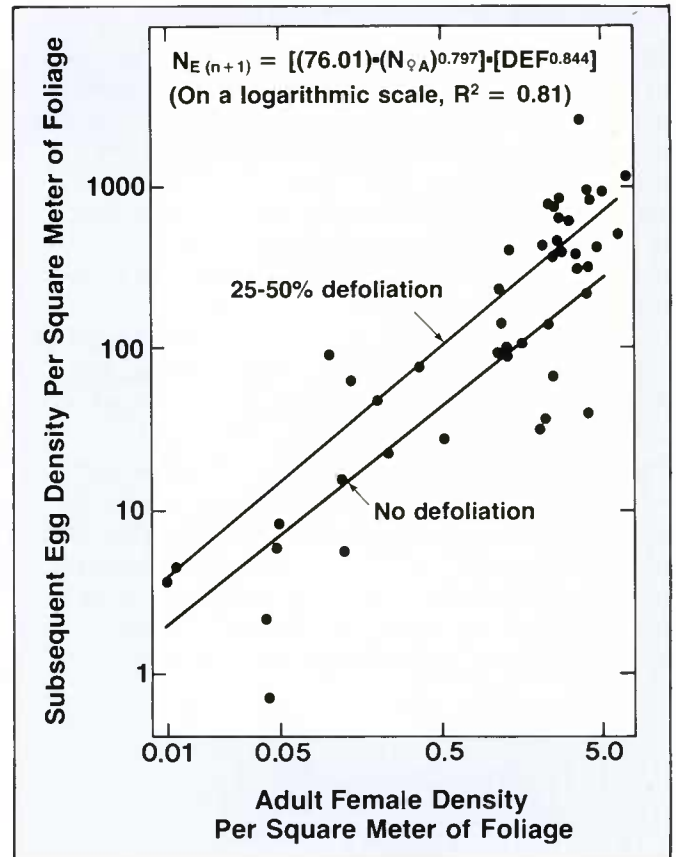
Figure 6-9—Density of emerging adult females ($N_{\female A}$) and an index of defoliation (DEF), versus subsequent egg density ($N_{E(n+1)}$). Data from populations studied in the Pacific Northwest (1978–82).

Chapter 7

Site and Stand Characteristics
N. William Wulf and Rex G. Cates

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This chapter is a synthesis of documented relations between budworm and characteristics of sites and stands. These correlations have been woven into a theory of interaction between western budworm and its host forests.

Outbreaks of western budworm occur over a wide geographic range, and populations are successful from warm, dry interior Douglas-fir types to cool, moist subalpine fir/spruce types. This wide distribution across environmental gradients and forest types could simply suggest that the budworm has broad adaptability. Outbreak frequency and infestation intensity vary considerably, however, which suggests budworm populations may be responding to an ecological similarity that exists among these seemingly diverse habitats. The common feature appears to be physiological stress in host trees.

Mott (1963b) defined stand susceptibility to budworm as the probability of infestation, and stand vulnerability as the probability of tree damage resulting from a given budworm density. He recognized that the environmental characteristics that predispose a stand to infestation may not be the same as those that account for tree damage after a stand is attacked. Susceptibility thus encompasses the influence that forest conditions have on budworm populations, and vulnerability refers to the damage the budworm causes to the forest. Susceptibility is a measure of the quality of budworm habitat and serves as an index to the population density supported by a stand during outbreaks. Vulnerability, on the other hand, is an expression of tree injury that accrues in a stand because of a budworm infestation.

Stand characteristics strongly influence the number of budworms inhabiting a stand. Stand susceptibility has two components: intrinsic habitat quality and extrinsic sources of population gain or loss. This extrinsic component of susceptibility is derived from the location of the stand with respect to active budworm infestations. Insects produced in these stands can drift or actively emigrate to adjacent stands, some of which may be marginal habitat. Thus, some stands that appear to have low intrinsic susceptibility may harbor fairly high budworm populations simply because they are downwind from infested stands (Mott 1963a). On the other hand, inherently susceptible stands may not be infested because they are isolated from active budworm infestations.

The amount of damage from a budworm infestation depends not only on the density and persistence of the budworm population but also on how trees respond to and recuperate from defoliation. Susceptibility to infestation and vulnerability to damage are closely related in that more budworm generally means more damage and vice versa. Susceptibility and vulnerability are both recognized as related to the same site and stand characteristics. These relations, along with descriptive indexes that could be used to quantify them, are listed in table 7-1.

Table 7-1—The relation of site, tree, and stand characters to susceptibility and vulnerability to western budworm

Character[1]	Susceptibility	Vulnerability	Indexes
Site	Warm, dry > cool, mesic > cold, wet	Warm, dry > cool, wet[2]	Habitat type Soil type Elevation Topographic position Site index
Tree species	True fir > spruce > Douglas-fir > western larch > nonhost	True fir > spruce > Douglas-fir > western larch > nonhost	Shade tolerance Successional status
Stand composition	Pure climax host > mixed host > pure seral host > mixed nonhost > pure nonhost	Pure climax host > mixed host ≥ pure seral host > mixed nonhost > pure nonhost	Percent climax Host stocking Ratio of host/nonhost stocking
Intraspecific genetic variation	High-quality foliage > nutritionally poor resistant foliage, early budbreak > late budbreak	Short needle retention > long needle retention Physiological response to defoliation	Artificial selection intensity Frequency and severity of past infestations
Tree and stand vigor	Nonvigorous > vigorous	Nonvigorous > vigorous[2]	Live crown ratio Current radial or height increment Basal area increment/sapwood area Level of pathogens Stand growth relative to site potential Basal-area stocking relative to maximum stocking Crown-competition factor
Stand density	Dense > open	Dense > open	Total trees per acre Total basal area per acre Crown closure
Crown class	Dominant > codominant > intermediate > overtopped	Overtopped > intermediate > codominant > dominant	Amount and exposure of foliage
Stand structure	Uneven-aged > two-storied > even-aged	Uneven-aged > two-storied > even-aged	Variation in tree heights, diameters, or ages
Tree and stand maturity	Old > young	Old > young[2]	Tree or stand age Tree or stand diameter

[1]Each character is assessed individually as if all other characters are held constant.
[2]Relations pertain to relative vulnerability—that is, percent growth reduction caused by infestation. In absolute terms, volume loss may be greater in fast-growing stands than in slow-growing stands.

In the following sections, we discuss how site, tree, and stand characteristics relate to susceptibility and vulnerability. The effect of each characteristic is considered separately, and we draw general conclusions about its influence, assuming all other factors are held constant or otherwise accounted for. In reality, however, budworm responds to its habitat as a whole, and therefore, the influence of any particular habitat characteristic may be obscured or confounded by the net effect of others. Site and stand variables—as we and others have distinguished them—are themselves interrelated, and often these interactions have not been recognized in reported analyses. For these reasons—and because sample data may represent a limited range of site and stand conditions—conclusions should not be drawn on the basis of a single correlation. We look for commonality among all of the available evidence and test our interpretation against what is known about the population dynamics and behavior of budworms.

Under each variable believed to be important in budworm population dynamics, we first describe reported correlations from the literature and current studies. At the end of each section, we synthesize the information into a description of how the variable influences budworm populations.

Several site characteristics have been found to be significantly related to the amount of defoliation caused by the western budworm. Fauss and Pierce (1969) determined that defoliation varied inversely with site index, and more defoliation of Douglas-fir occurred on dry, hillslope sites than on moist, productive, bottomland sites in western Montana. In the Bitterroot National Forest, Sutherland (1983) found that Douglas-fir trees were more likely to be defoliated on Douglas-fir habitat types than on grand fir or subalpine fir habitat types. For all three habitat series, defoliation increased as elevation decreased. In the drier habitat types, defoliation was more extensive on slopes steeper than 46 percent than on more gentle slopes. In the Gallatin Canyon of south-central Montana, Despain (1981) showed that defoliation on Douglas-fir tended to increase with decreasing elevation and increasing slope steepness. Defoliation was more severe on southerly exposures and on ridges and upper slopes.

In the Clearwater National Forest of north-central Idaho, Stoszek and Mika (1983 unpubl.) found heavier defoliation on grand fir habitat types than on western redcedar types, and on subalpine fir habitat types compared to mountain hemlock types. They also observed more defoliation on ridgetop sites and on southwesterly facing slopes. Defoliation was seen to increase with increasing elevation in the western hemlock series and with decreasing elevation in the subalpine fir series. Stoszek and Mika define habitat series according to Daubenmire and Daubenmire (1968)—the western hemlock series includes western hemlock, western redcedar, and grand fir habitat types.

More defoliation was found on ridgetops and upper slopes than on lower slopes in the Payette National Forest in central Idaho (Stoszek and Mika 1983 unpubl.). In the Salmon National Forest, these investigators found that defoliation on Douglas-fir increased with increasing elevation up to 6,000 ft (1830 m); thereafter, defoliation decreased with increasing elevation. This same mid-elevation banding pattern of defoliation was also detected on aerial photographs of north-central Washington and central Idaho by Heller and others (1981 unpubl.). In British Columbia, defoliation is seldom observed in the valley bottoms (Thomson and others 1984).

Kemp (1983) studied the distribution and frequency of budworm infestations that have occurred in Washington, Oregon, Idaho, and Montana between 1948 and 1978. He identified three infestation-frequency zones within this four-State area (see fig. 6-1) and found that infestations have been more common in areas with lower annual precipitation and lower winter temperatures. In addition, he found that soils with low available moisture and no volcanic ash mantle were associated with the high outbreak-frequency zone, and available soil moisture and volcanic ash depth increased as outbreak-frequency class decreased.

Some investigators have related the amount of growth reduction or other expressions of stand damage to site characteristics. Terrell and Fellin (1959 unpubl.) observed that the greatest amount of defoliation and tree mortality of Douglas-fir occurred on dry sites, usually with south and east exposures, and where timber productivity was marginal. Williams and others (1971) reported that Douglas-fir in eastern Montana died after about 5 years of severe defoliation if they were growing in shallow soils on dry knolls, but on wetter sites, they could endure as much as 40 years of defoliation. Extensive tree mortality occurred in dense stands on dry, rocky slopes. Carlson and others (1983) found radial-growth reductions were highest in dry Douglas-fir habitat types at low elevations and on steep slopes in western Montana. Forests on cooler and wetter habitats did not sustain nearly as much injury. The probability of stocking after a regeneration harvest was reduced by western budworm about 30 percent on dry Douglas-fir, dry subalpine fir, and moderate subalpine fir habitat types, but no influence was found on the more moist or cold habitat groups (Carlson and others 1982 unpubl.).

Based on the correlations between site variables and western budworm defoliation and damage, we conclude that warm, dry sites are generally more susceptible to infestation and more vulnerable to damage than cool, wet sites (fig. 7-1). Site variables are expressions of the interaction between local climate and edaphic features of a site. This interaction determines the potential of the site for timber production. We suspect that within similar climatic regimes, poor sites are more susceptible than productive sites. These contentions may be substantiated by a closer look at the relation between weather, moisture stress, and budworm population dynamics.

In northern Idaho, western Montana, and eastern Montana, Hard and others (1980) determined that infestation expansions between 1969 and 1979 were preceded by periods of relative drought and higher than average spring temperatures. Twardus (1980 unpubl.) showed that warm, dry periods preceded outbreak initiation in north-central Washington. Extensive studies of regional climate and weather patterns related to eastern budworm outbreaks show that dry, sunny summers favor population increases and that periods of relative drought often precede outbreak development (Greenbank 1956, 1963a; Ives 1974, 1981; Pilon and Blais 1961; Wellington and others 1950). Once stands are in a susceptible condition, weather cycles are believed to determine the general incidence of eastern budworm outbreaks in time and place (Baskerville 1975; Blais 1954, 1968; Morris and others 1958b).

The prevailing weather, as mediated by geographic location and local topography, can have direct and indirect effects on budworm populations. Warm weather in the spring and early summer hastens the emergence, growth, and development of larvae (Wagg 1958). Larvae emerge from hibernacula earlier at warmer low elevations than at higher elevations (Wagg 1958). Presumably, the early and more rapid development of larvae and pupae ensures that the

Figure 7-1—Severe defoliation and tree mortality occurs on steep, dry sites—which are marginal for timber production (Gallatin Canyon, south-central Montana).

overwintering stage is entered before the onset of cold temperatures in the fall. Blais (1958) observed that cooler than average temperatures were, in part, responsible for the delayed development of eastern budworm larvae at higher elevations. As a result, pupae often failed to give rise to moths, some eggs failed to hatch, and many first instars were killed by cold weather in the fall. Thomson (1979) estimated that western budworm eggs will not hatch if the temperature is below 60 °F (15.6 °C) or the relative humidity is below 50 percent or above 75 percent. Warm, dry summer weather promotes mating of eastern budworm (Greenbank 1963a) and could have a similar effect on western budworm. Extended larval and pupal development under cool regimes would presumably allow predators more time to find and destroy them. Late spring frosts can decimate populations of exposed budworm larvae or result in starvation if the expanding foliage of host trees is killed (Fellin and Schmidt 1973a, Johnson and Denton 1975, McKnight 1971).

The interaction of climate and site characteristics affects the synchrony between new foliage development and emergence of the larvae from hibernation and, thereby, indirectly influences budworm success. Budburst in host conifers is ultimately regulated by increases in soil temperature in the spring (Lavender 1981, Cleary and Waring 1969). Budburst occurs earlier on sites with warmer soils and air temperatures. Such sites are likely to be at lower elevations, and have southerly aspects and relatively dry soil. Wagg (1958) observed that in dense forest stands that retained a snow cover later in the spring, shoots began to grow later and larvae developed before the new foliage. Kemp (1983) showed that spring larval emergence and development were related to air temperatures, but one year when a deep snow pack persisted, host budburst was markedly delayed relative to larval emergence. Beckwith and Burnell (1982) suggest that larval emergence before budburst promotes mining of old needles and subsequent dispersal, both of which increase mortality. Eastern budworm larvae that are obliged to feed on old foliage because they emerge before budburst have higher mortality rates and reduced fecundity (Blais 1952, 1953; Greenbank 1956; Miller 1963a). Western budworm fed old foliage in the laboratory also had increased mortality rates (Blake and Wagner 1983 unpubl.).

We postulate from these observations that western budworm larvae generally emerge somewhat before the host foliage flushes, thereby increasing the chance of larval mortality and limiting population growth. Under warm, dry weather patterns and, more frequently, on warm droughty sites, foliage budburst occurs earlier and is synchronized with peak larval emergence. Larval survival increases markedly in response to the immediately suitable and available food supply, and this, along with high fecundity, causes the population to expand rapidly.

The frequency and severity of outbreaks of certain plant-feeding insects appear to be related to moisture stress in the host plants (Blanche and others 1983; Kemp 1983; Leonard 1974; White 1969, 1974, 1976). Plant moisture stress, caused by deficient or excess soil water, may induce chemical changes in the plant tissue that improve its suitability as food for some insects and its nutritional quality. The intensity of moisture stress depends not only on the amount of precipitation but also on various site characteristics such as exposure, soil type, and soil texture. Cates and others (1983b, 1984a unpubl.) found that the current year's needles of moisture-stressed Douglas-fir trees growing on a south-facing slope were higher in alpha-pinene and soluble nitrogen but lower in known and suspected feeding-resistance terpenes than were the needles of nonstressed trees growing on a north-facing slope. Associated with this change in the foliage quality of the stressed trees was a 69-percent increase in the survival of third through sixth instars and a 30-percent increase in the dry weight of adult females. Because female dry weight is highly correlated with fecundity (Kirkbride and Wagner 1983b unpubl.), the larger females on the stressed trees were likely more fecund. Site characteristics and weather patterns that cause moisture stress in host trees may precipitate budworm outbreaks by affecting both the availability and quality of the new foliage and providing an environment conducive to budworm survival.

Several studies have shown certain site characteristics are related to budworm defoliation. Based on these studies and the documented effects of climate on budworm survival, we conclude that warm, dry sites are more susceptible to infestation than cool, wet sites. The percentage of growth reduction suffered by a stand because of an infestation is also likely to be greater on the warmer, drier sites. Because budworm-caused mortality is sporadic and concentrated in the small size-classes, however, the greatest absolute loss of merchantable timber volume may occur on sites that are more mesic because these sites are inherently more productive.

7.4 Stand Characteristics

The stand characteristics that appear to influence susceptibility to infestation and vulnerability to damage from budworm include species composition, intraspecific genetic composition, vigor, density, crown-class structure, and maturity (see table 7-1).

7.4.1 Tree Species

The principal hosts of western budworm are interior Douglas-fir, grand fir, white fir, Engelmann spruce, subalpine fir, and western larch (Fellin and Dewey 1982). Susceptibility appears to differ among them.

Williams and others (1971) found higher larval densities on subalpine fir than on Douglas-fir and Engelmann spruce in the Bitterroot National Forest in western Montana. Schmid and Farrar (1982) note that egg-mass densities are generally greater on Douglas-fir than white fir in New Mexico but found higher larval densities on white fir. In a laboratory feeding study, Blake and Wagner (1983b unpubl.) calculated various nutritional indexes for Douglas-fir, white fir, and corkbark (subalpine) fir from Arizona. They found that larvae fed Douglas-fir foliage had higher relative growth rates and were more efficient in converting food to body weight than larvae fed the other hosts. The total ingested foliage, relative consumption rate, and resulting pupal weights were equal for the three species, however.

Several investigators have compared the defoliation among host species (figs. 7-2 to 7-5). In eastern Oregon, grand fir sustained heavier defoliation than did associated Douglas-fir or Engelmann spruce; spruce ranked intermediate (Williams 1966). Carolin and Coulter (1975) also reported from eastern Oregon that grand fir suffered more defoliation than did adjacent Douglas-fir but could not attribute this difference to higher insect densities. Stoszek and Mika (1983 unpubl.) found that grand fir and subalpine fir generally incurred more defoliation than did Engelmann spruce and Douglas-fir across infestation areas in central Idaho.

Figure 7-2—Seral Douglas-fir on the left remains lightly defoliated, while adjacent grand fir on the right suffers severe defoliation (Payette National Forest, central Idaho).

Figure 7-3—Climax grand fir in the foreground suffers severe defoliation, while seral Douglas-fir in the background remains green (Payette National Forest, central Idaho).

Figure 7-4—Defoliation on intermediate seral Douglas-fir in foreground is less than on surrounding overstory climax grand fir. Here species is more important in determining tree susceptibility than crown position (Payette National Forest, central Idaho).

Figure 7-5—Climax subalpine fir is severely defoliated, while intermingled Engelmann spruce and Douglas-fir receive only slight defoliation (Okanogan National Forest, north-central Washington).

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Tree damage resulting from an infestation has been shown to differ among the host species. Grand fir suffered more bud-killing and top-killing than did adjacent Douglas-fir in eastern Oregon (Carolin and Coulter 1975). Williams (1967) found grand fir sustained the greatest relative reduction in radial growth, followed by Engelmann spruce and Douglas-fir. Incidence and severity of top-kill was highest in grand fir, intermediate in spruce, and least in Douglas-fir. Mika and Twardus (1983 unpubl.) showed that an infestation in north-central Washington resulted in an average reduction in radial growth of about 20 percent for Douglas-fir and between 30 and 35 percent for grand fir and subalpine fir. Top-kill and mortality rates were also greater for the true firs than for Douglas-fir. In central Idaho, Ferguson and Stage (1983 unpubl.) found that subalpine fir was more prone to top-kill than associated host species. Johnson and Denton (1975), in an exhaustive review of the western budworm in the northern Rocky Mountain area, state that in mixed-species stands of grand fir and Douglas-fir, white fir and Douglas-fir, and subalpine fir and Engelmann spruce, the first-named species often is more heavily damaged. Further, the frequency of budworm-caused mortality has been greatest in pure stands of Douglas-fir.

Carlson and others (1983) conclude that shade-tolerant host species are more vulnerable to damage than the relatively intolerant host species. Budworm larvae often sever the terminal shoots of western larch seedlings and saplings, in contrast to feeding solely on the buds and foliage as they do on the other host species (Fellin and Schmidt 1967, 1973b). Although this type of damage amounted to an average height-growth reduction of 27 percent in pure young larch stands (Schmidt and Fellin 1973), no direct comparison with other host species has been made in mixed stands.

Comparisons of the defoliation and damage that occur among the host species indicate that the relative susceptibility and vulnerability of the host species rank according to their relative shade tolerance (table 7-2). Relative shade tolerance among these conifers is an indication of their successional status when two or more of these species occur on the same site. In the Bitterroot National Forest in western Montana, Sutherland (1983) found that Douglas-fir was more severely defoliated on sites where it is the climax tree species than on sites where it is seral. Thus, the late successional or climax host species are the most susceptible to western budworm.

Table 7-2—Relation of apparent host susceptibility and vulnerability to shade tolerance and timing of budburst when the species occur on the same site

Host species	Budworm susceptibility and vulnerability	Shade tolerance	Budburst phenology[1]
Western larch	1 (least)	1 (least)	1 (earliest)
Interior Douglas-fir	2	2	5 (latest)
Engelmann spruce	3	3	4
Grand fir or white fir	4	4	3
Subalpine fir	5 (most)	5 (most)	2

[1]Budburst phenologies do overlap because of variations in genotypes and microsites.

The relative budburst phenologies of the host trees are also shown in table 7-2. Except for western larch, budburst tends to occur earlier on the more susceptible species under the same environmental conditions. Asynchrony between budburst and spring larval emergence has been shown to be an effective resistance mechanism for the host tree species of eastern budworm (Blais 1957, Eidt and Cameron 1971, Eidt and McGillivray 1972, Graham 1951, Greenbank 1956). Delayed budburst in Douglas-fir has been related to reduced western budworm success as well (Cates and others 1983b). This suggests that host shoot phenology may be, in part, responsible for the variations in susceptibility between host species of the western budworm.

7.4.2 Stand Composition

In mixed Douglas-fir and ponderosa pine stands in western Montana, Fauss and Pierce (1969) found that average defoliation on Douglas-fir increased as the percentage of stocking of Douglas-fir increased. Stoszek and Mika (1983 unpubl.) showed that average host defoliation was positively correlated with percentage of host basal area in stands in central Idaho. Heller and others (1981 unpubl.) determined from aerial photographs that host defoliation increased as the percentage of host increased.

Larvae may disperse to nonhost trees in the fall or spring, but many starve because they are unable to use the foliage. Survival rates of eastern budworm larvae have been shown to decrease as stocking of nonhost trees increases (Kemp and Simmons 1979, Mott 1963a).

Nonhost or seral host trees may buffer a stand against growth reductions caused by budworm infestations. In western Montana, Carlson and Theroux (1982) showed that host-tree vulnerability, as indicated by radial-growth reduction, increases as percentage of host stocking increases. The growth of ponderosa pine sometimes accelerates in response to the defoliation of competing Douglas-fir (Carlson and McCaughey 1982). In one of eight case histories, seral Douglas-fir showed an increase in radial growth rate after adjacent climax grand fir sustained heavier defoliation (Williams 1966). The mere presence of nonhost species makes the stand less vulnerable than a pure stand of the most vulnerable host because per-unit area growth losses resulting from an infestation would be less.

Stand susceptibility to infestation and vulnerability to damage are both directly related to the proportion of host species in a stand and the proportion of climax or late successional host species represented. The most susceptible and vulnerable species composition is pure stands of climax host trees. For example, Douglas-fir is most susceptible and vulnerable at the warm, dry end of the environmental spectrum, where it often appears in pure, climax stands.

7.4.3 Intraspecific Genetic Resistance

Phenotypic variation in defoliation between two adjacent Douglas-fir trees of similar size and crown position has been observed (Cates and others 1983b; McDonald 1981; Redak and Cates 1984) (fig. 7-6). We have observed the same phenotypic variation in grand fir and white fir.

Characteristics of the tree that affect resistance to feeding and ovipositional preference appear to be highly heritable characteristics in Douglas-fir from Idaho and Montana. In a preliminary progeny test of half-sib Douglas-fir seedlings, McDonald (1979) found that defoliation was related to source stands and observed a within-family pattern of defoliation similar to other physical traits of Douglas-fir. The results of a subsequent progeny test indicated a strong family heritability for defoliation and a significant relation between oviposition preference and source stand (McDonald 1981; in press). The observed heritability of feeding resistance in Douglas-fir appears sufficient for obtaining significant genetic gains from a selective breeding program, but it is probably insufficient to be of use in extensive silvicultural approaches (McDonald 1981). These laboratory experiments were designed to synchronize budburst and larval application, and hence do not fully account for the phenological component of genetic resistance.

Figure 7-6—Phenotypic variation in defoliation of two adjacent Douglas-fir trees of similar size and crown position (Deerlodge National Forest, near Boulder, MT).

Budburst phenology is a highly heritable trait and is strongly correlated with budworm success; delayed budburst in Douglas-fir resulted in lower densities of budworm, less defoliation, and smaller females (Cates and others 1983b, Redak and Cates 1984). Although asynchrony between food availability and larval emergence has been shown to be effective for some host species of the eastern budworm, variation in foliage phenology does not explain the variation in apparent susceptibility between red spruce, black spruce, and their hybrids (Manley and Fowler 1969).

Provenance differences are known to occur in some of the soluble nitrogen components of Douglas-fir foliage (van den Driessche and Webber 1975), which suggests some genetic control of nutritional quality of the host tissue. Budworm larval survival and adult fecundity have been related to soluble and total nitrogen in Douglas-fir foliage (Cates and others 1983b, 1984a unpubl.; Redak and Cates 1984). In three different studies, some form of nitrogen entered into the multiple-regression models, but nitrogen was always less important than terpenes in affecting larval development and weight of adult females (Cates and others 1983b, 1984a unpubl.; Redak and Cates 1984).

Terpenes are under strong genetic control (Hanover 1975; von Rudloff 1975; von Rudloff and Rehfeldt 1980), and have been shown to affect western budworm adversely. Individual terpene content, as well as certain qualitative and quantitative combinations, were inversely correlated with infestation intensity, larval survival, and adult dry weight (Cates and others 1983b, 1984b unpubl.; Redak and Cates 1984). Heron (1965) found that the glycoside pungenin reduced eastern budworm larval feeding.

The evidence for chemical resistance to western budworm in the current year's foliage of Douglas-fir has been derived mainly from field studies and was correlative. Using synthetic diets, Cates and others (1983a, 1984a unpubl.) have shown that higher concentrations of bornyl acetate—typical of the natural quantities in the current year's foliage of Douglas-fir—significantly decreased larval growth rate and increased larval and pupal mortality. Higher concentrations of beta-pinene, on the other hand, stimulated larval growth and resulted in lower larval and pupal mortality. Growth responses to various amounts of nitrogen used in the diet differed in budworm populations from different places (Cates and others 1984a unpubl.). This suggests that the western budworm is adapted by provenance to use the more common tissue quality represented by the host. Genetic races of western budworm have been identified (Willhite and Stock 1983). McDonald (in press) explains some unexpected anomalies in the results of progeny tests for resistance as indicative of mismatches between budworm race and host ecotype.

7.4.4 Tree and Stand Vigor

Cates and others (1983a, 1983b) studied the nutritional quality and terpene chemistry of Douglas-fir trees in Montana and New Mexico. Trees of similar diameter, age, height, and crown class were selected on similar sites in each study area. They found that budworm success, as indicated by larval density and adult dry weight, was significantly related to the terpene chemistry of the foliage. In addition, dry weight of adult females—an indicator of fecundity—increased as the 5-year radial-growth increment of trees decreased. In a related study (Cates and others 1983b, 1984b unpubl.), Douglas-fir trees on a south slope were placed under moisture stress by root trenching. Larval survival and dry weight of adult females were compared for insects reared on these stressed trees to insects reared on nonstressed trees growing on a north-facing slope. Associated with the stressed trees was a 69-percent increase in larval survival, a 30-percent increase in weight of adult females, and a substantial difference in the terpene chemistry of the foliage. Subsequent feeding studies in the laboratory (Cates and others 1983a, 1984a unpubl.) showed the cause and effect relation between terpene chemistry and budworm survival and growth.

Blake and Wagner (1983b unpubl.) found no effect of host vigor, as indicated by the ratio of basal-area growth to sapwood area, in a laboratory feeding study where excised branches placed in water were offered to western budworm larvae. Sample size in this study was limited, and the palatability of the foliage was probably affected by removing the branches from the tree. In a greenhouse study, where 3-year-old Douglas-fir and white fir seedlings were fertilized with various amounts of nitrogen, phosphorus, and potassium, budworm success (larval mortality, adult emergence, and total development time) was highest at intermediate nitrogen levels (Brewer and others 1980 unpubl.). Cates and others (1984a unpubl.) found that larval survival increased as the nitrogen in synthetic diets increased, and that maximum survival occurred when nutritional quality was high and defensive terpene chemistry low. Schmidt and Fellin (1983) fertilized young western larch stands with various amounts of nitrogen, phosphorus, and potassium and found that budworm feeding increased over that in untreated stands. Nitrogen elicited the greatest response.

Williams (1967) compared defoliation on associated grand fir, Engelmann spruce, and Douglas-fir in eastern Oregon. Grand fir, the most vigorous species as measured by preoutbreak radial growth, suffered the greatest defoliation. His data indicate for each species, however, that defoliation tends to increase as preoutbreak radial growth decreases. Stoszek and Mika (1983 unpubl.) found a positive correlation between average tree defoliation and stand basal-area growth on the Douglas-fir habitat series in the Salmon National Forest. Nevertheless, they recognized a declining preoutbreak growth trend in the host stands suspected of being most susceptible. Despain (1981) found that defoliation on Douglas-fir in south-central Montana tends to increase as tree height and live-crown ratio decrease. On aerial photographs of central Idaho, Heller and others (1981 unpubl.) observed that defoliation increased as average crown diameter decreased.

Tree damage resulting from western budworm infestations also seems to vary inversely with tree vigor. Data of Williams (1967) from eastern Oregon show that the percentage of radial-growth reduction incurred by grand fir and Engelmann spruce tends to increase as preoutbreak radial growth decreases. The most vigorous spruce trees accelerated in radial growth during the outbreak, but those that were growing poorly before the outbreak declined. Top-kill was more common in trees that were growing poorly before the outbreak. The radial growth of Douglas-fir trees increased during the infestation, and the increase was greater on the trees that were growing faster before the outbreak. Ferguson and Stage (1983 unpubl.) studied the effects of defoliation on host trees less than 5 inches (12.7 cm) in diameter throughout central Idaho and found that trees with short live-crown ratios had a higher probability of zero or negative height growth. Schmidt and Fellin (1983) found more shoot damage in fertilized young western larch stands than in unfertilized stands. In young western larch, however, growth recovery after outbreak collapse was greater and more rapid in stands with fewer trees, and hence greater vigor (Schmidt 1980).

B

In general, we believe stand susceptibility to western budworm infestation increases as host vigor decreases (fig. 7-7). Undoubtedly, subtle changes in the complex foliar terpene chemistry can profoundly affect budworm populations. Vigorous trees appear well defended, but the application of fertilizers may override or upset this chemical defense and, in doing so, improve the nutritional quality of foliage. The eastern budworm is also known to respond favorably to fertilized trees (Roberts and Chow 1977, Shaw and Little 1972, Shaw and others 1978) and is sensitive to the natural variation in foliar components of balsam fir (Shaw and Little 1977). Stoszek and Mika (1983 unpubl.) have found inconsistent relations between defoliation and accumulated duff and woody debris among habitat series. From this, they speculate that nutrient stress may be related to stand susceptibility.

Balch (1958) suspects that for most—if not all—damaging forest insects, tree vigor is inversely related to vulnerability. Correlative evidence indicates that this principle also applies to western budworm. We reason that vigorous trees have more productive foliage per unit of total biomass and more carbohydrate reserves stored in their roots than nonvigorous trees. Given the same amount of defoliation, then, vigorous trees will have more remaining foliage and this necessarily implies a smaller relative growth reduction. Also, with greater carbohydrate reserves, vigorous trees are better equipped to continue growing and survive during the infestations and to recuperate once defoliation subsides. Starch reduction resulting from defoliation by the Douglas-fir tussock moth has been shown to be significantly less in faster growing trees (Webb and Karchesy 1977). Although vigorous trees and stands are relatively less vulnerable to damage compared to their slow-growing counterparts, this does not necessarily hold true when damage is expressed in absolute terms. A relatively small reduction in the rapid growth of a vigorous stand could represent a greater loss of timber volume than that associated with a large relative growth decline in a slow-growing stand.

Figure 7-7—White fir seedling growing in a canopy opening remains vigorous and escapes dispersing budworm larvae (A), while in surrounding dense stands understory white fir is severely defoliated (B). Effects of stand density and vigor override crown position in determining tree susceptibility (Carson National Forest, northern New Mexico).

The vigor of nonhost trees may also affect stand vulnerability. The growth of ponderosa pine sometimes accelerates in response to defoliation of competing Douglas-fir (Carlson and McCaughey 1982). Overmature or suppressed nonhost trees may not release when competition is reduced by the defoliation or death of neighboring host trees. Vigorous nonhost trees that are competing with host trees, however, can release quickly during infestations and will, at least partially, compensate for the growth decline in the host component.

7.4.5 Stand Density

In western Montana, Fauss and Pierce (1969) found that defoliation on Douglas-fir increased as crown closure increased. Williams and others (1971) observed higher defoliation and larval populations on open-grown trees than on trees growing in closed stands, but neither stand populations nor survival rates were studied. In Idaho, Stoszek and Mika (1983 unpubl.) found that defoliation increased as stand basal area increased on the subalpine fir habitat series, but the opposite was true on the western hemlock series. Stand composition was not included in this analysis. On Douglas-fir habitat types, defoliation was shown to increase as the basal area of susceptible stands decreased. Despain (1981) found defoliation on Douglas-fir tends to increase as tree density increases in stands on Douglas-fir habitat types in south-central Montana. Heller and others (1981 unpubl.), using photography of infestations in north-central Washington, found that defoliation increased as stand closure decreased.

Stand density, in conjunction with species composition, has an important influence on the larval mortality associated with fall and spring dispersal of the eastern budworm (Miller 1958, 1975; Morris and Mott 1963; Mott 1963a). More larvae fall to the ground in open stands than in dense stands because the tree crowns are farther apart and windspeeds within the canopy are greater. By trapping dispersing western budworm larvae within and beneath a canopy, Beckwith and Burnell (1982) demonstrated the filtering effect of tree crowns. Many larvae that reach the forest floor likely succumb to starvation, exposure, or ground-dwelling predators such as ants, spiders, and beetles (see chapter 6). In stands containing nonhost trees, starvation and dispersal-related mortality would probably be accentuated. Life-table analysis (Mott 1963b) and dispersal studies (Kemp and Simmons 1979) confirm that the survival of young eastern budworm larvae is greater in dense stands. Batzer (1967) showed that defoliation on balsam fir decreased as thinning intensity increased, but Crook and others (1979) detected no effect from thinning balsam fir unless species composition was also altered. Carlson (personal communication) found a 30- to 50-percent decrease in defoliation for thinned stands in western Montana compared to adjacent unthinned stands. Elsewhere in the West, thinnings have apparently reduced defoliation (fig. 7-8).

We believe that dense stands are generally more susceptible than open stands, although differences in species composition and site characteristics can obscure this relation (fig. 7-9). Stand density generally increases from the warm, dry sites to the cooler, wetter sites. Because of the site conditions, larval populations and defoliation on individual trees may be greater in open stands—even though dispersal-related mortality would also be high. Open stands on dry sites may also have higher moisture stress, and thus favored food compared to closed stands on more productive sites. On similar sites, however, dense stands would be expected to have better foliage quality because of moisture stress induced by intertree competition. We might expect that shade-tolerant conifers would be more common in dense stands than in open stands. In the western hemlock habitat series, dense stands might include more nonhost species; conversely, on the grand fir or Douglas-fir series, dense stands may have a higher proportion of preferred host species. But with similar stand composition and on similar sites, dense stands are more susceptible because survival of dispersing larvae is higher and foliage quality improves as intertree competition raises moisture stress.

Figure 7-8—Dense stand of grand fir and Douglas-fir receives severe defoliation (A), while a nearby thinned stand remains lightly infested (B). (Payette National Forest, central Idaho).

Figure 7-9—Dense stand of Douglas-fir on the left is more defoliated than the sparse stand on the right. Stand density can override effects of site variations in determining susceptibility (Bitterroot National Forest, southwestern Montana).

Williams and others (1971) observed less damage on relatively open-grown trees than on trees in closed stands in western Montana. They suggested that open-grown trees, even though supporting higher larval populations, could withstand greater stress from defoliation and survive better than trees that must compete for moisture in dense stands. In 10-year-old infested western larch stands in western Montana, Schmidt (1980) found that the percentage of dominant trees with severed terminal leaders decreased as stand density increased when budworm populations were low. The incidence of damage to crop trees, however, was not affected by stand density during the outbreak. The magnitude of the growth release after collapse of the outbreak was greater as stand density decreased. We reason that dense stands would be more vulnerable to damage than lightly stocked stands because they contain more trees or timber volume at risk. MacLean (1980) suggested that the greater the density of preferred host trees in eastern spruce–fir stands, the more vulnerable the stand. On similar sites, dense stands are probably less vigorous than open stands, which also indicates that relative stand vulnerability is greater in dense stands.

7.4.6 Crown-Class Structure

Using variation in tree age as an index of crown-class structure, Stoszek and Mika (1983 unpubl.) showed in a multiple-regression analysis that defoliation tends to increase as the canopy structure becomes more uniform on both the subalpine fir and western hemlock habitat series. Species composition was not explicitly accounted for in these models. When single variables were tested for significance (including variation in age, height, and diameter), defoliation was seen to increase as the crown-class structure became more diverse on the subalpine fir series and less diverse on the western hemlock series. Defoliation in the Payette National Forest tended to increase as the deviation in tree age decreased, but stands that had the overstory removed were generally less defoliated than selectively logged or unmanaged stands. No relation between defoliation and crown-class structure was detected for the Douglas-fir series in the Salmon National Forest. Defoliation on trees less than 3 inches (7.6 cm) in diameter was not included in the expression of stand defoliation used in constructing these correlations.

In the Bitterroot National Forest in western Montana, Sutherland (1983) observed that defoliation was more common in stands that had been harvested by salvage cutting, overstory removal, or selection methods than those that had been clearcut or thinned. Clearcuts suffered slightly less defoliation than seed-tree or shelterwood cuttings. Carlson and others (1983) concluded that the western budworm does not feed extensively on regeneration in managed stands in the northern Rocky Mountains. Host seedlings 1 to 20 years old in stands regenerated through proper silvicultural systems are not particularly vulnerable to western budworm for several reasons: they are a small target for dispersing larvae, the budworm is more vulnerable to predation on these small trees, and fewer adults are found in cut stands than in adjacent uncut stands.

Williams and others (1971) observed that nearly all understory trees were killed by western budworm in most Douglas-fir stands examined in south-central Montana. Johnson and Denton (1975) suggest that overtopped trees are more likely to succumb to budworm because they intercept a disproportionate share of large larvae, which do most of the feeding, and because these subordinate trees are often suppressed. Mika and Twardus (1983 unpubl.) found that single-storied stands in north-central Washington generally incurred a larger reduction in total growth than did multistoried stands. Multistoried stands of mixed composition, however, had a greater relative basal area and volume-growth reduction than did single-storied, mixed stands. Across all stands, top-kill was more common in the smaller diameter classes.

The crown-class structure of stands affects budworm population dynamics. Intermediate and understory trees intercept larvae as they spin down or drop from the upper canopy. If the subordinate trees are host species, the falling larvae can establish a feeding site, complete development, and contribute to the succeeding generation. Moreover, if these subordinate trees are suppressed, they may be producing foliage that is high-quality food for budworm. If no subordinate trees are present or if they are nonhost, the dropping larvae will fall to the ground and perish or starve on inadequate foliage.

Multistoried stands are generally more susceptible than single-storied ones of the same host species because of the inevitable downward drift of large larvae. Uneven or all-aged stand structures that provide for more crown exposure of both the dominant and subordinate trees are more susceptible than closed-canopied, multistoried stands because of improved microenvironments for feeding and egg deposition (fig. 7-10). The survival of large eastern budworm larvae is affected by the microclimate of the feeding site, which improves with increasing exposure to sunlight (Mott 1963b, Wellington 1948b). Larval development may be delayed in the lower crown strata because of the lower temperatures in shaded feeding sites (Régnière 1982). Because the development rate of western budworm larvae also increases with temperature (Wagg 1958), their survival might be higher on exposed tree crowns.

Mature tree crowns exposed to sunlight are preferentially selected by eastern budworm moths for egg-laying (Graham 1951, Greenbank 1963b, Mott 1963b, Wellington 1948a, Wilson 1964). Western budworm moths also tend to deposit more eggs in the upper and middle crown areas of large host trees (Campbell and others 1984b, Carolin and Coulter 1971, Schmid and Farrar 1982). An all-aged stand structure with its irregular canopy would seem to provide the ideal budworm habitat. Large, mature trees with deep, exposed crowns have more preferred egg-laying sites and warmer feeding sites than short-crowned trees in closed-canopied stands. The microclimate of subordinate crowns is warmer and drier when the upper canopy is broken. Budburst of these understory trees would logically be earlier than overtopped understory trees in multistoried stands, and thus new foliage would be available to early dispersing larvae. Shaw and Little (1977) have measured a progressive decrease in the nutritional quality of current balsam fir foliage as it expands from buds and develops.

Figure 7-10—Subordinate host trees in an uneven-aged stand intercept dispersing budworm larvae and become severely defoliated (Payette National Forest, central Idaho).
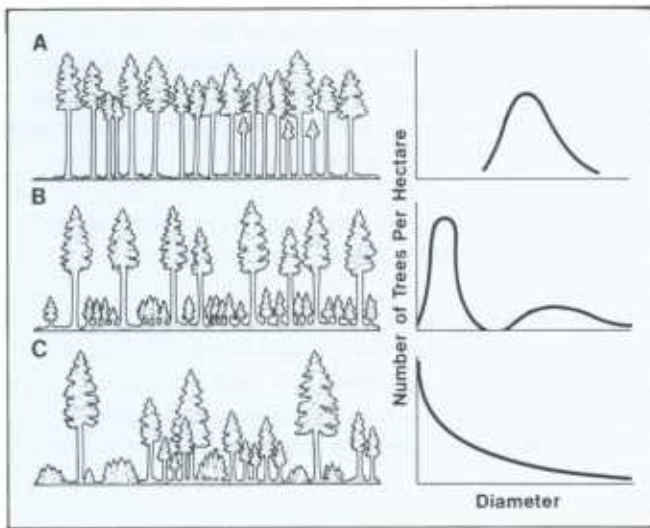
Figure 7-11—Stand structures, in order of susceptibility, from least to most susceptible: even-aged, top; storied, middle; and uneven-aged, bottom.

Figure 7-12—Intermediate Douglas-fir is being top-killed while the overstory remains lightly defoliated (Lubrecht Experimental Forest, western Montana).

We rank uneven-aged crown-class structures as most susceptible, multistoried structures intermediate, and even-aged structure least (fig. 7-11). But crown-class structure is often related to species composition, density, and vigor—and these interrelations might explain anomalies in correlations between stand structure and defoliation. We also suggest that uneven-aged or multistoried structures are generally more vulnerable to damage than even-aged structures because subordinate trees tend to be top-killed or die (fig. 7-12).

7.4.7 Tree and Stand Maturity

In central Montana on the Douglas-fir habitat series, Cates and others (1983b) found a greater infestation intensity (defoliation × number of larvae) on the older trees in a 55-year-old Douglas-fir stand. They also found a significant positive correlation between tree age and dry weight of adult females (an index of fecundity) in a 38-year-old Douglas-fir stand in New Mexico. The sample trees in these studies were of similar age, stem and crown diameter, and height.

In a multivariate correlation analysis, Stoszek and Mika (1983 unpubl.) detected that mean overstory age was inversely related to defoliation on both the western hemlock and subalpine fir habitat series in north-central Idaho. Single-variable correlations indicated that defoliation increases as average stand diameter decreases on the western hemlock series. But on the subalpine fir series, larger diameter stands appeared more susceptible. On the Douglas-fir habitat series in the Salmon National Forest, defoliation also tends to increase as the mean diameter of overstory trees increases. Across all habitat series in the Payette National Forest, defoliation appears heavier in stands of large-diameter overstory trees.

As a stand matures, stand basal-area stocking generally increases, as does average tree diameter. In the beginning, stocking accumulates rapidly but then levels off as the site becomes fully occupied. Associated with an increase in stocking is a general decline in tree vigor brought about by competition. On productive sites, crown closure occurs early—followed by diversification of crown classes. On poor sites, crown closure may never occur. Without disturbance, succession advances with time, with consequent changes in species composition and structure. Shade-tolerant species may first develop under seral overstory canopies and later grow into dominant positions as the often longer lived, seral species degenerates. The many possible stand-development and successional patterns confound the interpretation of stand age as an indicator of budworm susceptibility. When the expected interactions between stand age and density, vigor, crown-class structure, and species composition are recognized, the relation between tree age and budworm success becomes more revealing. We (Cates and others) have found that across a rather narrow range of age classes, budworm success was significantly improved on older trees. Foliage-quality characteristics were more important than tree age in describing budworm success. This fact leads us to speculate that the defensive terpene chemistry or nutritional quality of Douglas-fir foliage may vary directly with tree age because marked differences in tree vigor would not be expected across a narrow range of age. Also, we have observed that on habitat series where host trees are exclusively the climax species, defoliation increases with age and tree size. We believe stand susceptibility generally increases as a stand matures. Increasing stand age may represent a progressive increase in the quantity and quality of food, egg-laying sites, and overwintering habitat for western budworm.

Young seedling stands represent poor habitat for budworm. Rarely are these small trees selected by adult females for egg deposition, and such trees lack the rough bark surfaces used for overwintering. Batzer (1969) attributed the establishment of eastern

budworm populations in seedling and sapling balsam fir stands to the presence of scattered overstory trees that attracted egg-laying moths and provided overwintering habitat. Small seedlings are a small target for spring-dispersing larvae from adjacent stands, so many will land on the ground or on vegetation unsuitable for food. Larvae that happen to encounter a host seedling are vulnerable to predatory ants that can effectively search the small crown of seedlings close to the ground (Campbell and others 1984a). Host seedlings and saplings less than 20 years old that become established after even-aged regeneration cutting suffer negligible damage from western budworm infestations (Carlson and others 1983). As a stand grows from seedling–sapling into pole size, foliage biomass increases. Thus, more food becomes available and larval mortality during dispersal is reduced. As tree heights increase, the effectiveness of ground-dwelling predators declines (Campbell and Torgersen 1983b).

Flower production is a symptom of maturity in host conifers, and western budworm seems to feed preferentially on reproductive buds and cones (Chrisman and others 1983, Fellin and Shearer 1968). Reproductive buds burst earlier than vegetative buds and may be more nutritious. Kimmins (1971) found higher amino acid concentrations in the new foliage of flowering balsam fir than in nonflowering trees, and White (1974) interprets this as improved nutrition for eastern budworm. Staminate balsam fir flowers provide succulent food for eastern budworm and more favorable microclimates for spring-emerging larvae than vegetative buds (Blais 1952, Greenbank 1963b, Wellington 1948b).

Mature stands attract egg-laying moths, and as the bark of trees becomes more furrowed, overwintering habitat expands. Young balsam fir stands have been shown to lose more moths than neighboring mature stands (Morris and others 1958b). Kemp and Simmons (1979) have found a positive correlation between stem and crown diameter of balsam fir and survival of eastern budworm larvae, indicating that older stands are more susceptible. Aside from crown-class diversification, increasing age implies increasing basal-area stocking, which results in greater intertree competition and perhaps a stress-induced change in foliage quality. Moreover, a gradual improvement in foliage quality may occur as tree vigor declines through senescence.

We interpret the physiological changes that occur in aging trees as representing an increase in vulnerability to budworm damage. With age, crown size decreases relative to stem volume, which results in a diminished ratio of carbohydrate production to respiration. The loss of apical dominance accompanies the reduction of shoot growth in aging conifers. As tree vigor declines, the growth-rate depression caused by defoliation increases. Because old stands may be growing slowly to begin with, however, the absolute volume loss represented by this growth-rate depression may be less than in younger, more rapidly growing stands. Damage from top-killing also would represent a greater loss in volume growth in immature stands that are still growing rapidly in height, compared to older stands in which height growth has culminated. Top recovery, however, would occur more rapidly in younger stands that are more vigorous and have stronger apical dominance. Although western budworm seldom kills otherwise healthy, mature trees, it could predispose them to attack by bark beetles or root pathogens. Older stands are thus more vulnerable physiologically and more prone to tree mortality; immature stands may be more vulnerable to growth loss from nonlethal defoliation.

7.4.8 Stand Size and Forest Diversity

Outbreaks of the eastern budworm have occurred in forests composed extensively of mature balsam fir stands (Balch 1946, Craighead 1924, Morris and others 1958b, Mott 1963b, Prebble and Morris 1951). Mature balsam fir stands that were isolated from dispersing larvae and adult moths by nonhost stands have remained uninfested or quickly lost their populations during large-scale outbreaks (Baskerville 1975, Morris and others 1958b, Mott 1963b). Turner recognized these areas as "zones of survival" where balsam fir stands were receiving protection from infestation sources by lakes or hardwood stands. Because of high dispersal losses suffered by early instars and moths, stand conditions are the essential predisposing cause of eastern budworm outbreaks, and outbreaks do not develop where the forest is sufficiently discontinuous or variable (Morris and others 1958b). Van Raalte (1972) has suggested that isolated stands of less than 100 acres (40 ha) are nonsusceptible to infestation by eastern budworm. Thus, some degree of homogeneity of high-quality budworm habitat is apparently prerequisite for a sustained outbreak.

A forest could be so diverse in stand susceptibility that budworm dispersal and migration losses would exceed the population's reproductive capacity, and widespread outbreaks would be precluded. Given that habitat quality varies among stands, population release—in response to induced stress and phenological synchronization—occurs first in the most susceptible stands. Larval dispersal is largely passive, and drift to adjacent stands is inevitable. If adjacent stands are also susceptible, most of these drifting larvae may live, but not if the stand is surrounded by poor quality habitat. Nonhost stands, nonforest areas, and marginally susceptible stands thus function as population sinks for drifting larvae.

Moths fly away from defoliated trees because the trees lack sites for egg-laying (Blais 1953, Greenbank 1957, Morris 1963b). Although western budworm moths are known to deposit eggs on nonhost trees, survival of larvae emerging on them is much reduced. Presumably, the farther a budworm moth must fly, the greater the risk of mortality. As energy is expended in flight, fecundity and egg viability may be lowered. Marginally susceptible stands and nonforest areas thus promote mortality during moth migration and larval dispersal.

Extrinsic stand susceptibility may also be influenced by the action of budworm parasites and predators. These natural enemies are generally regarded as ineffective in exerting significant control of outbreak populations but may be more effective when budworm populations are low (Carolin 1976; Carlson and others 1983; Fellin and Dewey 1982; McGugan and Blais 1959; Miller 1963a, 1975; Morris 1963a; Morris and others 1958b; Neilson 1963; Prebble and Morris 1951; Thomson 1979). Tothill (1923) recognized that predatory birds may have a controlling influence on spruce budworm where the host trees occur in patches, and Graham and Orr (1940) suggested that the decimation of birds may have been a contributory cause of an eastern budworm outbreak in Minnesota. Recent studies have confirmed that predatory birds and ants can have a major influence on the survival of western budworm larvae and pupae when budworm populations are low (Torgersen and Campbell 1982, Campbell and others 1984a).

In a diverse forest where extrinsic stand susceptibility is generally low, incipient budworm outbreaks are localized in the susceptible stands—thus affording the mobile parasites and predators an opportunity to concentrate on the isolated rising budworm population. In homogeneous forests of high susceptibility, the effect of natural enemies is diluted because budworm populations would be expanding more uniformly over a larger area. Nonsusceptible stands and ecotones in diverse forests may be providing necessary habitat for the natural enemies of budworm by harboring alternative hosts and prey species. When the budworm populations increase in the susceptible stands, these natural enemies would already be abundant in the adjacent nonsusceptible areas and could switch their attack to budworm—thus avoiding the lag associated with a direct numerical response to the rising budworm population. The nonsusceptible stands in a diverse forest may function as reservoirs of these opportunistic natural enemies, thereby lowering the extrinsic susceptibility of the inherently susceptible stands.

Stand susceptibility is composed of both intrinsic and extrinsic components; either component can partially override the other. Inherently marginal habitat may be inundated with immigrating budworm, or inherently susceptible habitat may be protected from infestation because of its isolation. Large, relatively homogeneous stands are therefore more susceptible than a mosaic of diverse stands—even when average stand susceptibility is similar. The degree of spatial heterogeneity at which outbreaks would be precluded is unknown, but, no doubt, varies directly with the intrinsic susceptibility of the stands.

7.5 The Western Budworm and Forest Succession

Our analyses of the site and stand characteristics affecting stand susceptibility indicate that budworm habitat generally improves with increases in the warmth and dryness of the site, the proportion of shade-tolerant host species, the density and maturity of the stand, and the diversity of crown-class structure. When viewed collectively, these conditions are characteristic of mature climax forest communities on Douglas-fir, grand fir, white fir, spruce, and subalpine fir habitat types. Seral communities on these and other habitat types may be infested if they include host trees. A common characteristic of most, if not all, infestation areas of the western budworm, however, is a preponderance of late successional or climax forest stands. Outbreaks of the western budworm appear to be an integral component of climax associations that support host trees.

Succession may be defined as the cumulative change in the composition or structure of plant communities that, without disturbance, progresses toward a predictable and apparently stable endpoint (Daubenmire 1968). The endpoint or climax state is reached when the vegetative community ceases to exhibit clear evidence of unidirectional change (Daubenmire 1968). Thus, we consider a forest stand to be climax when the most shade-tolerant or climax tree species has achieved nearly complete dominance in the mature main canopy and in the understory regeneration.

As plant communities succeed from seral stages toward climax, several ecological changes occur that indicate an increasing potential for tree stress. These trends are summarized in table 7-3. As the climax state is approached, the ratio of community production to respiration approaches unity, and net primary production falls to zero (Odum 1969, 1971). Three interactive processes seem to be responsible for this gradual loss of community vigor: a change from exploitive seral species to conservative climax species, a general increase in biomass, and a slowing of energy and nutrient cycling.

Seral species exhibit an exploitive growth strategy exemplified by inherently fast growth rates and rapid but incomplete utilization of the site resources. Late successional species grow at more conservative rates but are able to compete successfully with seral species because of their greater efficiency in using light, water, or nutrients (Bormann and Likens 1979). Physiological studies have shown that late successional and climax trees have slower rates of photosynthesis than seral trees but are able to maintain a better carbohydrate balance in shade (Bazzaz 1979). Water-use efficiency (amount of water transpired per unit of carbon assimilated) apparently decreases as shade tolerance increases, and late successional plants are less capable of surviving if subjected to water limitations (Bazzaz 1979).

Table 7-3—Trends to be expected in the development of succession (modified from Odum 1969, Daubenmire 1968)

Attributes	Seral stages	Climax stages
Environmental tolerance of plant species	Similar and broad	Complementary and narrow
Gross production/community respiration	Greater or less than 1	Approaches 1
Gross production/standing-crop biomass	High	Low
Biomass supported/unit energy flow	Low	High
Net community production	High	Low
Total organic matter	Small	Large
Mineral cycles	Open	Closed
Nutrient exchange rate between organisms and environment	Rapid	Slow
Proportion of nutrients retained in organic matter	Small	Large
Role of detritus in nutrient regeneration	Less important	Important

Among western budworm hosts, the true firs—which are the most shade tolerant—are also less tolerant of drought than Engelmann spruce or Douglas-fir (Minore 1979). Engelmann spruce ranks intermediate in both shade and drought tolerance, Douglas-fir is more drought resistant than spruce, and seral pine species are more drought resistant than Douglas-fir (Brix 1979, Minore 1979, Lopushinsky and Klock 1974). As shade tolerance increases, drought resistance apparently decreases. Therefore, because of the change in species associated with forest succession, moisture stress in host trees is more likely to occur in climax ecosystems than in seral ecosystems.

As forest succession proceeds from seral towards climax stages, total biomass in vegetation generally increases. Higher amounts of living biomass might represent more intense competition for water and nutrients, and the accumulation of both living and dead organic matter means an increasing proportion of the nutrient capital is incorporated into the biomass. In this sense, succession represents the aging of the ecosystem similar to the maturing of a tree; both processes result in the eventual decline of vigor characterized by senescence. The amount of biomass may culminate with the maturation of the climax community, or biomass stocking could be regulated at some subclimax stage by insects or disease. Unmanaged stands of grand fir have been found to attain higher stocking than Douglas-fir stands on similar sites (Cochran 1979). Stoszek and Mika (1983 unpubl.) speculate that peak biomass—and, therefore, nutrient stress—might culminate in subclimax stages. They provide correlations between defoliation and woody debris or duff accumulations that could conceivably indicate a direct relation between nutrient stress and defoliation.

Successional patterns are highly variable in western coniferous forests because of the complex interrelations between physiography, fire history, and diseases and plant-eating insects. Generalizations about the successional stages at which biomass culminates are therefore not warranted. Nevertheless, the high biomass stocking associated with later successional stages may indicate near complete utilization of available soil moisture and nutrients, such that stress could be induced by the trees themselves. Simulations of nutrient and energy cycles show that as forest biomass builds, flow rates decline; consequently, the ecosystem becomes less able to resist change when the environment fluctuates (DeAngelis 1980). Early successional species are perhaps better able to adjust to environmental stress (Bazzaz 1979), and seral forest ecosystems, which are still accumulating biomass, appear to be inherently more stable than late successional stages when subjected to potentially destabilizing climatic events (Bormann and Likens 1979).

Western budworm outbreaks have been linked to regionally and temporally dry weather patterns, and infestations are associated with inherently unstable or stressed ecosystems composed of drought-sensitive conifers. Western budworm infestations typically result in the death of overtopped seedlings, saplings, and some intermediate pole-sized trees. Dominant, mature, host trees seldom succumb (Johnson and Denton 1975).

Seed production in Douglas-fir and western larch can be severely limited during outbreaks because the larvae feed on the reproductive buds and developing cones (Chrisman and others 1983, Dewey 1970, Fellin and Shearer 1968). The more extensive top-killing and loss of vigor on the preferred climax hosts might preclude seed production of those species long after infestations subside (Shearer 1980a). These effects retard succession on true fir, spruce, and Douglas-fir habitat types; on western redcedar and western hemlock habitat types, succession is promoted by outbreaks.

In mixed-species stands on the true fir, spruce, and Douglas-fir habitat series, budworm infestations favor seral trees. Defoliation and mortality of the more shade-tolerant host trees promote growth acceleration of established, competing seral trees (Carlson and McCaughey 1982, Williams 1966). Differential prevention of host-tree cone crops coupled with reduced stocking encourages regeneration of seral trees. In pure stands of climax hosts, outbreaks are likened to a thinning from below. Secondary disturbances, such as bark beetle infestations, may further recharge the nutrient pool, relieve moisture stress, and move the system toward a younger, more productive state. Infestations by the Douglas-fir bark beetle occasionally have been reported in forests heavily damaged by budworm (Johnson and Denton 1975, McGregor and others 1983).

In dry environments, where competitive stress is more a function of the climate than tree stocking, outbreaks are generally prolonged. In mesic environments, they tend to be short and episodic. The budworm has not demonstrated an ability to cause the death of large, mature, or open-grown trees directly, so it appears limited as a regulator of production. In dry environments, the mortality of the small, suppressed trees that develops during infestations does not sufficiently reduce moisture stress to end the outbreak. High budworm populations have persisted in open stands of Douglas-fir on grassland and steep, rocky sites for longer than 30 years in central Montana. This chronic infestation may represent a new ecological equilibrium, where the annual alleviation of stress brought on by defoliation nearly equals the annual increase in stress that occurs with basal-area growth. Thus, the western budworm functions to perpetuate and regulate the climax ecosystem, causing only slight retrogression by depleting understory layers. In addition, budworm defoliation of overstory trees, in conjunction with other sporadic damaging agents such as root disease, may initiate mortality and gap-phase regeneration.

On more mesic sites, the outbreak pattern in stands goes up and down sharply, with the infestation usually lasting 3 to 10 years in any given stand. The infestation is shorter on the more mesic and cooler sites and longer on the warmer, drier ones. The period between infestations in stands varies widely depending largely on regional climate, amount of tree mortality and defoliation that have occurred, and how quickly the stands grow back or succeed into a susceptible (stressful) condition.

Fire has historically had a strong influence on the ecology and development of most western forests (Arno 1980, Davis and others 1980, Fischer and Clayton 1983, Habeck and Mutch 1973, Cooper 1961). Ground fires, which occurred frequently in the drier forest types, periodically eliminated understory trees and selectively reduced the stocking of shade-tolerant, fire-susceptible trees in larger size classes. Stand-replacement fires often burned during abnormally dry weather or sporadically where woody debris accumulations and stand structures with variable height classes provided fuel ladders to the main canopy. The frequency and intensity of natural fires varied by forest type and site conditions, but few stands—except the very wet western redcedar/ western hemlock and upper subalpine types—escaped fire long enough for the climax community to become established. Lightning-caused fires perpetuated a mosaic of heterogeneous seral timber stands and nontimbered communities which—because of their diversity, species composition, regulated density, and often even-aged structure—precluded widespread budworm outbreaks.

In western Montana, fire-history studies indicate that the time since the last burn on most forest sites now exceeds the longest fire-to-fire interval that occurred over the two centuries preceding effective fire suppression (Arno 1976). McCune (1983) has determined that fire frequency has been reduced by two orders of magnitude in the low-elevation mesic forests of the Bitterroot Canyons. As a result of fire exclusion, dramatic changes have taken place in the composition, structure, and density of nearly all forest stands that were prone to burn. Open, even-aged, parklike stands composed of shade-intolerant seral species have now succeeded to dense, uneven-aged stands dominated by the shade-tolerant climax species (Gruell and others 1982).

Fire exclusion has so affected the conversion of
mature to newly regenerated stands that the once
mosaic pattern of diversity has been replaced with a
relatively homogeneous mixture of late successional
and mature persistent seral types. These late
successional and stagnated seral forest ecosystems
that fires historically prevented are now extensive and
often infested with budworm, bark beetles, dwarf
mistletoe, root diseases, and other pests. Moreover,
the intensity of budworm outbreaks, as measured by
radial-growth depression in grand fir and spruce, has
increased as a result of the cumulative change in
species composition caused by fire suppression
(McCune 1983).

Budworm and its primary hosts evolved when
frequent fires recycled or rejuvenated the
ecosystem—usually before the long-term carrying
capacity of the site was exceeded. The climax
communities were short lived and discontinuous, so
that budworm host trees at full site occupancy never
fully adapted to the vagaries of the climate. The
exclusion of fire as a major ecological force allows the
budworm's selective pressure to begin working anew
on host populations; however, the process of building
genetic resistance in hosts is slow and unpredictable
(Howe 1976). Until the forces of natural selection
define a new host–pest equilibrium in the absence of
fire, optimal production in the long term may be
compromised.

The frequency of budworm outbreaks—and the area
involved—are likely to increase because western
forests are now succeeding toward climax much more
rapidly than they are being turned back and
rejuvenated. The western budworm continues to exert
a regulatory influence on tree stress and forest
succession, in part replacing the functional role of
natural fire.

The probable consequence of a long history of
coevolution between plants and their usual consumers
is a mutualistic relation in which insect grazers
function as regulators of primary production and
nutrient cycling (Mattson and Addy 1975, Rafes 1970).
Insect feeding varies inversely with the vigor and
productivity of the host system and thereby tends to
ensure constant and optimal plant production over the
long term.

The western budworm is a native insect that also
seems to function as a stress regulator. Good habitats
for budworm are dense, mature stands composed of
shade-tolerant host species on xeric sites, reflecting
an increase in susceptibility as tree and stand vigor
decrease. When all interrelated habitat
characteristics—including diversity in crown-class
structure—are analyzed collectively, budworm habitat
improves as forest succession advances and net
production of the ecosystem declines. Evidence
shows that tree moisture stress increases tree
susceptibility, and correlations indicate reduced tree
vigor improves foliage quality. Susceptibility to
infestations and vulnerability to damage are closely
aligned, and the stands and trees that are least
productive or most stressed tend to receive the
greatest relative damage.

Outbreaks of many diverse, plant-feeding insects have
been explained by climatic events that induce plant
moisture stress (White 1969, 1974, 1976, 1978).
Insects are characteristically produced in
overabundance, which ensures population survival
even with limited food supply. Only occasionally,
when the host plants become stressed, does the food
tissue become sufficiently rich in nitrogen to improve
survival. White (1974) speculated that outbreaks of
both western and eastern budworm might be caused
by similar qualitative changes in the foliage of their
hosts. Survival does not have to be large to effect
significant population increases from one generation
to the next. A 2-percent survival means a doubling of
the population for an insect species that lays about
200 eggs, like the budworm; a 10-percent survival
translates into a tenfold increase.

Chemical defenses emitted by the host plants are known to be important in limiting the food supply of insect grazers (Hanover 1975, Rhoades and Cates 1976). Abnormally warm, dry weather in spring and summer often precedes western budworm outbreaks (Hard and others 1980, Twardus 1980 unpubl.), and the frequency of outbreaks is directly related to increasingly dry climates (Kemp 1983). Nitrogen fertilization can elicit an increase in budworm populations (Schmidt and Fellin 1983), and feeding studies have shown that foliage nitrogen and terpene chemistry interactively affect budworm survival and fecundity (Cates and others 1984a unpubl.). Any condition that reduces defensive chemistry and increases nutritional quality favors larval growth, survival, and adult fecundity. Such changes can be caused by moisture deficiency, which may be induced by abnormal weather or by succession.

Several processes of population change are undoubtedly important in the initiation of an outbreak of western budworm. The net effect of these processes on population survival and reproductive rates can be indexed by site and stand conditions. Each stand may be considered to have a threshold of population density above which population growth overwhelms the mortality caused by the budworm's natural enemies (parasites, predators, and diseases). The threshold of escape is defined by the prevailing weather and certain characteristics of the stand (see table 7-1), which collectively index the amount of competitive stress on host trees. Outbreaks arise in stands whenever and wherever the quantity and quality of the food resource is sufficient to impart a substantial increase in the survival rate of the small larvae that cannot be compensated for by mortality from natural enemies.

Natural enemies are important in regulating low-density populations but cannot keep pace with a rapidly growing population under favorable environmental conditions. Low budworm populations may reach the threshold of escape density in just a few stands or simultaneously over large forested areas, depending on the successional and climatic homogeneity of the stands and the degree of stress imparted by the general weather conditions.

Budworms disperse from the most susceptible stands—transported by the wind as small buoyant larvae or as weak-flying moths seeking foliated shoots for egg deposition. Additional budworm thus reach adjacent, less susceptible stands. Should the threshold of natural-enemy control be exceeded with this immigration, a widespread outbreak ensues. Stands that are poor habitat for budworm, inherently not very susceptible, often suffer outbreaks because the tremendous number of immigrants overwhelms local biocontrols. Populations may begin to increase in highly susceptible stands perhaps 3 to 4 years before defoliation becomes noticeable from aerial surveys (Blais 1973).

Budworm infestations persist in stands until the internal competitive stress between host trees is relieved and immigration falls off, allowing reestablishment of natural-enemy regulation in conjunction with mass starvation of young larvae. Weather—for example, early spring frost—may intercede to cause larval starvation and consequent dramatic population reductions, but unless loss of the food resource is sustained, budworm populations will quickly resurge to outbreak.

Infestations may continue indefinitely, where host stress is a function of the prevailing climate and advanced successional stage of the stand, or may be episodic, where abnormal weather induces host stress periodically. In either case, stand conditions represent the underlying cause of outbreaks because ultimately the effects of weather and natural enemies on budworm populations are mediated by the quantity and quality of available food.

Chapter 8

Modeling Budworm and Its Hosts

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William P. Kemp, and J. J. Colbert

8.1 Introduction

Modeling the budworm life system has been a major goal from the beginning of CANUSA-West. Preprogram planning called for an organized collection of studies, and the managers of the program proposed models as the means to integrate results. Research on budworm biology, ecology, and population dynamics was balanced with studies on the forest environment, tree and stand dynamics, and budworm–forest management options. Results from these and earlier studies on budworm and host dynamics have been integrated through the Prognosis–Budworm Model. Two previously developed extensions of the Prognosis Model—for Douglas-fir tussock moth (Colbert and others 1979, Monserud and Crookston 1982) and mountain pine beetle (Crookston and others 1978)—provided a preliminary coupling framework for the Budworm Model.

The Prognosis Model is used as a management and planning tool over a large portion of the budworm range. It predicts growth and yield of a forest stand under a variety of management options by use of standard inventory and sampling information. The combined Prognosis–Budworm Model allows integration of budworm effects into forest management and planning. The Prognosis Model can simulate most silvicultural prescriptions: precommercial and commercial thinning; selection, shelterwood, seed-tree, and clearcutting; postharvest site preparations; and regeneration establishment. The Budworm Model simulates various pest-management prescriptions. The combined model is already being used to develop an environmental assessment for budworm management on a National Forest. The combined model will simulate various management options, project differences between scenarios, and account for interactions between budworm and forest.

The remainder of this chapter provides a brief overview of the Prognosis Model structure and the additions or extensions to the Prognosis Model required to simulate budworm populations and their effects on forest growth and yield. Descriptions of the linkage of the Budworm Model to the Prognosis Model and the details of the Budworm Model are organized to follow the order of actual computations. Next, we describe the requirements and options for input and output, and the way output can be used in economic analyses. Finally, we provide the contacts for continued access to these models and describe mechanisms for coordinating continuing research and incorporating improvements as results become available.

Some of the variables and relations in the Prognosis–Budworm Model have been estimated by experienced scientists, pending further research. Some of these poorly understood variables and relations may have little effect on the model's predictions; a revised version of the model that simplifies them would then be in order. Other poorly understood variables and relations may significantly affect model predictions, which would underscore a need for additional research on them. Because the Prognosis–Budworm Model simulates the processes in budworm population dynamics, a manager might use the model to identify management techniques that exacerbate or mitigate effects of a particular variable or relation. When a range of assumptions is used for a particular variable or relation, the range in predicted results at least gives managers an idea of possibilities for the best case and the worst case.

8.2 Prognosis Model

The Prognosis Model for stand development (Stage 1973, Wykoff and others 1982) is a blend of silvicultural knowledge and growth data from sampled stands. The model represents these factors—albeit imperfectly—and uses them to estimate how stand conditions will change over time given specific management prescriptions. The Prognosis Model was designed (Wykoff and others 1982) to

● Use existing inventory methods to produce initial estimates of volume and growth.
● Apply to all timber types and stand conditions encountered in the inventory.
● Treat stands as the basic unit of management.
● Project growth as a function of interactions among trees.
● Incorporate growth of the current inventory into projections.
● Provide links to other components of the ecosystem and to economic-analysis procedures.

8.2.1 Prognosis Model Structure

The Prognosis Model is an individual-tree model that does not require mapped tree locations. The Prognosis Model stores several attributes for each sample tree. Stand averages and total volume statistics are computed by summing attributes of individual trees. A typical Prognosis Model run consists of the following steps:

1. Site-specific data and run-control commands are entered for the stand.
2. A sample-based inventory of individual trees is entered. See Wykoff and others (1982) for a complete list of input requirements.
3. Periodic increment data are used to adjust growth equations automatically to reflect the uniqueness of the stand.
4. Current conditions are displayed.
5. Planned harvests are simulated.
6. Shrub and cover conditions are predicted (Moeur 1985).
7. Growth and mortality in the absence of pests are predicted.
8. The effects on tree growth and mortality of selected pests (Douglas-fir tussock moth, mountain pine beetle, budworm) are simulated.
9. Establishment of new trees is simulated (Ferguson and Crookston 1984).
10. Attributes of sample trees are updated to reflect conditions at the end of the growth period (usually 10 years).

11. Conditions at the end of the growth period are displayed.
12. Time is incremented. If the projection is incomplete, steps 5 to 11 are repeated; otherwise the run ends.

8.2.2 Parallel Processing

Budworm densities often rise quickly over a wide geographical area. These increases may result from adult dispersal or budworm responses to favorable conditions. Regardless of the causes, high populations in one stand may affect populations in other stands. Simulation of interactions between stands—such as the redistribution of budworms—requires projecting related stands in parallel.

Most stand-growth models cannot represent this kind of interaction among stands. Including it in the Prognosis Model required creation of an extension to process several stands at once—the Parallel-Processing Extension (PPE) (Crookston 1983 unpubl.). A simulation using the PPE involves the following steps:

1. The user enters PPE options and program control options. One of the PPE commands establishes a master starting year for the multistand projection.
2. The user enters Prognosis Model options and tree data applicable for one stand. This stand is processed normally by the Prognosis Model up to the master starting year, and the stand data are then stored. This step is repeated for all stands.
3. The PPE reviews the status of each stand, and management or budworm options may be modified. For example, a user may specify that a particular stand be thinned from below when a minimum basal area is reached.
4. The PPE simulates each stand's development for one growth period (usually 5 to 10 years). Budworm interactions among stands are simulated using annual time steps.
5. Steps 3 and 4 are repeated until the end of the last growth period.
6. The user enters PPE commands necessary to print desired stand information, yield tables, and other output.

Figure 8-1 illustrates the differences between the base Prognosis Model and the PPE. The base Prognosis Model projects the development of one stand from the date of inventory to the scheduled end of the simulation. Simulation of several stands using this model requires that each stand be entered and simulated separately. The PPE, however, requires that all stands be entered at the start of the simulation. Growth in each stand is estimated during each growth period, and budworm population interactions may be simulated each year.

8.2.3 Prognosis–Budworm Model Linkage

Linkage between the Prognosis Model and the Budworm Model has the same general characteristics for both the standard Prognosis Model and the PPE. Therefore, the following discussion of the combined model does not distinguish between them.

The Prognosis Model calls the Budworm Model once during each year that budworms are active and provides information on foliage present at the start of the season. The Budworm Model then predicts how much foliage will be present at the end of the season and returns this information to the Prognosis Model. The Prognosis Model predicts the effects of defoliation on tree growth, top-kill, and mortality. Thus two steps link the Prognosis and Budworm Models: determination of the amounts of foliage present in a stand (see section 8.3), and translation of defoliation into damage to hosts (see section 8.6).
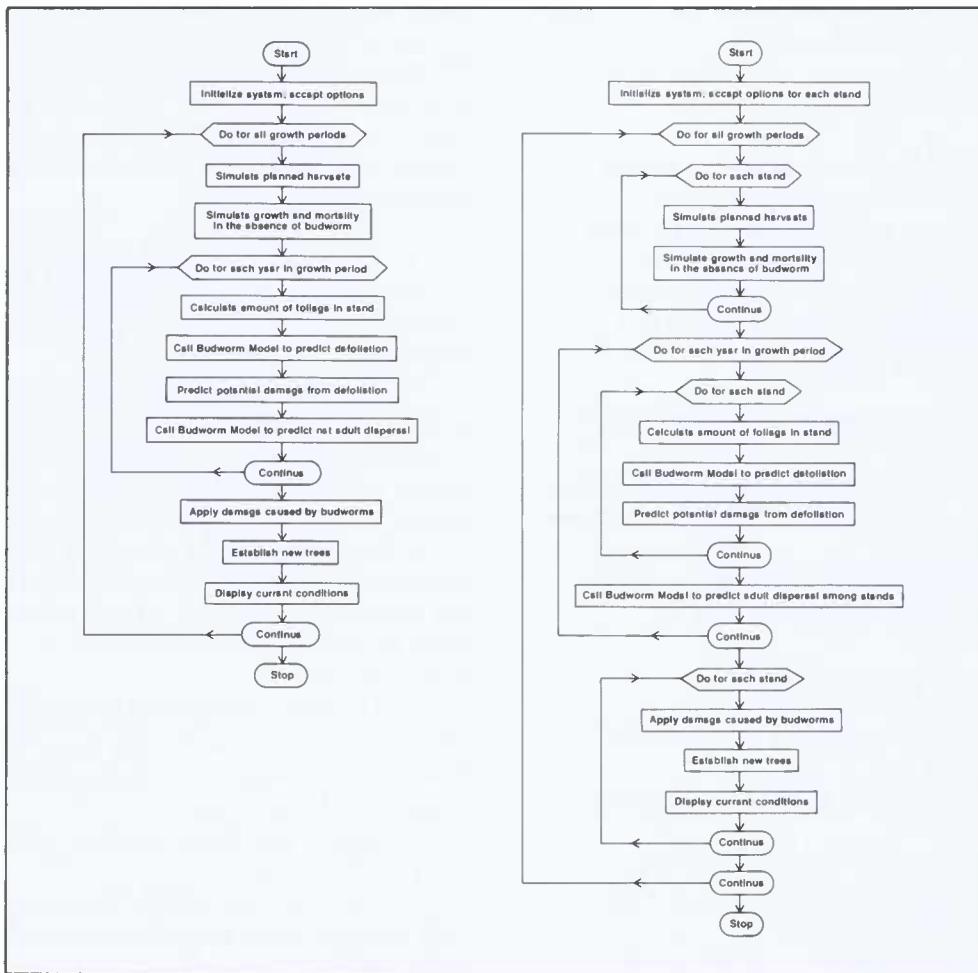
Figure 8-1—Simplified flowchart illustrating the schedule of events during the simulation of, left, one stand and, right, several stands in parallel using the Prognosis–Budworm Model.

8.3 Prognosis–Budworm Model Linkage, Part I

8.3.1 Prognosis Model Trees

The Prognosis Model simulates stand development by growing 2 to 1,350 sample trees. The following attributes of each sample tree are stored (see Wykoff and others (1982) for details):

1. Species,
2. Diameter breast height (d.b.h.),
3. Height,
4. Crown ratio,
5. Diameter increment (normal—that is, not affected by pests),
6. Height increment (normal),
7. Sampling probability (number of trees per acre represented by the sample tree),
8. Percentile in distribution of tree basal areas,
9. Height to point of permanent top damage, and
10. Probability of sample-tree death.

8.3.2 Budworm Model Trees

The Budworm Model has a set of three model trees for each host species and one set for all nonhosts. These model trees represent three classes of Prognosis Model trees: trees less than 23 ft (7 m) tall, trees 23 through 46 ft (7 through 14 m) tall, and those over 46 ft (fig. 8-2). The model is designed to handle six host species: Douglas-fir, grand fir, white fir, subalpine fir, Engelmann spruce, and western larch.

Each Budworm Model tree has an associated height and crown length obtained from the weighted average of all Prognosis Model trees represented by that tree. Budworm Model trees are partitioned into crown thirds, so that nine foliage cells are defined for each host species (three model trees, each with three crown levels).

Short (4-7 m)   Medium (7-14 m)   Tall (> 14 m)

- A set of three trees (one from each height class) is modeled for each host species.
- One set of three trees is modeled for all nonhost species.
- Each Budworm Model tree is divided into crown thirds.
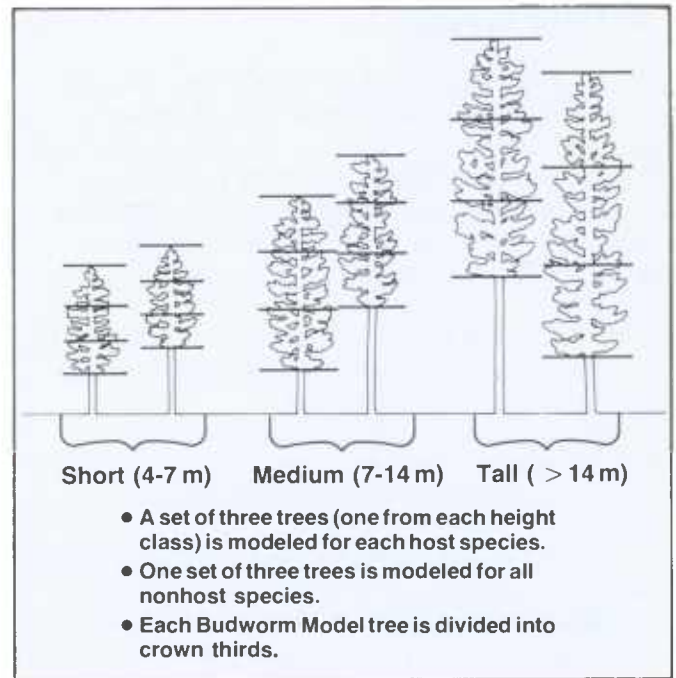
Figure 8-2—The Budworm Model trees.

8.3.3 Estimating Foliar Biomass

The amount of foliage on each Prognosis Model tree is computed using the equations of Moeur (1981) for total tree biomass. Total biomass is divided into crown thirds, by use of the proportions derived from data published by Jensen (1976; see also Jensen and Long 1983) and Schmid and Morton (1981). For each Budworm Model tree, the amount of foliage in a crown third is the weighted average of the corresponding crown thirds of the Prognosis Model trees that are represented by that Budworm Model tree. The weights are equal to the number of trees per acre that each Prognosis Model tree represents.

The foliage in each cell is further divided into four cohorts: new foliage, 1-year-old, 2-year-old, and remaining. These age classes are computed by multiplying the amount of biomass in each cell by the proportions expected for each cohort (derived from data published by Jensen 1976).

8.3.4 Foliage Dynamics

A model of the distribution of initial foliage biomass was developed for nondefoliated trees. A separate foliage-dynamics model has been developed to include effects of budworm defoliation. Each year, foliage ages into the next older class, some of the remaining foliage dies, and potential new foliage is predicted. The foliage dynamics model includes these assumptions:

● The amount of new foliage created each year is lower if the tree was defoliated in the previous year (hypothesized by Thomson 1979).

● During periods of defoliation, trees tend to retain old needles. The limit to the amount of retained old foliage is a function of the amount normally present.

● During periods of heavy, prolonged defoliation, even these retained needles will eventually drop.

● When defoliation stops, production of new needles returns to the predefoliation rate after a 1-year delay. Older needles that were retained because of defoliation drop off as new foliage is produced.

Weather has an important influence on any pest-management system (Bruhn 1980, .Hatfield and Thomason 1982). Several studies of western budworm have suggested that large-scale climatic features directly affect insect growth, outbreak initiation, and infestation collapse (Hard and others 1980; Ives 1981; Johnson and Denton 1975; Kemp 1983; Thomson and others 1984; Twardus 1980 unpubl.). On a shorter time scale, additional studies have illustrated the relation between western budworm and host phenology (Beckwith and Kemp 1984; Kemp and Beckwith 1983 unpubl.; Volney and others 1983b; Wagg 1958). Through the Weather Model, the effects of weather on both host and budworm may be included in the Prognosis–Budworm Model. The Prognosis Model calls the Weather Model to generate daily weather for each year that western budworm is active.

The Weather Model provides three options for predicting daily temperatures (maximum and minimum) and precipitation. Two options use weather records from a particular location to create a set of climatic parameters specific for that location. The Weather Model then uses these parameters to simulate daily weather. A third option allows a user to specify actual daily weather. These options and their uses are discussed in greater detail below.

8.4.1 Simulating Weather Data

The stochastic features of the Weather Model are based on work by Bruhn (1980) and Bruhn and others (1979). To begin, a long string of weather data from a particular location is used to derive a much smaller set of statistical parameters that characterize the climatic features of that location. The string of weather data must have no missing values and should contain at least 10 years of daily records. Standard methods for handling missing weather data are described by Kemp and others (1983).

Climatic parameters from several weather stations in the Pacific Northwest have been stored in the Weather Model; a user may specify the set that is most appropriate for a given stand. As an alternative, the user may develop and use climatic parameters from other weather stations.

The Weather Model uses climatic parameters to predict daily weather following methods developed by Bruhn and others (1979) and modified by Kemp (1982 unpubl.). Daily temperatures are a function of month, rainfall occurrence the previous day, and a random variable described by a normal probability distribution. In addition, maximum temperatures are affected by the previous day's maximum temperature, and minimum temperatures are affected by the current day's maximum temperature. Precipitation is a function of month, rainfall the previous day, and a random variable described by a uniform probability distribution. The amount of precipitation is influenced by month and a random variable described by a gamma probability distribution.

8.4.2 Actual Weather Data

Users may supply actual weather data. Although the volume of data required probably prohibits use of this option for long simulations, this option may prove useful for simulations of one or a few years.

The Weather Model will accept daily maximum and minimum temperatures and precipitation amounts. The model assumes no data are missing. Under this option, when the Prognosis Model calls the Weather Model for a given year, the actual values supplied for that year are returned for later use by the Budworm Model.

8.4.3 Onsite Weather Adjustments

Weather measured at a weather station may be very different from that occurring at a particular forest stand. The base temperatures are modified to account for differences in elevation, by use of the standard lapse rate of 6.3 °C/1000 m (Barry 1981). Additional procedures to improve the accuracy of local temperature predictions are being developed by Running (1981) and Running and Hungerford (1983). After further testing, these procedures may be incorporated into the Weather Model.

The Budworm Model integrates information from the literature and the collective expertise of numerous entomologists and foresters. When initial testing is completed, further details on the Budworm Model will be available, including a user's guide that will describe how to access the model and documentation of the model's organization, formulas, parameters, and other details. Publications are also planned that will describe model behavior and sensitivity. Instructions for using a stand-alone version of the Budworm Model will be included in the user's guide and documentation.

During each year of a budworm outbreak, the Prognosis Model creates Budworm Model trees, determines initial amounts of older foliage and potential new foliage in each cell, and calls the Budworm Model. The Budworm Model predicts how much foliage will be present in each foliage cell after defoliation. Budworm populations in each foliage cell are simulated separately, but not independently.

8.5.1 Initiation of Outbreaks

At present, two options for initiating outbreaks are included in the Budworm Model. One option allows the user to specify certain years when budworm populations will rise; the Prognosis Model will automatically start an outbreak during those years. A second option uses historical observations on frequency of outbreaks in different regions. Kemp (1983) reported the mean number of years that defoliation by budworm was visible from the air for regions in Oregon, Washington, Idaho, and Montana (table 8-1; see also fig. 6-1). Either the frequencies reported by Kemp (1983) can be used or another probability of outbreak occurrence can be specified. During each Prognosis Model cycle, the Prognosis Model will use those probabilities to predict whether an outbreak will occur in a given region during that cycle.

Table 8-1—Relevant statistics by outbreak-frequency region (from Kemp 1983)

Outbreak frequency code	Mean number of years with recorded defoliation divided by total number of years	Standard deviation	Range	Number of points analyzed[1]
High (1)	0.823	0.128	0.60–1.00	11
Medium (2)	.307	.130	0 – .48	19
Low (3)	.009	.018	0 – .04	13

[1]At each point, all forested acres within a radius of about 13 mi (21 km) were considered in the analysis.

Working in two areas (McCall, ID, and John Day, OR), Ulliman and Kessler (1983 unpubl.) found that, given an outbreak in a region, every stand that contained hosts showed some defoliation. Unless otherwise specified by the user, the Budworm Model assumes that initial densities are uniformly low in all stands; budworm populations in subsequent years will rise or fall according to weather, site and stand conditions, and other factors in the Budworm Model that influence budworm dynamics. Initial budworm densities for given stands may also be specified by the user.

Future versions of the Budworm Model may include a regional index currently being developed by Kemp and Long (personal communication). By using both temperature and precipitation, this index should predict the likelihood of an outbreak occurring in a given region.

A synoptic model of budworm population dynamics (Synoptic Budworm Model) is being developed by Campbell and Srivastava (personal communication). In contrast to the Budworm Model, which simulates the processes that affect budworm population dynamics in great detail, the Synoptic Budworm Model will summarize the net effects of those processes in a few steps. This model will predict both a sequence of budworm densities (eggs, fourth instars, pupae, residual pupae, adults, and adult females) and defoliation as functions of prior budworm densities, site and stand conditions, and weather. Coupled with the Prognosis Model, it is intended for use as an aid in long-range land-use planning.

During years with low budworm densities, the combined model could use the Synoptic Budworm Model exclusively. Given an outbreak, managers could either continue with the Synoptic Budworm Model or switch to the high-resolution Budworm Model. Decisions on which model should be used (once both models are available) will depend on the type of information sought by the managers and on results of tests of the behavior of the two models. Linkage to the Prognosis Model would be similar for either population model; both require some information about site and stand conditions at the start of the generation and both predict defoliation at the end of the season. Use of the Synoptic Budworm Model when the detailed information provided by the Budworm Model is not required should result in considerable savings in computer time and storage requirements.

8.5.2 Budworm Model Structure

Two separate components make up the Budworm Model: BWMOD and BWFLY (fig. 8-3). BWMOD simulates the budworm life cycle from egg hatch in the fall through adult emergence in the late summer, and is the component that predicts defoliation. BWFLY simulates adult dispersal and oviposition, thereby predicting the number of eggs per stand that will start the next season. When several stands are processed in parallel, the Prognosis Model calls BWMOD once for each stand during a year; BWFLY is then called once that year to simulate adult dispersal for all stands. The sequence of calls to BWMOD and BWFLY differs between simulations of one stand (fig. 8-1a) and several stands (fig. 8-1b).
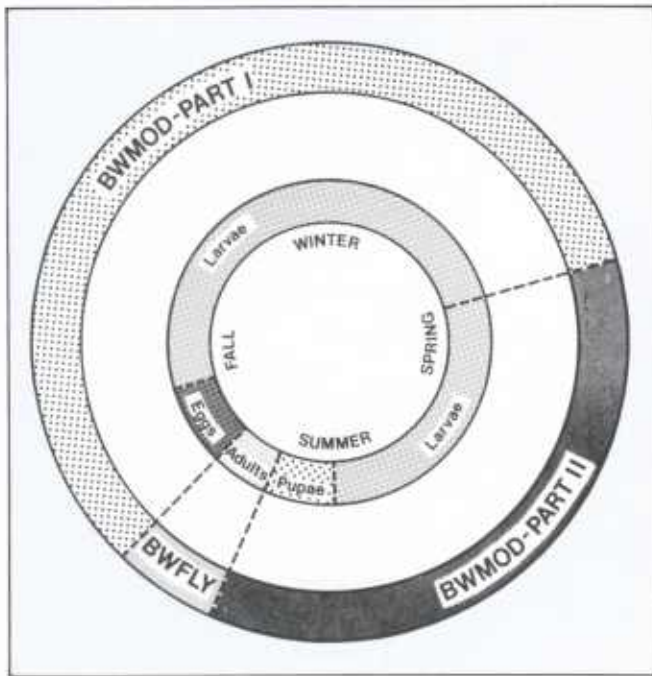
Figure 8-3—The two components of the
Budworm Model—BWMOD and BWFLY.

8.5.2.1 Eggs to Larval Emergence in Spring (BWMOD part I)—The Budworm Model begins by simulating egg mortality, fall larval dispersal, mortality of overwintering larvae, and a minimum dispersal mortality in the spring. The net effects of each event arc applied in order of occurrence.

The Prognosis Model passes to the Budworm Model either the total number of eggs laid in the stand (predicted by the Budworm Model during the previous year) or mean egg density (provided by the user as an option at the start of a simulation). The Budworm Model distributes these eggs to each of nine crown levels (crown thirds within three height classes), using relative egg-mass densities (based on information reported by Campbell and others 1984b; Carolin and Coulter 1972, 1975; Schmid and Farrar 1982; Waters and Volney 1981 unpubl., 1982 unpubl.). For a given crown level, the model distributes budworm eggs to host species according to the relative amounts of foliage for each host.

Two sources of egg mortality are included in the model: parasitism and nonviability. Low egg-mortality rates have been reported by Torgersen and others (1984), Carolin and Coulter (1959), and Waters and Volney (1981 unpubl.). The same rates are applied to budworms in each foliage cell because differences in mortality rates were not significantly related to host species, tree size, or crown third (Campbell and others 1984c). These mortality rates are applied independently; for example, the number of eggs killed by parasites is not affected by the number of nonviable eggs.

During fall dispersal, most larvae are thought to move inward and downward, and hibernacula are most commonly found on the bole and inner branches of the lower crown and just below the bottom of the live crown (Eldridge and Egan 1983a unpubl., McKnight 1969a). Mortality from fall dispersal and overwintering is therefore applied to all larvae on a given model tree, and not separately according to crown third. Fall dispersal and overwintering mortality rates have been studied by Eldridge and Egan (1983a unpubl., 1983b unpubl.) in north-central Washington and by Carolin and Coulter (1972) in central Oregon; their findings generally match those of Miller (1958) for eastern budworm.

Mortality during spring dispersal is separated into two parts: a base or minimum amount that occurs as larvae move from their hibernacula toward foliage, and the additional mortality that occurs as larvae search for suitable buds or needles to mine. This additional mortality is highly variable because it is affected by weather, stand conditions, and other factors; it is modeled separately in the more detailed, time-dependent part of the model (described below). Total rates of spring-dispersal mortality for a limited number of years have been supplied by Eldridge and Egan (1983a unpubl., 1983b unpubl.) for western budworm and by Miller (1958) for eastern budworm.

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8.5.2.2 Emerging Larvae Through Pupae (BWMOD part II)—At the conclusion of the first part of BWMOD, all larvae that remain have survived egg mortality, fall dispersal, and overwintering. Some of the larvae that will die while moving from hibernacula to foliage have also been excluded.

The Budworm Model divides the budworm life cycle from spring larval emergence through the pupal period into intervals based on budworm development. The developmental rate for budworm is assumed to be a direct linear function of temperature; at higher temperatures (above a given threshold), budworms are assumed to develop faster. Daily maximum and minimum temperatures supplied by the Weather Model are used to calculate the number of heat units that accumulate during each calendar day, measured as Celsius degree-days (Arnold 1960, Baskerville and Emin 1969). Each interval is 20 degree-days (°D) long, with °D calculated using budworm thresholds; typically it takes 7 to 8 calendar days to accumulate 20 °D in early spring and 1 to 2 days in midsummer. The lower and upper thresholds for budworm development are set to 5.5 °C and 35 °C, respectively, though users may specify other thresholds. Although developmental thresholds vary among populations (Volney and others 1983b) and larval development probably is not linear near lower and upper thresholds (Logan and Hilbert 1983), these difficulties are far outweighed by the problems inherent in predicting temperatures for the microsites occupied by larvae. Larvae developing in buds or in webs, for example, may experience temperatures that are 3 to 8 °C different from ambient temperatures (Shepherd 1958, Wellington 1950).

Budburst and shoot expansion are also functions of daily weather (Campbell and Sugano 1979, Thomson and Moncrieff 1982). Heat units are accumulated separately for each host, and different thresholds may be specified by host. Cleary and Waring (1969) and Sorensen and Campbell (1978) note that soil temperatures also affect host phenology, particularly in the early growing season. A planned improvement of the Budworm Model will adjust predicted daily ambient temperatures to account for snowpack and soil temperatures.
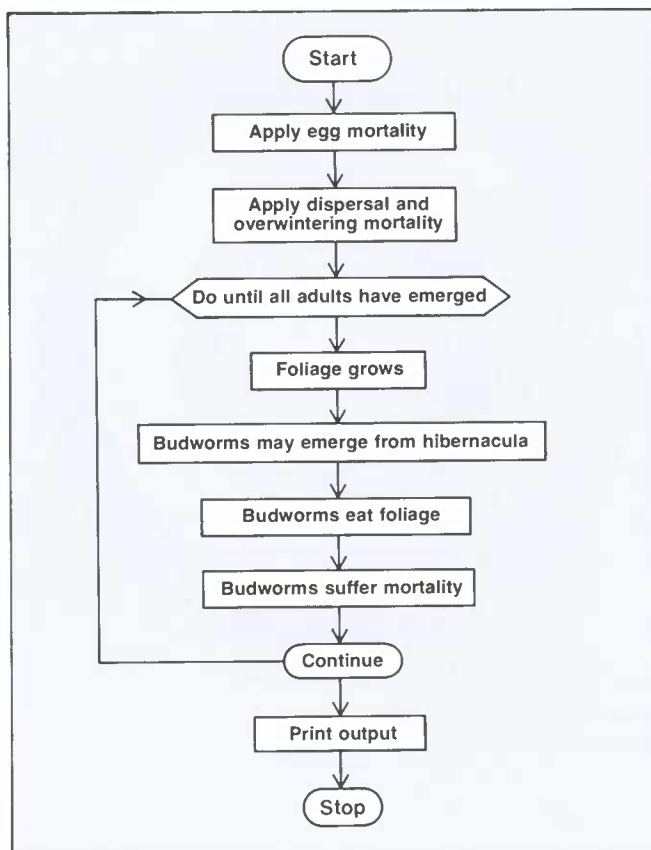
Figure 8-4—Flowchart describing the sequence of events simulated by BWMOD.

During each interval of 20 °D (accumulated using budworm thresholds), several events occur: foliage and budworms grow, budworms may emerge from hibernacula, larvae destroy foliage, and budworms suffer mortality (fig. 8-4). If specified by the user, the status of budworm population or foliage may be printed at the end of each interval. The Budworm Model repeats this cycle at each interval of 20 °D until all budworms have either died or emerged as adults. Once all adults have emerged, the number of eggs produced by each female is calculated. The total number of potential eggs per stand is stored for later use during adult dispersal and oviposition.

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8.5.2.2.1 *Host and Budworm Phenology*—Host phenology is based largely on logistic models developed by Beckwith and Kemp (1984) that predict shoot expansion during a season as a function of accumulated °D. Separate models were developed for each crown third for Douglas-fir and grand fir. At present, the Douglas-fir models are used for Engelmann spruce, and the grand fir models are used for subalpine fir and white fir. Host-biomass production is assumed to parallel shoot elongation; studies currently in progress will relate biomass production directly to accumulated °D. Biomass produced per each interval of 20 °D is the product of total number of buds, mean total biomass produced per bud (over the entire season), and percentage of shoot elongation during the interval.

Budworm phenology is also determined by accumulated heat units. Data from Beckwith (personal communication) were used to estimate the mean °D accumulated per instar. Female budworms require more accumulated °D to complete development than males (Beckwith, personal communication). The life stage of each budworm cohort (those that emerge from hibernacula during one interval of 20 °D) is updated every 20 °D until all surviving budworms have emerged as adults.

8.5.2.2.2 *Larval Emergence*—During each interval of 20 °D, the Budworm Model checks to see if all successfully overwintering larvae have emerged from their hibernacula; if so, the model skips this section. The Budworm Model assumes that larvae in hibernacula do not emerge until a minimum number of °D have accumulated. Once this minimum requirement has been met, peak larval emergence occurs shortly, although a few larvae emerge late (Volney and others 1983b) (fig. 8-5).

Larvae emerging from hibernacula on a given Budworm Model tree are distributed among crown thirds proportional to the amount of foliage present. Waters and Volney (1981 unpubl., 1982 unpubl.) and Carolin and Coulter (1972) reported no consistent, significant trend in budworm densities among crown thirds when they sampled second and third instars in needles and expanding buds. Male and female budworms are assumed to have identical emergence patterns.
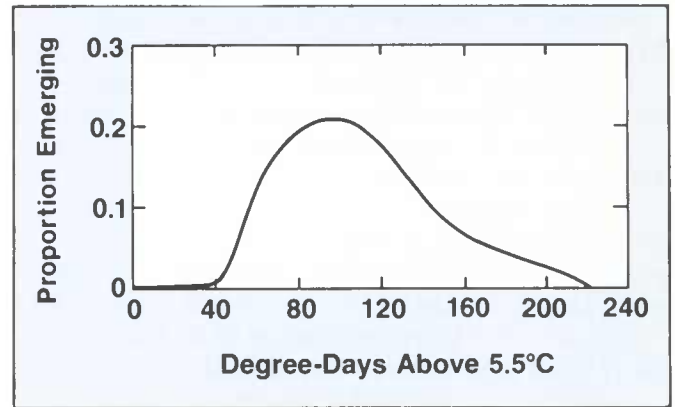
Figure 8-5—Pattern of budworm emergence from hibernacula (data from Volney and others (1983b), table 7, Dry Lakes Flat (b) at 25 °C.

Once larvae have arrived at a particular foliage cell, some larvae disperse immediately while the rest search for needles or buds to mine. Larvae first search for buds that are suitable for mining. Reproductive and vegetative buds are considered suitable if they have expanded enough for mining; vegetative buds also must not have been mined previously. A small proportion of buds are considered effectively "hidden" from larvae and therefore not eligible for mining. If there are more larvae than eligible buds, larvae that do not get a bud to mine will either disperse or mine needles. Most of these estimates are based on limited field observations. Further testing of the model is needed to see how sensitive it is to these variables.

8.5.2.2.3 *Larval Feeding and Foliage Destruction*—The Budworm Model next calculates the total potential amount of foliage that would be destroyed if all larvae fed on new foliage. Total potential foliage destroyed includes both foliage actually consumed and foliage wasted during larval feeding—ends of needles that were clipped off but not consumed, for example. Blake and Wagner (1983b unpubl.) and Beckwith (personal communication) reported feeding rates specific to instar, sex, and host as well as destruction/consumption ratios specific to instar and host, all based on laboratory studies. These feeding rates and destruction/consumption ratios were adjusted upward to reflect higher metabolic requirements and greater foliage wastage under field conditions (Beckwith, personal communication).

The potential foliage destroyed by larvae in a given foliage cell is compared to the amount of new foliage available in that cell. A small portion of the foliage present is considered effectively hidden from larvae, so that larvae will not consume every needle present during one interval of 20 °D. If enough new foliage (excluding "hidden" foliage) is available, all larvae feed on new foliage, and the amount of new foliage present is reduced accordingly. All young larvae that were not able to feed on new foliage will disperse; a portion of older larvae may feed on older foliage and the rest disperse. Larval dispersal is described below. Separate feeding rates and destruction/consumption ratios are used for larvae feeding on older foliage to calculate amounts of older foliage destroyed.

Depending on the timing and extent of feeding, larvae may damage or kill developing buds (Carolin and Coulter 1975, Thomson 1979). In the model, bud-killing is a function of both percentage of shoot elongation and percentage of defoliation, and occurs early in the growing season (if at all). When a larva consumes a given amount of foliage biomass, the effect is much greater if the shoot has just begun to expand than if the shoot has nearly finished elongating because of the lost "potential" foliage that would have been grown by the expanding shoot. Damaged buds represent this lost potential foliage.

At present, the Budworm Model calculates two measures of defoliation: visible defoliation (foliage destroyed divided by foliage actually grown) and effective defoliation (foliage destroyed divided by total potential foliage grown—including foliage from killed or damaged buds). These defoliation measures are displayed for the user's information; the actual amount of foliage remaining is provided to the Prognosis Model at the end of the season. Additional work is needed on the effect of killed and damaged buds on current foliage production, and on measures of defoliation that are related to tree growth and mortality rates (section 8.6.1).

Mean female weight gain for an interval of 20 °D is calculated for each foliage cell for later use in predicting the number of eggs produced per female. First, the amount of foliage consumed per female is multiplied by the efficiency-of-conversion index (Waldbauer 1968); host-specific values for this index have been supplied by Blake and Wagner (1983b unpubl.) and Beckwith (personal communication). Female weight is also influenced by foliage quality (Cates and others 1983a), although measures of foliage quality are not simulated directly by the Prognosis Model. Cates and others (1983b) related foliage quality for budworms to tree stress, particularly water stress. The Budworm Model uses host species and habitat series (Pfister and others 1977) as an index to stress on trees. Budworms are assumed to grow larger on trees under greater stress.

8.5.2.2.4 Budworm Mortality—Four sources of mortality are explicitly modeled during each interval of 20 °D: larval dispersal, natural enemies, foliage quality, and (as an option) insecticide application.

Larval Dispersal—In simulating larval dispersal, the Budworm Model first calculates the proportion of dispersing larvae that land on nonfoliage. This proportion is a function of the amount of host and nonhost foliage below and beside each larva's original crown level. All larvae landing on nonfoliage are assumed to die. Silvicultural practices that reduce total foliage present in a stand—such as thinnings—thus greatly affect larval mortality during dispersal.

Next, the proportion of larvae leaving a given crown level that will land in each of the other crown levels is determined. This is a function of both instar (younger larvae are almost equally likely to move downward, laterally, or upward, but older larvae primarily move downward, with some lateral movement) and total amount of foliage present in each crown level (larvae are more likely to land in crown levels with more foliage).

In each crown level, larvae are apportioned to tree species according to the relative abundance of each species (including nonhosts). Young larvae that land on nonhost species are assumed to die. Older larvae landing on nonhosts may redisperse once or twice.

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Natural Enemies—Four groups of natural enemies are represented: birds, ants, parasites that attack in the fall, and parasites that attack in the spring.

The number of budworms killed by birds (for the entire stand) during an interval of 20 °D is influenced by the number of birds in the stand, the number of budworms eaten per bird per day, and the number of days per each interval of 20 °D. Five bird guilds are modeled separately: flockers, ground foragers, foliage gleaners, shrub gleaners, and flycatchers. At present, the number of birds of each guild in a stand is estimated as a function of successional stage (Garton, personal communication). Future work by Garton will use site and stand variables provided by the Prognosis Model to predict numbers of birds present for each guild; this modification will allow the effects of silvicultural treatments on bird populations to be simulated by the model. The number of budworms eaten per day is calculated using a density-dependent equation; specific parameters for each guild have been provided by Garton (personal communication). The number of calendar days occurring in each interval of 20 °D is stored by the subroutine that uses daily weather to calculate accumulated degree-days.

In open-grown stands in the Pacific Northwest, variation in mortality from ants has been related to budworm density, budworm life stage, host species, predation by birds, tree size, and crown level (Campbell and others 1983a unpubl.; Campbell and others 1983c, 1984a; Campbell and Torgersen 1982, 1983). Users may specify the standwide mortality from ants or use the default value provided by the model.

Budworm mortality from ants and birds for the entire stand is then apportioned to specific crown levels and hosts. Campbell and others (1983a unpubl.) reported that birds caused greater budworm mortality in the upper two-thirds of the crown of trees about 30 ft (9 m) tall than in the lower third, but ants were more active in the lower crown third. Ant predation in the middle crown third was affected by the extent of bird predation. The model therefore recognizes two stand-canopy layers for birds and three layers for ants; the absolute heights of canopy boundaries and the proportion of total mortality that occurs in each canopy layer are based on Campbell and others (1983a unpubl.), but these values may be reset. Mortality within a canopy layer is partitioned among foliage cells occurring in that layer according to relative budworm abundance in each cell. A small proportion of the budworms in each cell are considered effectively hidden; thus, predators cannot eat every budworm during one interval of 20 °D.

Some parasites, primarily *Apanteles fumiferanae* and *Glypta fumiferanae,* attack budworms in the fall and emerge from fourth and fifth instars during the following spring (McKnight 1971). The model assumes that these parasites do not affect budworm feeding rates until shortly before the budworms are immobilized and therefore does not separate parasitized larvae before immobilization. Torgersen and others (1984) reported 7- to 44-percent parasitism by this guild in the Pacific Northwest; Waters and Volney (1981 unpubl.) found 22- to 45-percent parasitism in the Southwest. Neither group of investigators found significant differences in parasitism rates among hosts or crown levels (Torgersen, personal communication; Volney, personal communication). The model assumes that parasites emerge uniformly from mid-fourth to mid-fifth instars, and that males and females are parasitized equally.

Parasites that attack budworm larvae in the spring and emerge shortly before or during pupation form the other parasite guild. The model assumes that larvae parasitized by this guild do not alter their foliage consumption. Waters and Volney (1981 unpubl., 1982 unpubl.) reported 0- to 49-percent mortality from this guild, and Torgersen and others (1984) noted 0- to 59-percent mortality. Again, no significant differences were observed in parasitism rates among hosts or crown levels (Torgersen, personal communication; Waters and Volney 1982 unpubl.). In the model, these parasites emerge uniformly during the pupal period. The overall rate of parasitism by both guilds may be reset by the user.

Foliage Quality—Cates and others (1983b) have observed that foliage quality affects budworm survival and that tree stress affects foliage quality. A tree-stress index, similar to the index that influences female weight gain, has been included. Both host species and habitat type affect this index, with greater tree stress assumed for drier habitat series and for host trees that are climax for the habitat series. Tree stress is assumed to enhance budworm survival.

Insecticide Application—A user may specify spray application when budworm densities exceed a minimum and when either a certain percentage of shoot elongation or a certain mean instar has been reached. Mortality rates vary with instar and sex. A pair of currently available models (Dumbauld and others 1980, Force and others 1982) predict instar-specific mortality based on insecticide, dosage, budworm population genetics, application techniques, meteorological conditions, and so on. These models can be used to estimate efficacies for use in the Budworm Model.

8.5.2.3 Adult Dispersal and Oviposition

(BWFLY)—After all adults have emerged, the Budworm Model calculates the number of potential eggs produced by females emerging from the stand. Kirkbride and Wagner (1983b unpubl.) have provided regression equations to predict potential eggs per female based on female pupal weight; the number of potential eggs produced in each foliage cell is calculated and then summed for the entire stand. If several stands are being processed at once, all stands must be brought to this point before the adult dispersal and oviposition subprogram (BWFLY) is called.

Unfortunately little specific information exists on adult dispersal of western budworm. Two options are presently available. The user may either specify the net results of immigration and emigration for each stand, or use the conceptual submodel (based on few data) described below. Another adult dispersal submodel that requires information on distances between stands is currently being developed by Long (personal communication).

For each stand, the adult dispersal submodel begins by applying a low preflight mortality rate. This mortality represents eggs from those females that die before laying any eggs (because of predation, incomplete wing expansion, and so on).

Next, a portion of the eggs are laid in the stand of origin. Two options are available: one assumes that each female lays one egg mass, and the other that females lay a certain proportion of their total potential eggs. In general, eastern budworm females are thought to lay at least one egg mass before long-distance flight (Greenbank 1973, Harvey 1977); further, Greenbank and others (1980) observed that females leaving stands carry about 50 percent of their total egg complement.

8.6.2 Damage Models

Earlier in each growth cycle, the Prognosis Model predicts height and diameter growth and the probability of mortality (in the absence of budworm) for each Prognosis Model tree. The damage models predict changes in these attributes and simulate top-kill.

8.6.3 Diameter Growth

Defoliation-induced changes in diameter growth are based on a model developed by Scott and Nichols (1983 unpubl.) that predicts the proportion of expected basal-area increment. This model uses two independent variables: the percentage of foliage biomass retained (one minus the averaged past 5 years' current defoliation), and the outbreak duration in years minus the number of years since the outbreak ended (effective outbreak duration). The Prognosis–Budworm Model assumes that a minimum of 20-percent defoliation occurs during an outbreak year.

Greater defoliation (reflected by a lower percentage of biomass retained) results in greater loss of basal-area increment (fig. 8-6). This effect is magnified by effective outbreak duration. For example, consider a situation where an outbreak has sustained a 5-year average of 40-percent defoliation (percentage of biomass retained is 60 percent). If the outbreak has been going on for 7 years (effective outbreak duration equals 7), then 48 percent of normal basal-area increment is expected, but if the outbreak has been going on for only 5 years, 68 percent of normal basal-area increment is expected.

8.6.4 Height Growth

The height-growth reduction model is identical in form to the diameter-growth reduction model. The measure of percentage of biomass retained is taken from the top third of the tree crown (rather than the tree average, as is done for the diameter model). The behavior of this model is the same as the diameter-reduction model (fig. 8-7). For example, if a 7-year outbreak subsided 2 years ago (effective outbreak duration equals 5) and percentage of biomass retained is 70 percent or higher, then 78 to 88 percent of normal height growth is expected. If this 7-year outbreak ended four or more years ago, however, then normal height growth is expected.
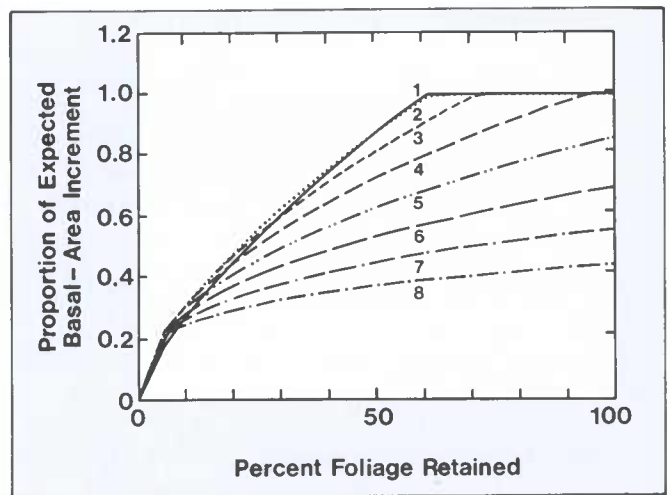
Figure 8-6—Proportion of expected basal-area increment as a function of percentage of foliage retained and effective outbreak duration (numbers on lines). Effective outbreak duration is the length of the outbreak in years minus the number of years since the outbreak ended. After Scott and Nichols (1983 unpubl.).
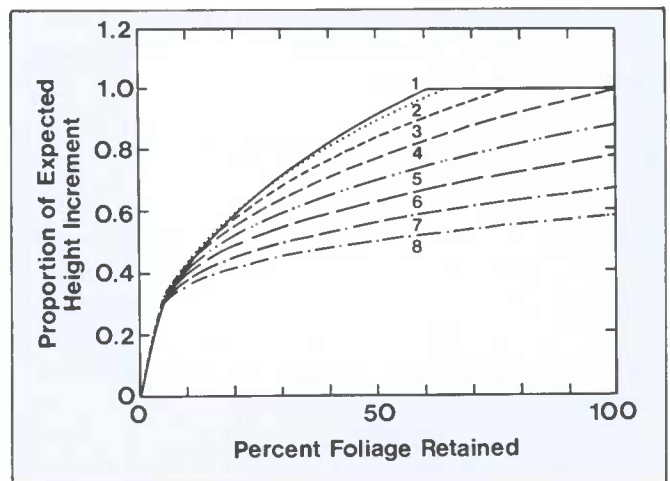
Figure 8-7—Proportion of expected height growth as a function of percentage of foliage retained and effective outbreak duration (numbers on lines). Effective outbreak duration is the length of the outbreak in years minus the number of years since the outbreak ended. After Scott and Nichols (1983 unpubl.).

8.6.5 Top-Kill

Three types of top damage are simulated: total loss of height growth for 1 year, top-kill that does not result in permanent damage to the tree, and top-kill that does result in permanent defect. The model assumes that permanent defect occurs when no merchantable volume will grow above the base of the killed top.

Budworm-caused damage that falls into the first category is accounted for in the height-growth reduction model. Models that predict top-kill with or without permanent damage are not available. Users may enter the probability of top-kill and the proportion of the crown that is top-killed during a Prognosis Model growth period. Using this option, users can take advantage of their own observations of top-killing. If the diameter at the point of top-kill is greater than an arbitrarily set limit (4 inches, 10 cm), the damage is considered permanent. Top-kill options may be specific to species, tree height, and diameter.

8.6.6 Mortality

The Prognosis Model predicts background mortality as a function of diameter, density of the stand relative to normal stocking, and density relative to a theoretical maximum for the site (Wykoff and others 1982). In studies designed to measure the effects of budworm defoliation, mortality was usually rare and sporadic. Alfaro and others (1982) recorded heavy mortality in one Douglas-fir stand in British Columbia that had undergone heavy defoliation for several years. They were able to relate mortality to tree diameter and to cumulative defoliation. To predict mortality, the Prognosis Model uses a combined and modified version of the two models developed by Alfaro and others (1982).

As defoliation increases, so does the predicted probability of mortality (fig. 8-8). Trees that are small relative to the stand average have a greater risk of dying than relatively larger trees with the same defoliation. If cumulative defoliation is 300 percent, for example, relatively small trees (less than half the stand's average) have a probability of dying equal to 0.80, but large trees (twice the stand's average) have a probability of dying equal to 0.04.
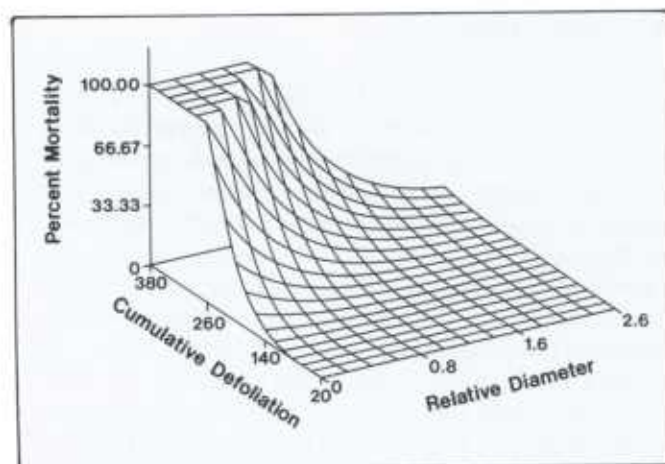
Figure 8-8—Percentage of mortality as a function of cumulative defoliation (5-year sum) and diameter relative to the mean stand diameter. Derived from two models published by Alfaro and others (1982).

8.6.7 Regeneration Establishment

The Regeneration Establishment Model (Ferguson and Crookston 1984, Stage and Ferguson 1982) has recently been added to the Prognosis Model. This extension predicts the probability that a 1/300-acre (13.5-m^2) plot will be stocked with regeneration and (given that it is stocked) the species, number, and heights of the established trees. The extension is used to predict regeneration several years after a disturbance.

Ferguson (personal communication) has found that the probability of stocking and the size and numbers of host trees are all reduced in areas where budworm-caused damage is high in the residual overstory or nearby stands. This result is currently being added to the combined models.

8.7 Model Input and Output

8.7.1 Model Input

Stand information required by the Prognosis–Budworm Model is identical to that required by the Prognosis Model (documented by Wykoff and others 1982). Crookston (1983 unpubl.) describes changes needed to process several stands in parallel. In brief, the Prognosis Model expects information on

● Inventory design used to measure the stand (basal-area factor or fixed-plot area, critical diameter when small trees are measured on fixed plots and large trees on variable radius plots, and so on);
● Site conditions (slope, aspect, elevation, and so on);
● Individual-tree measurements (species and d.b.h. are required; options or subsamples include periodic diameter increment, crown ratio, tree height, and so on).

Through a keyword system, users can simulate a wide range of management actions. Examples include thinning from above or below to a specified residual number of trees per acre (or basal area per acre) and establishment of regeneration after harvest. The effects of mountain pine beetle or Douglas-fir tussock moth may also be simulated.

Weather data (maximum and minimum temperatures, and precipitation) may be used directly. As an alternative, the Weather Model will generate stochastic daily weather from climatic parameters. A user may select a set of climatic parameters from one of several weather stations in the Pacific Northwest. These sets are included in the Weather Model. Climatic parameters from other weather stations may also be generated by the user. Daily weather may be adjusted for a specific location's elevation, latitude, slope, and aspect.

The Prognosis and Weather Models provide most of the information required to run the Budworm Model, but many options are available that allow the user to tailor a simulation to a certain situation.

The daily weather that is required by the Budworm Model is supplied by the Weather Model. Defoliation history (percentage defoliation of 1-year-old, 2-year-old, and older foliage for each host) is optional—necessary only if the user wishes to start a simulation in the middle of an outbreak. The adult-dispersal submodel requires either net dispersal into a stand or stand distances (for each stand, distances in kilometers to all other stands being modeled); work is proceeding on a submodel that simulates among-stand dispersal without requiring input of stand distances.

The Budworm Model usually begins simulation of the budworm life cycle at the egg stage—it needs to know the number of budworm eggs in each foliage cell. Several options are available for determining initial budworm densities. Unless otherwise specified by the user, the model begins an outbreak by assuming uniformly low initial densities of budworm eggs on host foliage of all stands in the outbreak. A user may specify budworm densities at the start of the simulation or at the beginning of an outbreak by supplying one of the following:

● Egg-mass densities (estimated for the whole stand or midcrowns of 23- to 46-ft-tall [7- to 14-m] trees). Relative egg-mass densities and mean number of eggs per mass are used to determine the number of eggs per foliage cell. Stand-specific values for eggs per mass are optional.

● Adult densities for previous generation (estimated for the whole stand from samples of pupal exuviae). Stand-specific values for potential eggs per female are optional. The adult dispersal submodel is called once to determine the number of eggs that will be laid in each stand by the dispersing adults.

● Larval densities (second through fourth instars may be sampled, estimated for the whole stand or midcrowns of 23- to 46-ft-tall trees). If the user supplies an estimate of degree-days accumulated to date (by using percent shoot elongation as an index, for example), the model may start the simulation at the instar sampled. Otherwise, mean survival rates will be used to predict the number of eggs that had to have been laid to result in the number of larvae observed, and the simulation will start at the egg stage.

Finally, the user may also specify a wide range of parameter options, such as specific parasitism rates, number of eggs per egg mass, and so on. The Budworm Model user's guide and documentation will describe these parameters in detail—how they are used, as well as literature and recent research results that were used to determine their default values. A user will thus be able to make use of additional local information or to test the sensitivity of the Budworm Model to these parameters.

8.7.2 Model Output

Unless otherwise specified by the user, no output is produced by the Prognosis–Budworm Model beyond that normally produced by the Prognosis Model. Wykoff and others (1982) describe Prognosis Model output in detail. In brief, four tables are produced:

- Input summary and calibration statistics (initial conditions);
- Stand composition (number of trees per acre, stand volume, growth, mortality, and so on);
- Individual-tree attributes (for six trees, their species, d.b.h., height, crown ratio, diameter growth, and so on);
- Stand-development and management-activity summary (volume grown and removed for the stand, mean height of dominant trees, years when thinnings occurred, and so on).

The last three tables are updated at the end of every growth cycle (usually 10 years), so that a user may follow the progress of a stand during the simulation.

The user may direct the Weather Model to print the daily weather predicted for given months of specific years.

Three independent options are available for output from the Budworm Model—two give detailed information about the status of budworm populations or foliage during a season, and the third gives a yearly summary of budworm and foliage conditions.

The two detailed options produce output every 20 °D for each foliage cell. The budworm population output prints Julian day, percentage shoot elongation, percentage defoliation, mean instar, density, and number of males and females for each life stage. The foliage output prints mean instar and budworm density; percentage shoot expansion; percentage defoliation; number of live, dead, and damaged buds; and amounts of new, 1-year-old, 2-year-old, and older foliage. Users should not specify these options for simulations of many stands or many years—the amount of output produced would be overwhelming!

The summary option prints the following information once each year: egg-mass density, nominal fourth-instar density, percentage shoot elongation at nominal fourth instar, final percent defoliation, final amounts of foliage for each age class modeled, and percentage mortality from dispersal, natural enemies, foliage quality, or insecticides.

8.8 Economic Models

In forest planning, the Prognosis Model provides stand-yield projections used by other programs (such as FORPLAN, Johnson and others 1980 unpubl.) that optimize the allocation of forest resources. Projected stand volumes that incorporate effects of budworm defoliation (including changes in distributions of species and diameters) will increase the accuracy of forest plans. Plans can be composed to retain the integrity of management units, allowing consistency in local, forest, and larger regions, and in various sectors of economic communities.

Several programs can be used to evaluate the incidence and magnitude of economic impacts of budworm defoliation. A computer program (Medema and Hatch 1982) available to users of the Prognosis Model will assist in making stand-by-stand economic analyses. The user can perform benefit-cost analyses for existing stands and obtain soil-expectation values for regenerated stands.

Methods also have been developed to estimate budworm impacts for a wide range of economic objectives, from maximizing profit to stabilizing communities. Bible and others (1981) developed a model for determining how much of the losses attributable to budworm can be offset by changes in commercial thinnings and rotation policy. Bible (1982) and Berck and Bible (1984) developed methods that use output from the Prognosis–Budworm Model to evaluate impacts in the context of forest planning objectives. In expanding economic analysis to account for indirect losses to local communities, Bible (1983a unpubl., 1983b unpubl., 1983c unpubl., 1983d unpubl.) developed methods to assess such things as changes in local mill viability, employment, and subsequent regional tax and revenue bases.

8.9 Future Work

Additional publications such as user's guides and model documentation will be produced. Calibration and validation studies are planned for several areas. The USDA Forest Service is collecting data for comparing the models with recent outbreaks. These data will allow comparison of actual effects of defoliation on growth and yield with model predictions. Further, these data will provide information on past silvicultural practices over a range of habitat types. The models should be able to mimic these interactions.

The models will be updated as additional research results become available. Future entomological research will be coordinated by Research Work Unit 2201 at Pacific Northwest Forest and Range Experiment Station.[1] Future silvicultural research will be coordinated by Research Work Unit 1302 at the Intermountain Forest and Range Experiment Station.[2] Two management units are responsible for maintaining the operational versions. The Methods Application Group[3] will maintain the Budworm Model. The Timber Management Staff Unit[3] will maintain the Prognosis Model. The models will be available to Forest Service users through the Forest Service Data Processing System (FSDPS) and accessible to cooperating agencies and institutions through these management units.

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[1]Forest and Range Sciences Laboratory, Rt. 2, Box 2315, La Grande, OR 97850.
[2]Forestry Sciences Laboratory, 1221 S. Main St., Moscow, ID 83843.
[3]Fort Collins Computer Center, 3825 E. Mulberry St., Fort Collins, CO 80524.

Chapter 9

Recommendations
Russel G. Mitchell

Significant progress was made in the 6 years the CANUSA-West Program worked on developing new and improved techniques to manage forests susceptible to the budworm in the West. But the tyranny of time also showed that some projects, regardless of the intensity of effort, could not be initiated and completed in a 6-year span. The critical problem of impact assessment, for example, requires a long-term commitment for measuring not only growth reduction and mortality during an outbreak but also recovery of trees and stands long after it. Mathematical models needed for decision-support systems are just too complicated for quick construction and calibration for all areas where they might be used. Further, some fundamental research problems and questions developed during the research program could not reasonably be addressed in an applied program.

This chapter presents a list of areas where additional work is desirable if we are to reach the goal of integrating reduction of budworm impact with forest management. The order does not reflect priorities, but two areas are deemed absolutely critical to the completion and validation of CANUSA-West projected outputs—impact assessments in managed, unmanaged, and insecticide-treated stands and the extension, calibration, and validation of the decision-support system throughout the budworm range. Continued refinement of management applications and applied research requiring long-term plots are especially suitable for the research arm of the Forest Service in cooperation with Forest Pest Management in the United States and the Canadian Forestry Service and Provincial agencies. Fundamental research questions can also be addressed by the United States and Canadian forest services, but many questions might be answered more appropriately by other research organizations, such as universities.

The aim of future work is to determine:

For Host Trees

- Factors determining the extreme variability of top-kill and tree mortality from stand to stand.
- Normal production of new foliage for host species of all sizes and over a wide range of sites.
- Effects of defoliation on production of new foliage.
- Effects of defoliation on photosynthesis.
- Effects of defoliation on wood-volume production by hosts in both the short and long term.
- Effects of host defoliation on the growth of associated nonhost tree species.
- The genetic base for apparent resistance to budworm in individual trees.
- The influence of abiotic environmental stresses on resistance to budworm in individual trees.
- The nature of host stress and how it affects budworm populations.
- Interrelation of other pest organisms, particularly tree diseases.

For Western Budworm

- Whether preference some larvae show for seed cones and others for foliage is genetically based.
- Effect of tree size on differences in vertical distribution of egg populations among hosts.
- Which factors are most likely to upset the normal sex ratio of budworm populations and how much deviation will have a significant effect on egg production.
- Whether bud-killing on different host species can be related to host phenology and budworm density.
- The role of olfactory and other stimuli in close-range communication of adults.
- Whether inconsistencies in host preference have a genetic base.
- Whether genetic changes occur when low populations change to outbreak, and if selective changes in genetic makeup can result from applications of insecticides.
- Regional variation in lepidopterous species associated with the western budworm and which species add significantly to the damage caused by budworm.

For Population Monitoring and Assessment

● Further testing and developing of automatic egg-mass counter for field use.

● The relation of adult males caught in pheromone traps to subsequent populations on host trees.

● Whether sampling methods, such as lower crown beating, developed for various budworm stages are applicable in all locations and stand conditions.

For Population Ecology

● Techniques for verifying population dynamics studies over the range of habitats in the West, featuring why populations remain low, increase, remain in outbreak status, and collapse.

● A better understanding of survival in early instars and how that survival affects population trends.

● The ecology of ant and avian predators, their role in maintaining low budworm populations, and what factors can be exploited to improve their efficiency.

● More clearly how weather affects the timing of budworm emergence from hibernation and the development of new growth on host trees.

● Effects of foliage chemistry on budworm populations and of defoliation on foliage chemistry.

● Better ways of evaluating adult dispersal and its effect, if any, on initiating localized and general outbreaks.

For Stand Management

● For intermediate stand culture, the appropriate precommercial and commercial thinning schedules, the intensity of thinning, and the levels of growing stock in host species that are required for optimum stand growth and reduced budworm activity.

● Whether prescribed underburning can be used in budworm-susceptible stands to promote succession toward a forest type with reduced vulnerability to budworm.

● How stand hazard ratings can be improved for evaluating relative susceptibility among stands.

● Whether climatic zones reflecting hazard can be made more site specific.

● Which silvicultural treatments in established demonstration areas show the most promise for reducing budworm damage.

● Relations of stand characteristics to the effectiveness of insecticide treatments over the long term.

For Control

● Whether pheromone treatments can be used to suppress populations through trapping or confusion techniques.

● The long-term effect of direct suppression by various means on population stability and growth patterns in host and nonhost tree species.

● Whether new disease organisms can be found that are lethal to budworm.

● Further guidelines for conserving and augmenting major predators—for example, preserving ant habitat or putting out bird boxes.

For the Decision-Support System

● Procedures and opportunities for updating the Prognosis–Budworm Model as appropriate new research is completed.

● Procedures and opportunities for calibration and validation of the Prognosis–Budworm Model over wide areas of the West.

● Opportunities for linking the Budworm Model with stand-growth models other than Prognosis.

Glossary[1]

Abietoideae: Subfamily of the pine family (Pinaceae) that includes all the hosts of budworm.

Adfrontals: In caterpillars, a pair of elongated, hardened plates on the front of the head extending from the base of the antennae to the top of the head where they meet, forming two sides of a triangle.

Adult: Fully grown, sexually mature stage of an insect—in budworm, the moth.

Advance regeneration: Young trees that have become established naturally before regeneration cuttings are begun.

Adventitious foliage: Shoots arising from buds produced by conversion of mature tissue into meristematic tissue.

Aggregated distribution: Clumped distribution of a population in space.

Allele: One of a pair of genes, or of multiple forms of a gene, at the same locus of paired chromosomes.

Allelochemics: Secondary compounds produced by plants that affect the behavior of organisms feeding on or associated with them. For example, many plants produce toxic compounds that deter insect feeding.

Allopatry: Geographic separation of species or races sufficient to prevent gene exchange.

Anal shield: In caterpillars, a hardened plate on the upper surface of the last body segment.

Analysis of variance: Statistical procedure typically used to separate the variation (sum of squares of differences from the mean) into portions, each attributable to a defined source.

Apical dominance: The growth of the terminal bud at the expense of lateral buds whose development is inhibited while the terminal bud is actively growing.

Arthropods: Invertebrate animals with segmented bodies and paired, jointed appendages—for example, insects and spiders.

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[1]Terms are defined as used in this book.

Bark beetles: Common name applied to the family Scolytidae, a group of beetles whose adults bore through the bark of host trees to lay their eggs, and whose larvae tunnel and feed under the bark.

Basal area: The area of the cross section of a tree inclusive of bark, at breast height (4.5 ft, 1.37 m).

Benefit-cost analysis: An economic appraisal technique used to rank alternatives based on expected return on investment.

Benefit/cost ratio: A financial measure obtained by dividing the anticipated gains from a project by its anticipated costs.

Billion International Units (BIU's): The International Unit (IU) is an expression of the potency of B.t. formulations based on that of a particular strain of *Bacillus thuringiensis* used as a reference standard; strain HD-1-S-1971 is currently used as the reference standard in the United States.

Bioassay: Determination of the relative strength or specificity of a substance—for example, sex pheromone—by comparing responses of test organisms.

Biomass: Total quantity at a given time of living organisms of one or more species or tissue per unit area.

BIU's: (see Billion International Units).

Board foot (foot board measure, fbm): Unit of measurement represented by a board 1 ft long, 1 ft wide, and 1 inch thick.

Bole: The trunk or stem of a tree.

Budburst: Opening or flushing of vegetative buds; beginning of shoot and foliage growth.

Canopy: The more or less continuous cover of branches and foliage formed collectively by the crowns of adjacent trees and other woody growth.

Canopy closure: In a stand, the progressive reduction of space between crowns as they spread laterally, increasing the canopy density.

Chemosystematic (chemotaxonomic): Pertaining to the use of chemical characteristics for the separation and classification of organisms.

Chi-square test: Test of the mathematical goodness of fit of a hypothesized frequency to an observed frequency.

Chlorogenic acid: An organic acid found in the foliage of conifers which, in high concentrations, inhibits browsing by deer.

Cholinesterase inhibitor: A chemical that interferes with the normal transmission of nerve impulses.

Clearcutting: Removal of the forest stand completely in one cut.

Climax species: Species capable of perpetuation under the prevailing climate and soil conditions; the culminating species in plant succession in a given environment.

Clinal variation: Gradation in measurable characters of a species or other group of related organisms associated with changes in environmental conditions—for example, changes in latitude, longitude, or elevation.

Cluster analysis: A statistical tool for segregating individuals into groups based on similarities of measurable characteristics.

Clypeus: In insects, a hardened plate on the lower front of the head located just above the upper lip.

Codominant: Trees with crowns at or near the top of the canopy. In silviculture, one of the four main crown classes, recognized on a basis of relative status and condition in the stand.

Cold hardiness: The ability to survive exposure to below-freezing temperatures.

Color morphs: Different colored forms of an insect species occurring in the same population.

Community: An assemblage of populations of plants and animals in a given place.

Copulation: Mating.

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Covariance analysis: Statistical procedure used to separate the variation in a response variable that is systematically related to another variable (covariate) from the variation related to treatment. For example, budworm weight gain may be related to several test diets and to starting weight. The test diet is the treatment and the starting weight is the covariate.

Cover type, forest: Forest vegetation type now occupying the ground, with no implication as to whether it is seral or climax.

Crown height (base of live crown): Of a standing tree, the vertical distance from ground level to the base of the crown, measured either to the lowest live branch whorl (termed upper crown height) or to the lowest live branch (lower crown height).

Crown kill: Portion of crown with foliage killed by defoliation or secondary causes.

Crown length: The distance from the top of the tree to the base of the live crown.

Crown ratio: The ratio of crown length to tree height of a standing tree.

Damage: Any effect of insect feeding deemed deleterious to some management objective or objectives.

Decision tree: A systematic way of illustrating alternatives and their outcomes over time.

Defoliation: Reduction in the amount of foliage through actions of insects, fungi, or other agents, as distinct from natural leaf fall.

Defoliation prediction model: A model or algorithm used to predict amounts of defoliation.

Degree-day: A measure that accounts for both time and temperature during that time; 24 hours at a temperature that is 1° above a specified threshold temperature equals 1 degree-day (°D).

Dendrology: The science of the identification and systematic classification of trees.

Dependent variable: A variable whose value is determined by the value of one or more other independent variables in a function.

Detection: Procedure used to discover outbreaks of forest insects and diseases; detection surveys may be made by observations from aircraft or the ground.

Diameter breast high (d.b.h.): Diameter of a tree at 4.5 ft (1.37 m) above the ground.

Diameter inside bark (d.i.b.): Diameter of a tree less the bark thickness.

Diapause: Condition of suspended animation or arrested development during the life cycle of an organism—for example, overwintering budworm larvae undergo diapause.

Dieback: Progressive dying from the extremity of any part of a plant.

Discriminant analysis: A special case of multiple linear regression where the dependent variable is a class or group—for example, low, medium, and high.

Dispersal: The act or result of dispersing or scattering; usually refers to the distribution of adults or to the redistribution of larvae after eggs have hatched—for example, dispersal of early instars.

DNA: Deoxyribonucleic acid; hereditary material found in the chromosomes that stores and transmits genetic information.

Dominant: (1) A plant species within a community, or more narrowly defined assemblage of components, that exerts the greatest influence because of its abundance or activity; (2) a tree or group of trees occupying the uppermost layers of the forest canopy and that are largely free growing.

Dormant (latent) bud: A bud in a resting state with growth and development suspended until triggered by some environmental cue.

EA: (see Environmental Assessment).

Early larvae: Larvae that have recently issued from eggs; usually first and second instars.

Ecology: The study of plants and animals in relation to their environment.

Economic-selection cutting: Logging only of the highest value trees from a stand; exploitation cutting, often called "high grading."

Ecosystem: An assemblage of living plants and animals and their environment.

Ecotone: Transition zone between two adjoining communities—for example, a forest edge forms an ecotone between forest and meadow.

Efficacy: Effectiveness, as of an insecticide; ability of a product to control the specified target pest or to produce the specified action.

Egg mass: Eggs deposited in a group by a single female.

EIS: (see Environmental Impact Statement).

Elastic demand: (see also Price Elasticity of Demand.) Demand is elastic if a decrease in price results in a greater than proportional increase in demand. Similarly, increase in price results in decrease in total revenue.

Electrophoresis: Movement of suspended particles through a fluid under the action of an electromotive force; compounds can be separated based on differences in the rate of movement.

Entomological unit: Portions of the susceptible host type usually defined by physical features or stand composition.

Entomopathogenic: Refers to microorganisms and viruses capable of causing disease in an insect host.

Environmental Assessment (EA): Public document providing results of environmental analysis of the impact of a proposed action; used to determine the need for an Environmental Impact Statement.

Environmental Impact Statement (EIS): Public document, required by Federal law, which documents the significant environmental effects of any major action on federally owned land that may alter the quality of the human environment.

Epicormic branching: Growth of foliage and branches long after normal laterals have elongated; originating from buds that may have been suppressed for many years.

Esterase: An enzyme that mediates or promotes synthesis and hydrolysis of an ester.

Evaluation survey: A survey in which the current or potential significance of an insect or disease outbreak is appraised.

Even-aged: The condition of a forest or stand composed of trees having no or relatively small differences in age.

Fecundity: Productivity (numbers of offspring) of an organism. The fecundity of the budworm is measured in numbers of eggs produced per female.

Fixed-size plots: Sampling method using plots of a predetermined and fixed size.

Foot board measure (fbm): Measurement of lumber (see Board Foot).

Formulation: Packaged active ingredient plus various other materials that a manufacturer of pesticides produces.

Frass: Waste product of insect digestion.

Free thinning: A thinning to favor only the trees considered most suitable to form the final crop, in whatever layer of the canopy they may be found.

Gene frequency: The proportion of individuals in a population carrying a given gene.

Genetic polymorphism: Existence in the same population of genetically different forms.

Genitalia: Sexual organs and related structures.

Genotype: Genetic constitution of an individual or a species.

Granulosis virus (GV): Virus causing disease of insects characterized by minute granular inclusions in infected cells.

Gravid: Pregnant.

Group selection: A modification of the selection system in which trees are removed in small groups.

Guild: A group of organisms that share a definable ecological trait—for example, conifer-gleaning birds or larval parasites of western spruce budworm.

Habitat: The place occupied by a plant or animal considered in relation to all the environmental influences affecting it.

Habitat series: Collection of habitat types that share a common overstory climax species.

Habitat type: The units of land capable of producing similar plant communities at climax.

Hazard: Probability of attack or damage by a pest.

Hazard rating: An index of relative likelihood of attack or damage by a pest.

Head-capsule: The hardened portions of the larval head that form a rigid compact case, which is shed with the skin at each larval molt.

Height-class structure: Stand structure expressed in terms of variation in tree heights.

Hemolymph: Body fluid of an invertebrate organism having an open circulatory system.

Hibernaculum (pl., hibernacula): Silken shelter spun by a budworm larva and in which it overwinters.

Host: Any organism on or within which another organism lives.

Host type: Forest composed primarily of tree species that are hosts for budworm.

Hybridization: Mating between members of different populations of the same species with different gene complexes, or between members of different species.

Hyperparasite: A parasite that lives in or on a primary parasite.

IGR's: (see Insect Growth Regulators).

Impact evaluation survey: (see Evaluation Survey).

Implant (technique): Method used to introduce chemicals into tree tissues by drilling a hole into the woody tissue and implanting the chemical in a solid form. The chemical is slowly absorbed and translocated by the tree (see also Injection).

Independent variable: A variable whose value determines that of one or more other variables.

Inelastic demand: (See also Price Elasticity of Demand.) Demand for a product or quantity is inelastic if a change in unit price causes a change in the same direction of total revenue—that is, if unit price increases, so do total revenues and vice versa.

Infectious: Able to produce infection—that is, able to enter into a susceptible host, to multiply, and to produce disease; said of certain microorganisms and viruses.

Infestation: In budworm, presence of insects in sufficient numbers to produce visible defoliation.

Infinitely elastic demand: (See also Price Elasticity of Demand.) Demand is infinitely elastic if changes in quantity offered by producers do not affect product price.

Injection (technique): Method used to introduce chemicals into tree tissues by injecting a liquid formulation of the chemical into the wood.

Insect growth regulator: Insect hormones, hormone mimics, or molt inhibitors that affect the ability to develop normally, survive, or reproduce.

Instar: Period or stage between molts in an insect larva.

Internal rate of return: The interest or discount rate that equates the present value of a project's benefit and costs.

Internode: The part of a stem between two adjacent nodes.

Intolerant species: A kind of plant that grows poorly or dies in competition with other plants (as for light, moisture).

Isoenzymes: Functionally like enzymes with similar amino acid sequences; may be separated electrophoretically or by chromatography.

Isomer: Chemical compound that contains the same number of atoms of the same elements as another compound, but differing in structure and properties.

Kairomone: A chemical compound produced by one species that affects other species.

Larva: The immature form of an insect that undergoes complete metamorphosis: a caterpillar, maggot, or grub.

Late (large) larvae: Mature larvae near the end of the feeding period, usually fifth and sixth instars.

Leader: Terminal, topmost shoot.

Life table: Tabulation of mortality factors acting on a population that displays the relative importance of each factor and permits estimation of survival; the information on survival, coupled with a knowledge of fecundity, allows estimation of the size of the succeeding generation.

Lignification: Hardening of the cell walls in a woody plant by conversion of cell-wall constituents to lignin.

Linear function: Any relation between variables which when graphed yields a straight line.

Linear regression: A statistical modeling technique in which a response (dependent) variable is assumed to be a linear function of independent variable(s) plus an associated normal error.

Locus (gene locus): Fixed position of a gene in a chromosome.

Loss function: Relation describing how cost of making an error changes with the size of the error.

Lower crown: That portion of the tree crown whose main branches originate from the lower third (usually) of the tree crown.

Maturity: Loose term for the stage at which a tree has attained full development, particularly height, and is in full seed production.

Meristematic tissue: Undifferentiated tissue capable of further division and specialization.

Mesic: Pertaining to relatively moist habitats.

Metamorphosis: The process of change in which an organism passes through several developmental stages; for example, budworms develop from eggs to larvae to pupae to adults.

Midcrown: Portion of the tree with branches originating from the middle third (usually) of the crown.

Model: Formal description that represents a system or process.

Molt: Shedding of the larval integument, a process that allows for growth.

Molt inhibitor: Chemical that interferes with the process of molting.

Monomorphic: Existing in only one form.

Monoterpene: A hydrocarbon in the terpene group composed of one unit of the basic terpene structure (see Terpene).

Morph, color: (see Color Morphs).

Net present value: Value of an investment measured by discounting all future returns minus associated costs.

Node: In plants, the part of a stem where leaves and axillary buds arise; in decision trees, the point on a branch that gives rise to two or more branches.

Nomenclature: System of terms or names used to describe organisms.

Nucleopolyhedrosis virus (NPV): Virus causing disease of insects, mainly larvae of certain Lepidoptera and Hymenoptera, characterized by the formation of polyhedra in the nuclei of infected cells; usually fatal.

Operational suppression: Use of biological or chemical compounds for the large-scale suppression of insect populations.

Outbreak: Period of high insect (budworm) numbers during which conspicuous defoliation occurs.

Overstory: The portion of trees, in a forest of more than one story, forming the upper or uppermost canopy layer.

Parameter: A quantity that is considered constant for a particular situation, although it may differ in other situations.

Parasite: An organism that develops in or on a host organism at the host's expense.

Phenology: Observational science dealing with the time of appearance of periodic events in the life cycle of organisms, particularly as these events are influenced by local conditions.

Phenotype: Expression by visible characters of an organism of the interaction of genotype and environment.

Pheromone: A chemical compound produced by an organism that affects others of the same species.

Photoperiod: Variation in light and dark periods (day length), which affects plant development. For example, flowering in many plants will occur only under certain photoperiods.

Photosynthesis: Process in green plants of conversion of carbon dioxide and water to carbohydrates and oxygen by the energy of sunlight.

Phytophagous: Feeding upon plants.

Pilot test: A test of the efficacy of a pesticide against its target organism over a fairly large area before the pesticide is used operationally.

Pistillate bud: Structure that forms the female cone in conifers.

Pole: A still young tree from the time its lower branches begin to die up to the time when the rate of height growth begins to slow down and crown expansion becomes marked.

Pole pruner: Sectional pole with cutting shears and a basket on the upper end for collecting branch samples from the tree crown.

Pollen cones: In conifers, male (staminate) structures that produce only pollen.

Polymorphism: (see Genetic Polymorphism.)

Population dynamics: The study of changes and the reasons for changes in population numbers.

Predator: A free-living organism that feeds on other organisms—for example, birds and ants that feed on budworm.

Pretreatment, posttreatment: Before and after treatment with insecticide.

Price elasticity of demand: For any quantity being sold, the percentage change in quantity divided by the percentage change in price.

Primary parasite: A parasite that establishes itself in or on a host that is not a parasite.

Prothoracic shield: In caterpillars, a hardened plate on the upper surface of the first body segment behind the head.

Provenance: Original geographic source of seed, pollen, or propagules.

Pupa: The resting, intermediate stage of an insect between the larva and the adult.

Race: (see Subspecies.)

Refoliation: Regrowth of foliage after defoliation.

Regeneration cutting: Any removal of trees intended to assist regeneration already present or to make regeneration possible.

Regional climate: Long-term weather averages over an area, such as western Montana or the northern Rocky Mountains.

Reproductive isolation: The prevention of mating between potentially interbreeding organisms by physical, temporal, or behavioral mechanisms.

Residual life: Length of time that a pesticide remains effective against its target organisms after application.

Residual properties: Ability of pesticides to remain efficacious for some time after application.

Residual pupae: Budworm pupae that survive predation by predators such as ants and birds but are subject to other mortality factors such as parasites.

Risk: Probability of an undesirable event occurring within a specified interval.

Salvage cutting: Harvesting of trees that are dead, dying, or deteriorating before their timber becomes worthless.

Sapling: Loose term for a tree no longer a seedling but not yet a pole; in the United States, a tree 2 to 4 inches (5 to 10 cm) d.b.h., in Canada, one-half to 3 inches (1.3 to 7.6 cm).

Sclerotization: The hardening of the body wall of an insect.

Seed cones: In conifers, female (pistillate) structures that bear seed.

Seedling: In general, a young tree grown from seed from its germination up to the sapling stage.

Seed-tree cutting: Removal in one cut of the mature timber from an area, leaving a small number of seed bearers singly or in small groups.

Selection cutting: Periodic removal of trees (particularly mature trees), either singly or in small groups.

Sequential sampling: Sampling with a variable sample size, in contrast to conventional sampling procedures that require a fixed number of sample units.

Seral species: A plant species characteristic of a stage in the development of forest communities (see Succession); not permanent (see Climax).

Setal areas: In caterpillars, areas of attachment on the body of stiff, erect hairs (setae).

Severity index: An index of the severity of previous budworm defoliation based on the magnitude of growth reduction.

Sex pheromone: Insect-produced chemical that stimulates a specific sexual attraction response by the receiving individuals.

Shade-tolerant: Said of plant species capable of growing and reproducing in shade.

Shelterwood cutting: Regeneration cutting in a mature stand designed to establish a new crop under the protection of the remaining stand.

Significance: Referred to generally as the significance level; when a statistical hypothesis is tested, it cannot be rejected if a calculated probability exceeds a given value.

Silvicultural system: A process whereby forests are tended, harvested, and replaced to result in production of crops of distinctive form; systems are classified by methods of felling that remove the mature crop with a view to regeneration.

Silviculture: Theory and practice of controlling the establishment, composition, constitution, and growth of forests.

Simulate: To use models to represent real systems.

Single-tree selection: Removal of individual, usually high-risk, mature trees from an even-aged forest to realize the yield and establish a new crop of irregular constitution.

Site climate: Regional climate modified by the slope, aspect, elevation, and edaphic characteristics at a particular site.

Site index: A measure of the relative productive capacity of a site based on the height of dominant trees in a forest stand at an arbitrarily chosen age.

Site potential: The potential productivity of a site.

Socioeconomic model: A collection of computer programs used to translate the volume of timber, water, and other factors into dollar impacts of a simulated outbreak.

Sparse population: A population at low density; sparse populations of budworms cause little or no visible defoliation.

Staminate bud: Structure that forms the male, pollen-producing cone in conifers.

Stand composition: The representation of tree species in a stand.

Stand density: Quantitative measure of tree stocking, usually expressed as number of trees, basal area, or volume per unit area.

Stand vigor: An expression, usually not quantitatively defined, of the general health of a stand.

Stereoisomer: (see Isomer.)

Stocking: In a forest, a more or less subjective indication of the number of trees as compared to the desirable number. More precisely, a measure of the proportion of the area actually occupied by trees as distinct from their stand density.

Strobilus (pl., strobili): Male or female inflorescence in most conifers; cone.

Stumpage: Harvested tree volumes, considered with reference to their quantity or marketable value.

Subclimax: The stage in plant succession immediately preceding climax.

Subspecies: Geographically defined group of populations of a species with different characteristics.

Succession: Replacement of one kind of community by another; the progressive changes in vegetation and animal life that may culminate in the climax.

Suppression: In pest management, reduction of pest populations below economically damaging levels.

Susceptibility: The probability that a stand will become infested by western spruce budworm.

Susceptibility index: A number representing the relative susceptibility of a stand to western spruce budworm.

Sustained yield: Continuous production; balance, over time, between net growth and harvest.

Sympatry: Overlap in the geographic ranges of related species.

Synonomy: A chronological list of all the scientific names assigned to a particular taxonomic group, such as a species.

Taxonomy: The orderly classification of plants and animals according to their presumed natural relationships.

Technology transfer: Communication of research and development information to potential users that results in a change or improvement in procedure.

Terpene: General name of hydrocarbons having the formula $C_{10}H_{16}$, many of which occur in volatile oils of plants.

Thermoperiod: Effect of cyclic alternations of temperature between day and night on plant processes. For example, plant growth is increased in some species when cool night temperatures alternate with moderate daytime temperatures.

Thinning: A felling made in an immature crop or stand primarily to accelerate diameter growth; also, a selection made to improve the average form of the trees that remain.

Threshold development temperature: Critical temperature above which some biological process, such as growth, begins.

Tolerant species: A kind of tree that grows well under specific conditions, most commonly in the shade of or in competition with other trees.

Top-kill: death or dieback of the leader and more or less of the upper part of the crown.

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Toxicity: Poisonous quality, especially its degree or strength.

Toxicology: Science dealing with poisons and their effects on specific organisms.

Translocation: Movement of dissolved substances through the vascular tissue of a plant.

Tribe: A category in the Linnaean classification system between family and genus; a group of genera.

Understory: Generally small trees and woody species growing under the main tree canopy.

Uneven-aged: Said of a forest, crop, or stand composed of intermingling trees that differ markedly in age.

Unit elasticity: (see also Price Elasticity of Demand.) Demand for a quantity or product relative to its selling price is said to be of unit elasticity if a change in price is counterbalanced by a change in demand so that total revenues remain unchanged.

Variable: A quantity that may assume any one of a set of values.

Vegetative buds: Buds that give rise to roots, stems, or leaves, and not to reproductive parts such as flowers.

Virus isolate: A virus that has been isolated from contaminants and associated microorganisms.

Vulnerability: Probability that damage will occur in a stand, given an infestation of western spruce budworm.

X-ray energy spectrometry (XES): An x-ray technique whereby elements and their relative amounts in insect tissues are determined.

Xylem: Woody tissue of higher plants, which functions in support and water conduction.

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