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Chapter 7

Site and Stand Characteristics

N. William Wulf and Rex G. Cates



7.1 Introduction

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.

7.2 Susceptibility and Vulnerability

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 \geq 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

¹Each character is assessed individually as if all other characters are held constant.

²Relations 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.

7.3 Site Characteristics

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).

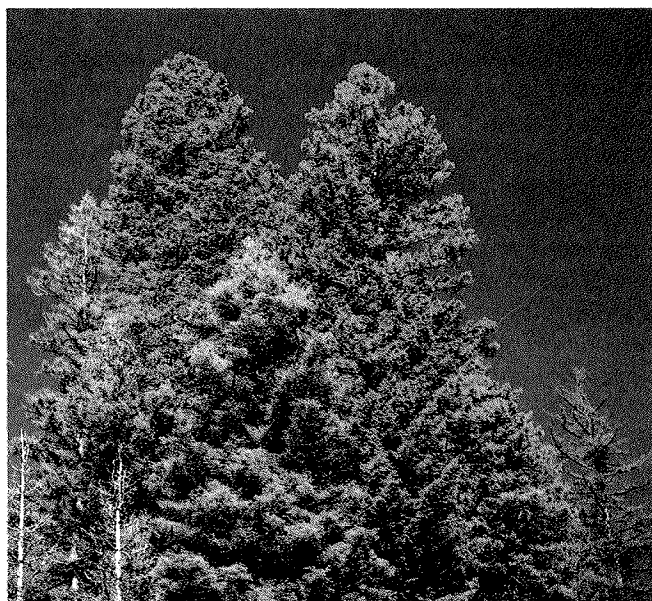


Figure 7-3—Climax grand fir in the foreground suffers severe defoliation, while seral Douglas-fir in the background remains green (Payette National Forest, central Idaho).



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).

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

¹Budburst 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).



A



B

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).

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 7-9—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 7-12—Intermediate Douglas-fir is being top-killed while the overstory remains lightly defoliated (Lubrecht Experimental Forest, western Montana).

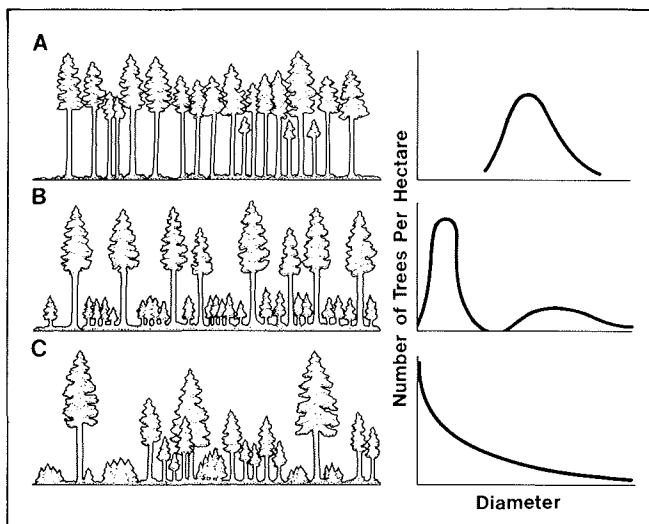


Figure 7-11—Stand structures, in order of susceptibility, from least to most susceptible: even-aged, top; storied, middle; and uneven-aged, bottom.

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 \times 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).

7.6 Site and Stand Conditions As the Predisposing Cause of Budworm Outbreaks

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.