

Management strategies for forest insect defoliators in British Columbia

Roy F. Shepherd

Department of Natural Resources Canada, Pacific Forestry Centre, 506 West Burnside Road, Victoria, B.C., V8Z 1M5, Canada

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Abstract

In a synthesis of outbreak characteristics of common defoliating insects in British Columbia, two types emerge: those with fast-cycling outbreaks and those with sustained outbreaks. Species with fast-cycling outbreaks rise quickly to visible defoliation levels, cause significant growth loss, tree deformation and mortality, and disappear just as quickly. Impact is closely related to the severity of defoliation during the first year of an outbreak; consequently, the objective of managing these species should be to reduce populations before defoliation occurs, i.e. to prevent the outbreak. To accomplish this objective, identification of susceptible habitats and monitoring with sensitive pheromone traps in areas of expected outbreaks are necessary to detect upwelling populations. Species with sustained outbreaks cause significant growth losses only after defoliation continues for a number of years. Tree mortality usually is not important except where regeneration is being nurtured under a selective or shelterwood silvicultural system. Impact can be significant over the life of a stand because of the length and frequency of outbreaks, but treatments effective for only 1 year usually cannot be justified except where it is important to retain a full crown. Long-term cultural methods appear to be the preferred management system and, of these, utilizing non-host species or resistant or phenologically asynchronous host species may be the best option. Again, determining the location of expected outbreaks is an important component of a management system and, at present, identifying stands by frequency of outbreak within zones of climatic suitability would be useful in selecting treatment areas.

Keywords: Forest management; Pest management; Insect defoliator; Defoliation

1. Introduction

Demands upon our forests are increasing and becoming more diverse. A wide range of uses dictates that many management systems or techniques will be useful to meet these multiple objectives. The overall management of forests should include those integral components required to minimize losses to insects. In this paper, I discuss current and proposed pest management systems for common defoliators in British

Columbia, discuss their advantages and disadvantages, and provide guidance for the selection of the best systems to attain specified objectives. This review is based on a synthesis of our knowledge of the population ecology of these defoliators and of our attempts to reduce damage caused by these pests.

A knowledge of the population dynamics of pest insects is essential before sound management decisions can be made. In this paper, different types of dynamics are discussed from both

a theoretical and practical point of view and the implications upon management systems are pointed out. It is hoped that this will stimulate a more sophisticated and diverse approach to insect pest management than has been practised in the past and will identify areas where additional research is required to develop suitable strategies for specific pests in different situations. Recently introduced pests are not considered in this paper.

Strategies of insect pest management should be developed well in advance of need. These strategies should depend on the following factors: (1) the objectives of managing the forest and to what degree those objectives will be jeopardized by the insect damage and be alleviated by implementation of a pest management system; (2) the types and amount of damage caused by the pest to the stand and the associated cost–benefit ratios of treatment vs. non-treatment in economic, ecological, and sociological terms; (3) the types of management systems available and the feasibility of applying these in an effective and timely manner; (4) the outbreak characteristics of each pest population and their response to different available treatments.

2. Forest management objectives

The objectives for growing and managing forests have changed considerably over time. Earlier in this century, the maintenance of commercial stands until they could be cut was of prime importance. Later, the major concern was for the maintenance of the growing stock, and now, the maintenance and enhancement of the growing capacity of the site to sustain the local community is the first consideration. Vegetation management in parks and wilderness areas has similarly evolved from policies of 'let nature take its course' to the preservation of species diversity and maintenance of as many forest ecosystems as possible. The use of forests will undoubtedly increase over time and the objectives will change and diversify as the public's perception of their purpose evolves.

Insects can have a significant impact on forest

management objectives, sometimes with devastating effects. A range of management techniques should be available to minimize those effects within the objectives of managing that particular forest. With the current explosion of the human population, demands on forests, and expectations of forest use will multiply. This, in turn, will increase the need for a diversity of methods to handle insect pest problems, particularly for techniques which are less intrusive (Van Frankenhuyzen, 1990) than those often used in the past. It will also mean a greater integration of insect management systems with other management requirements of the forest.

3. Types of damage and their impact on the forests

Foliage is the food generator which provides the nutrients necessary to maintain the growth and health of the tree. When insects graze on the foliage, there can be immediate and long-term effects on survival, stem height and diameter growth, seed production, and bole form. Trees counter foliage and bud loss by concentrating resources on regrowing these food-producing tissues at the expense of other tissues. Immediately after partial defoliation, photosynthates are translocated away from the roots toward new shoots and branches (Parker, 1979; Bassman and Dickman, 1985). The capability of the tree to counter the effects of defoliation depends upon tree vigour, tree age, site conditions and the time of attack within the seasonal growth pattern of the tree (Fig. 1) (Shepherd, 1992). Considering timing, for instance, when buds of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, are destroyed by the western spruce budworm, *Choristoneura occidentalis* Freeman, early in the year, before flush, the latent buds in the axils of needles are immediately stimulated to develop and form a completed bud ready to flush the following year. In contrast, when the same host species is attacked by caterpillars of the Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough), later in the growing season after the buds have flushed and shoot extension is near completion,

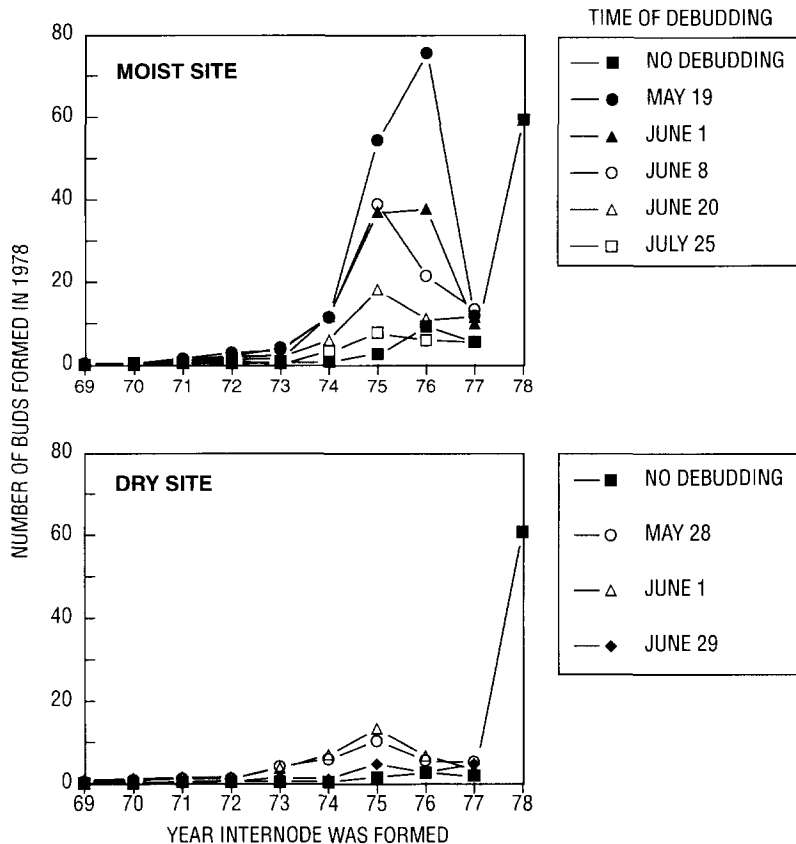


Fig. 1. Average number of latent buds formed on each internode of Douglas-fir during 1978 in response to bud removal in spring 1978 as related to site and time of debudding (from Shepherd, 1992).

it is too late in that season for the trees to respond with latent bud development. In this case, the consequences of defoliation are more serious, and mortality is more likely to occur. A similar timing response was found in artificial defoliation studies of sugar maple, *Acer saccharum* Marsh. (Gregory and Wargo, 1985). Mattson et al. (1988) also recognized the effect of timing of defoliation upon the severity of impact, and gave needle-feeding insects a much higher ranking for potential damage than bud-feeding insects.

Age of consumed needles can affect impact. Needles on 1-year-old internodes produce the most photosynthate; production is progressively less as needles age. Some insect species, notably those in the sawfly group, prefer older needles, and these pests have relatively less impact than species feeding on current or 1-year-old foliage.

The most obvious effect of defoliation is the loss of growth, both radially and terminally, as food production decreases. It appears, however, that most trees have a surplus of foliage to meet minor foliage losses, and defoliation must reach 30–50% before significant radial growth losses can be detected (Stark and Cook, 1957; Alfaro et al., 1982; Mason and Wickman, 1988), although more recent sophisticated analytical techniques may revise those findings (Alfaro and Shepherd, 1991).

Repeated defoliation over a number of years will have a cumulative effect upon growth (Fig. 2), and may even result in no radial growth and missing annual rings for a number of years (Evenenden, 1940). After an outbreak has declined and the damage ceased, the crown must be regenerated before normal growth can return (Fig. 3).

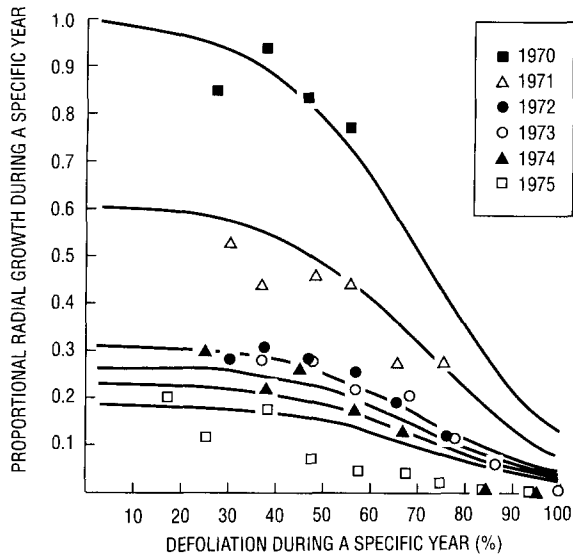


Fig. 2. Proportional radial growth of Douglas-fir trees as related to defoliation by western spruce budworm during a specific year and the accumulated defoliation up to that year in a stand experiencing continuous defoliation for 6 years (from Alfaro et al., 1982). Reproduced with the permission of the National Research Council of Canada.

A tree's capacity to grow new foliage, in itself, will be severely affected by defoliation (Embree, 1967), and a number of years may be needed before the trees acquire sufficient internodes of foliage to reach normal growth levels (Williams, 1967). In the case of western spruce budworm on Douglas-fir, a rule of thumb often used is that the number of years for recovery equals the

number of years of moderate to severe defoliation (Alfaro et al., 1982). Following severe defoliation, the crown may be restructured and growing conditions may have changed owing to mortality or crown thinning of surrounding trees; growth rates of survivors may, therefore, be higher or lower than pre-outbreak rates (Wickman, 1980; Alfaro and Macdonald, 1988).

As the terminal bud is often the primary site of larval feeding, height growth losses probably begin at lower insect densities than radial growth losses. The feeding of larvae on the terminal buds of the main stem can result in three effects: (1) reduction or prevention of height growth in the current year because of bud destruction, which can result in missing internodes (Van Sickle et al., 1983); (2) deformation of the main stem, which can result in trees of reduced merchantable height and reduced value (Shepherd et al., 1977); (3) dieback of one or more internodes which grew in previous years. The commercial significance of the combined effects upon height growth throughout a stand will depend upon stand age at the time of attack. If the infestation is in young stands, height loss will have a continuing impact on stand volume for the remaining growth period of the stand because shorter boles will form the basis for additional radial increments. If the infestation is in mature stands, then loss of height growth will have a negligible effect on final merchantable volume. In addition, growth capacity of a site may be underestimated

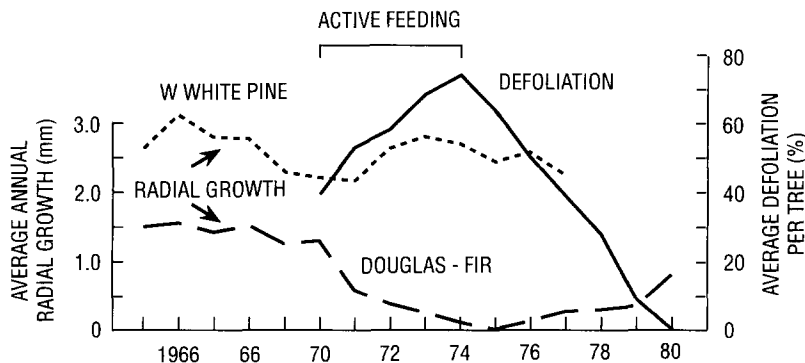


Fig. 3. Mean annual defoliation and radial growth at breast height for 64 Douglas-fir trees and one western white pine (*Pinus monticola* Dougl.) (a non-host species) before, during and after an outbreak of western spruce budworm (from Alfaro et al., 1982). Reproduced with the permission of the National Research Council of Canada.

if the height-over-age criterion is determined on trees containing undetected height losses acquired during the immature years (Van Sickle et al., 1983).

Mortality often results directly from defoliation. Where severe defoliation of Douglas-fir appeared suddenly in 1 year, as often occurs with Douglas-fir tussock moth, most mortality occurred in trees defoliated 90% or more (Silver et al., 1962; Alfaro et al., 1987; Mason and Wickman, 1988). Where defoliation by western spruce budworm accumulated over a number of years, mortality of Douglas-fir occurred only after trees had accumulated 175% or more defoliation over 5 years; mortality approached 80% in trees with a cumulative defoliation of 350% (Fig. 4) (Alfaro et al., 1982). Mortality of Douglas-fir during recurrent defoliation did not begin until after defoliation had occurred for a number of years (Fig. 5); once begun, mortality increased rapidly. Similarly, mortality of balsam fir, *Abies balsamea* (L.) Mill, attacked by eastern spruce budworm, *Choristoneura fumiferana* (Clem.), began after 4–7 years of defoliation (Blais, 1958; MacLean, 1980). Flowering balsam fir suffered greater defoliation and died sooner than non-

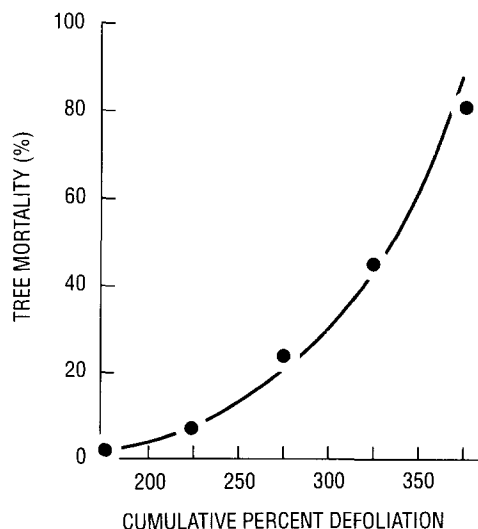


Fig. 4. Per cent mortality of Douglas-fir trees sustaining various levels of cumulative defoliation after 5 years of active defoliation by western spruce budworm (from Alfaro et al., 1982). Reproduced with the permission of the National Research Council of Canada.

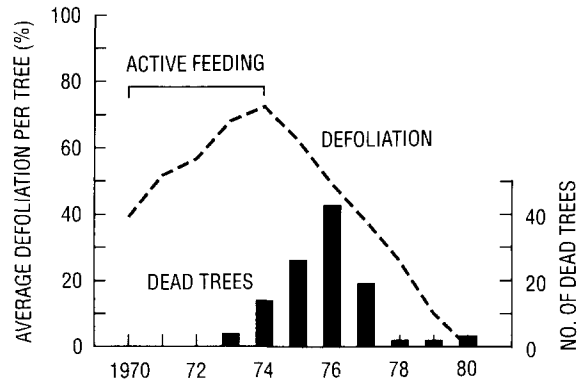


Fig. 5. Relationship between time of annual tree defoliation and mortality of Douglas-fir caused by western spruce budworm (from Alfaro et al., 1982). Reproduced with the permission of the National Research Council of Canada.

flowering trees, and there was greater mortality of trees on poor sites than of trees on good sites when defoliated to the same degree.

Defoliation may recur at different times in the life of a stand, and the accumulated losses can be significant. Alfaro et al. (1985) found that, in one 80-year-old stand that had experienced four outbreaks, 60 m³ ha⁻¹ of wood volume had been lost, 40 m³ owing to tree mortality and 20 m³ to growth reduction in the surviving trees. In addition, height growth was severely affected. In the same stand, an average of 11.4 m of height growth had been lost (Van Sickle et al., 1983).

Interactions of defoliation with other factors often can exacerbate the problem. Severe defoliation may increase susceptibility to bark beetles and lead to an outbreak which can devastate the stand (Thomas, 1958; Wickman, 1963, 1978a; Dewey et al., 1974; Shepherd, 1980). Site or growing conditions will interact with newly planted seedlings defoliated by black army cutworm, *Actebia fennica* (Tauscher), to increase mortality significantly (Maher and Shepherd, 1992). Defoliation diverts photosynthates from the roots to the shoots. This reduces the growth of roots and their ability to establish contact with soil water and nutrients, thus increasing the susceptibility of seedlings to drought. If Douglas-fir or lodgepole pine, *Pinus contorta* Dougl., seedlings are planted in a site not susceptible to drought, only a small proportion will die but,

when planted on a site which suffers from drought, mortality will increase dramatically after defoliation. Similar effects have been noted where roots are not handled properly during planting (Fig. 6). Reduction of root growth following defoliation has also been noted for tamarack, *Larix laricina* (Du Roi) K. Koch (Ives and Nairn, 1966), balsam fir, *Abies balsamea* (Redmond, 1959), white spruce, *Picea glauca* (Moench) Voss (Carlson, 1977), and Norway spruce, *Picea abies* (L.) Karst. (Långstrom and Hellqvist, 1989).

Stand structure may be affected by the preferential attack and subsequent mortality of certain crown classes of trees. Intermediate and suppressed crown classes of Douglas-fir suffered the greatest mortality when under attack by the western spruce budworm (Fig. 7) (Alfaro et al., 1982); intermediate trees also suffered the greatest defoliation during an outbreak of the green-striped forest looper, *Melanolophia imitata* (Walker) (Silver et al., 1962). In contrast, during an outbreak of western hemlock looper, *Lambdina fiscellaria lugubrosa* (Hulst), in a mature coastal forest, the larger western hemlock, *Tsuga heterophylla* (Raf.) Sarg., amabilis fir,

Abies amabilis (Dougl.) Forbes, and Sitka spruce, *Picea sitchensis* (Bong.) Carr., trees suffered a greater percentage of defoliation and subsequent mortality at all defoliation levels than smaller trees (Kinghorn, 1954). However, Evenden (1940) could find no relationship between crown class and survival or rate of recovery of ponderosa pine, *Pinus ponderosa* Laws., defoliated by pine butterfly, *Neophasia menapia* (Fielder and Felder); losses were wholly related to severity of defoliation.

Stand structure may be affected by differential effects of defoliation on different host species. In mixed stands, a consistently higher degree of damage and slower rate of recovery was experienced by grand fir, *Abies grandis* (Dougl.) Lindl., compared with Douglas-fir during an infestation of 8–10 years by western spruce budworm (Williams, 1966). However, Brubaker and Greene (1979) found that Douglas-fir tussock moth had a similar effect on radial growth of both Douglas-fir and grand fir, namely a severe, short reduction in growth followed by 3–4 years of recovery. However, Wickman (1978b, 1980) found, in some cases, that growth losses were partially recovered by enhanced growth of resid-

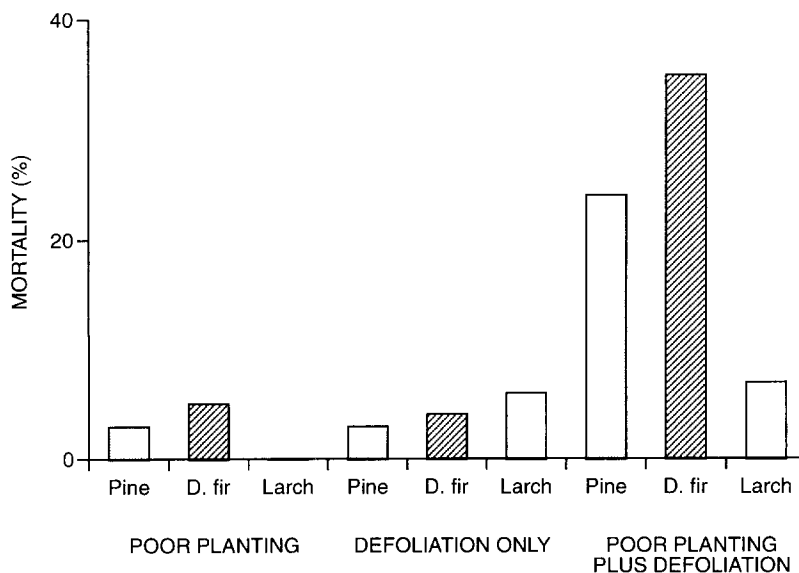


Fig. 6. Comparison of mortality by species between non-defoliated seedlings where mortality is due to poor planting only, well-planted seedlings defoliated 61% or more by black army cutworm, and poorly planted seedlings which are also defoliated 61% or more. Pine—lodgepole pine; D. fir—Douglas-fir; Larch—western larch (from Maher and Shepherd, 1992).

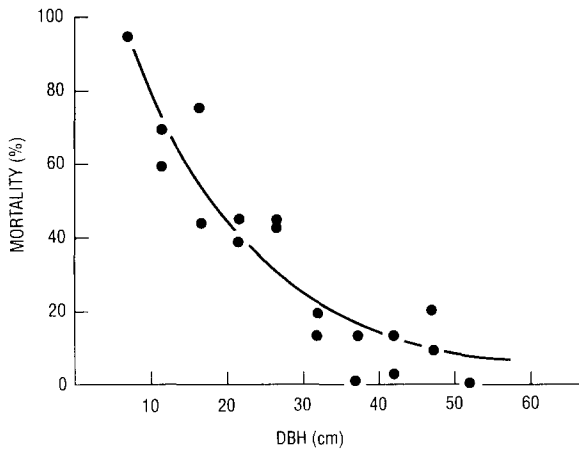


Fig. 7. Per cent mortality by 5 cm dbh classes among Douglas-fir trees in a multiple crown-layered stand defoliated by western spruce budworm (from Alfaro et al., 1982). Reproduced with the permission of the National Research Council of Canada.

ual host and non-host trees surviving within defoliated patches of trees which experienced some mortality.

The long-term effects of defoliators upon the ecosystem are not well understood. Currently, there is a strong interest in sustaining biodiversity by providing ecological reserves of sufficient size of suitable habitat to maintain all or at least most species. However, the effect of defoliation upon the insects, birds and other fauna in these habitats, as well as possible changes to the plant community, has received little study. Presumably, some species will be favoured and others will be at a disadvantage. Long-term and short-term impacts, both positive and negative, will depend upon the sensitivity of the various species to the effects of defoliation. Without that knowledge there is an inadequate basis for a decision on the need for or desirability of a treatment.

4. Control systems and their applications

The direct application of insecticides usually has an immediate effect upon the generation treated and is most useful where the population

is not expected to rebound during the following generation. Insecticides are also used in high-value stands such as seed orchards or small parks where no other choice is available, but in these cases a reinvasion from surrounding forests can be expected every generation and additional treatments of subsequent generations may be required to maintain stand values. Priorities for treatment can be based on insect density, potential damage, or impact on management objectives.

Control using an aerial application system is an efficient technique to reach rapidly millions of insects spread over a rough forest and terrain; however, many difficulties may arise which can lead to variable results. These difficulties can be attributed to many causes, but two stand out: variability in time of larval emergence and bud flush dates, and difficulties in obtaining even and adequate applications in mountainous terrain with uncertain weather conditions. For example, western spruce budworm larvae feed inside buds and are not usually accessible until after bud flush (Shepherd, 1992; Volney and Cerezke, 1992). By this time, the insects have reached the fourth to sixth instars and their susceptibility to biological diseases has decreased. In the case of viruses, there may not be sufficient time left between bud flush and the cessation of feeding to obtain good multiplication and spread of the pathogen. Also, because viruses are slow acting, feeding may not be inhibited until the larvae are close to pupation, and thus little foliage protection is obtained. Bud phenology varies considerably from tree to tree and from site to site; coordinating aerial applications with bud break over a large area is difficult, if not impossible. June, the month of most aerial applications in British Columbia, is also a month in which cold air masses often pass through with their accompanying unstable weather conditions. Unpredictable winds and changeable fallout rates result in the loss of finer droplets from the spray deposit, resulting in inadequate and irregular insecticide distributions. In addition, the direct application of insecticides is becoming less acceptable to the public, who perceive aerial spraying as being more intrusive than many other methods. All of these

factors often result in compromises in spray operations and lead to less than satisfactory results.

The most desirable treatment has carry-over effects which reduce and maintain the population below tolerable damage levels for a number of generations. The nuclear polyhedrosis virus (NPV) treatment of Douglas-fir tussock moth is a good example where the population is reduced dramatically by the virus and remains at low levels throughout the remainder of that outbreak cycle (Shepherd et al., 1984b).

The use of pheromones in broadcast applications is a new control technology with promise. They block mating, and the oviposition of viable egg masses is reduced dramatically. These materials are highly specific and have little other environmental impact, but long-term effects and interactions with parasites and predators are, as yet, unknown. The disadvantage is that pheromones must be used one generation ahead of other materials to prevent damage.

The reduction of susceptibility of the forest to defoliator attack is a long-term objective in which cultural or silvicultural methods may be used to change the host species or provenances, manipulate stand structure, vary the time of planting, or increase host resistance through selection and breeding programmes. These methods can potentially reduce the rates of increase of the pests and thus decrease the probability of their reaching damaging levels. Susceptibility, in this sense, reflects a sum of habitat factors which regulate the probability of a net increase of the local population. However, a second component of susceptibility concerns the chance of an infestation occurring through immigration from other stands. In this case, the proximity of other outbreaks, the continuity of host type, the direction and strength of winds, and the air temperature during moth flight are some of the factors to consider.

Management systems which reduce susceptibility to attack have the potential to realize long-term effects in inhibiting population increases. These techniques are in their infancy and in many cases have yet to be proven; however, the potential pay-off is so high that they should be seriously considered when selecting future research

programmes. These methods include increasing the diversity of age classes and species composition, changing stand structure by using different harvesting techniques, and selecting trees which are biochemically resistant or phenologically asynchronous with the pest. The recent advances in bioengineering technology make tree resistance systems more appealing. However, from a research point of view, these cultural techniques will be difficult to field test with highly mobile populations such as western spruce budworm. Effects on small plots are masked by the dispersing insects, which overwhelm differences created by treatments (Hodgkinson et al., 1979; Alfaro and Wegwitz, 1988).

Silvicultural techniques for control by reducing susceptibility are usually viewed with great favour because they can be combined with other forest management practices. There are, however, few success stories using these techniques because other habitat and climatic influences often override differences caused by stand manipulations. Carlson et al. (1985) proposed silvicultural treatments for the northern Rocky Mountains of USA to reduce damage by western spruce budworm. The most effective recommendation was probably the conversion of the stands to seral species such as ponderosa pine and western larch (*Larix occidentalis* Nutt.) from the climax species grand fir and alpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Carlson et al. also recommended reducing uneven-aged multilayer stands to single crown levels, early harvesting of mature trees to reduce overall stand age and thereby increasing tree vigour, and varying the host type to break up the continuity of susceptible stands. In British Columbia there are fewer options available in the budworm-susceptible forests because Douglas-fir dominates most seral stages and fewer alternative species are available. Current forest management practices favour multilayer tree management through selective harvesting systems which may increase susceptibility to budworm damage. Silviculture treatments would need to be applied over large areas to avoid immigration of the pest. Benefits from such treatments are difficult to document.

If insects cannot be controlled in time to pre-

vent damage, then consideration should be given to increasing the vigour of the trees and improving recovery rates of damaged trees. In the case of early attacking insects, selection could be made for trees which respond to attack with increased latent bud production. This would decrease vulnerability to significant damage or mortality through the outbreak period and accelerate recovery after the outbreak subsides. However, insects such as western spruce budworm with sustained outbreaks may have a positive response to spacing or fertilization, and the resulting increased foliage production may lead to higher pest densities or prolonged outbreaks (Shaw and Little, 1972; Roberts and Chow, 1977). These types of interactions probably vary with the pest, the site, and the habitat. Only through careful experimentation can we determine where and when such systems could be useful.

The use of parasites and predators as control mechanisms is another system with potentially large benefits for a low initial investment. Successes have been limited largely to non-native pests which have been introduced accidentally, and established in our forests. Once parasitoids are established, pest populations may be reduced to low densities and maintained below damage thresholds without repeated releases. Parasites may complement other control systems to increase total effectiveness; for instance, when the insecticide diflubenzuron was used instead of the conventional organophosphorus or organochlorine compounds to suppress the pine looper, *Bupalus piniaria* L., parasitism of surviving larvae was increased significantly because adult parasites present at the time of application were not affected by the chemical (Barbour, 1988). Similarly, when applications of *Bacillus thuringiensis* Berliner are delayed from third to fourth instar spruce budworm, parasitism can be expected to increase (Nealis and van Frankenhuyzen, 1990). Synergistic combinations of different systems such as this should be sought and tested before outbreaks occur.

Different control systems may be required for each pest species. Each technique will have advantages and disadvantages and will probably have different degrees of success. If a variety of

techniques are available, pest management objectives are more likely to be reached in concert with other forest management programmes.

5. Outbreak dynamics of pest populations

It is useful, conceptually, to divide the more common defoliating species of insects into two types based on the characteristics of their outbreak dynamics: fast cycling and sustained. Characteristically, the fast-cycling defoliators appear suddenly in noticeable numbers, cause significant damage, and then rapidly drop to low densities, usually all within 1–4 years. Impact on the stand is related more to intensity of defoliation than to duration. Many species have recurrent outbreaks within specific habitats and a few may be periodic. The reason(s) for the sudden collapse of these fast-cycling populations is unknown for all species except the Douglas-fir tussock moth, in which case a nuclear polyhedrosis virus is often responsible. The roles of climate and virus in the dynamics of this insect have been described by Shepherd et al. (1988a,b), and a synthesis of the overall dynamics has been given by Mason and Wickman (1988).

In addition to Douglas-fir tussock moth, fast-cycling defoliators include: western blackheaded budworm, *Acleris gloverana* (Walshm.); black army cutworm, *Actebia fennica* (Tauscher); western hemlock looper; false hemlock looper, *Nepytia freemani* Monroe; greenstriped forest looper; saddleback looper, *Ectropis crepuscularia* (Denis and Schiffermuller). Tree mortality is commonly associated with outbreaks of all these species except blackheaded budworm.

Operationally, fast-cycling species are difficult to predict. They appear suddenly and there is little lead time available to plan a control programme. The explosive increase of populations often results in high densities of insects which cause the greatest damage during the first year of an outbreak at any one location (Fig. 8) (Wickman, 1978; Alfaro et al., 1987). Defoliation can be severe, resulting in significant mortality. In a sample of 61 stands sampled during and after a Douglas-fir tussock moth outbreak on Douglas-

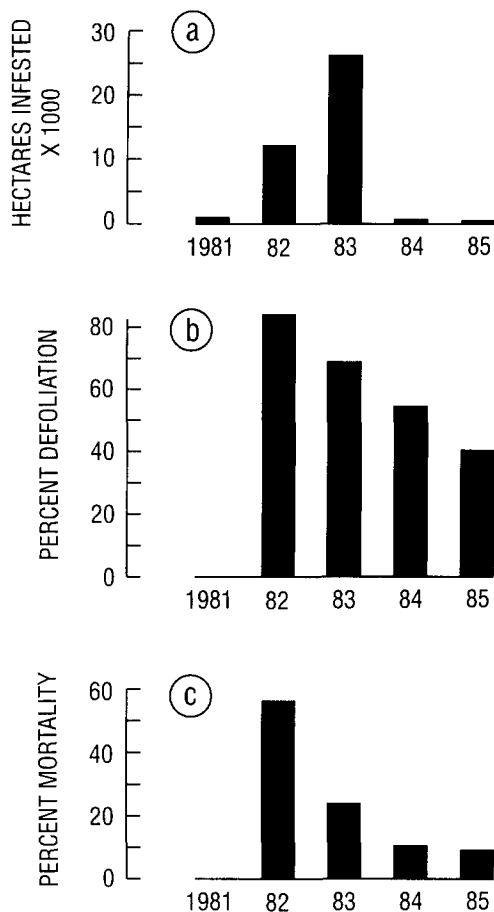


Fig. 8. Area infested (a), average per cent defoliation (b), and per cent of total tree mortality (c), by year, in a Douglas-fir tussock moth infestation (from Alfaro et al., 1987). Reproduced with the permission of the Canadian Institute of Forestry.

fir in 1982–1985, 51% of the trees were killed and 11% of the survivors had top kill (Alfaro et al., 1987). Only minor increases in mortality and top kill occurred through cumulative defoliation after the first year; defoliation intensity was more important than duration. Ninety-nine per cent of the mortality occurred in trees defoliated 90% or more. An almost identical association between defoliation intensity and mortality had been reported by Wickman (1978) for defoliation by the same insect on Douglas-fir in Oregon a decade earlier. Damage of this intensity can cause major changes in the ecosystem by conversion of the species composition to successional stages ahead

of or behind the current stage and by changing the stand structure. For instance, Kinghorn (1954) found that the contiguous single-layered crowns of an old-growth forest were broken up owing to defoliation and mortality caused by the hemlock looper. This resulted in a complete change of shrubbery and regeneration at ground level.

Most of the fast-cycling insects overwinter as eggs and hatch to feed on the flushed foliage. The current shoots along with the newly developing buds are usually killed. As new foliage disappears, feeding transfers to the older foliage, and defoliation is complete by July, at which time shoot growth and bud initiation for the year are complete; therefore, the trees cannot initiate new buds to replace foliage in the next spring and mortality is common in the first year of an outbreak. For survivors, ring growth effects appear in the following year (Wickman et al., 1980; Alfaro and Macdonald, 1988).

The severity of defoliation in the first year dictates that treatments should take place in the year before defoliation appears. In the past, we have detected and mapped defoliation at the end of the first year's feeding and planned treatments for the second year. We now know this is too late and emphasis must be placed upon early detection of upwelling populations. Pheromone monitoring systems are ideally suited for this purpose.

Fast-cycling insects appear to be habitat sensitive, i.e. even though the species may be found over a wide range of hosts and locations, outbreaks develop only where specific habitats prevail. By taking advantage of this characteristic, monitoring can be concentrated in susceptible habitats which are recognizable on the ground and can be mapped. In mountainous situations, distinct habitats with narrow ecotones are common. In flat or rolling country, where habitat changes appear as gradients, the concept is less useful.

In British Columbia, an ecological classification of habitats into Biogeoclimatic (BGC) zones and subzones has been developed (Krajina, 1965) and mapped. Climate, soils and vegetation in stands have been described and organized into a classification system with the zones

and subzones recognizable by the plant communities present. Temperature and moisture regimes are important limitations for the distribution of the subzones in the mountains. Outbreaks of the Douglas-fir tussock moth, black army cutworm and blackheaded budworm have been closely associated with specific BGC zones (Shepherd, 1977; Shepherd et al., 1988b, 1992). Monitoring systems have been developed for the first two species (Shepherd et al., 1985, 1992), and one is being developed for the third species. This emphasizes the need to relate population outbreak dynamics of the fast-cycling species with habitats to provide a valuable management tool.

In contrast to fast-cycling insects, populations of sustained defoliators do not follow a regular or predictable pattern. Numbers can remain at high density levels for many years and then drop to low levels for a few years only to rise again (Fig. 9). Rates of increase of sustained species are generally less than those of fast-cycling insects, resulting in a slower population build-up

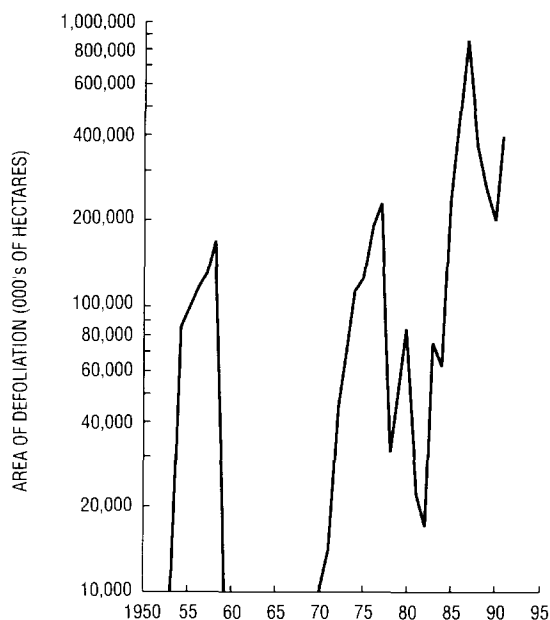


Fig. 9. Annual area of Douglas-fir forest with light to severe defoliation caused by the western spruce budworm in the Vancouver and Kamloops Forest Regions of British Columbia (data from annual reports, Forestry Canada, Forest Insect and Disease Conditions in Canada).

over time. The high mobility of these species in both the larval and adult stages tends to smooth out spatial differences; however, immigration of large numbers of insects can occasionally result in sudden increases in density. These insects are generally less habitat sensitive than the fast-cycling species and appear opportunistic: they are able to move into areas which may have a favourable climate only on a transitory basis. Severe damage appears only after a number of years of defoliation, and impact is more closely related to duration than intensity of defoliation. The sustained types of defoliators are typified by the various species of spruce budworms, *Choristoneura* spp., such as the western spruce budworm, the 2-year cycle budworm, *C. biennis* Freeman, and *C. orae* Freeman. All have caused significant defoliation for many years over extensive forests.

During the 43 year period from 1949 to 1991, defoliation by the western spruce budworm in British Columbia occurred in 28 of the 43 years somewhere in the Douglas-fir forests of the Vancouver and Kamloops Forest Regions (Forest Insect and Disease Survey of Canada, 1949–1991) (Fig. 9). Increases in extent of defoliation occurred in 20 of the 28 years with an average rate of increase of 2.6. Decreases in extent of defoliation occurred in only 8 years, with an average decrease of infested areas of 1/8.6. The rates of decline in defoliated areas are more dramatic than the rates of increase. This indicates that, during most years, the climate is probably favourable for modest increases in the area defoliated, which is surprisingly consistent from year to year. Occasionally, an unfavourable year occurs and the population collapses. The population trend depends upon the sequence of favourable and unfavourable years. Major collapses occurred in generations which would have caused defoliation in 1959, 1978, 1981 and 1988; minor decreases occurred in the generations leading to defoliation in 1982, 1984, 1989 and 1990. As only two of these eight recorded decreases were included in the previous weather analysis (Thomson et al., 1984), a re-analysis of trends by regions could be useful.

Budworm larvae, upon hatching from eggs in late summer and again after emerging from ov-

erwintering, spin off the foliage on silk threads and are dispersed by wind throughout the stand. Larvae continue to crawl and spin until they find an unoccupied bud or are lost. Only one larva becomes established in a bud (McDonald, 1985), which, together with the high dispersal capacity, provides an ideal strategy to ensure that the maximum number of larvae find feeding niches without overloading the carrying capacity of the host.

Detailed studies of field populations have shown that larvae which emerge from overwintering before the buds swell cannot penetrate the buds and are forced to disperse and mine old needles with accompanying high losses (Shepherd, 1992). Larvae which emerge as the buds begin to swell can penetrate the buds and spend most of their feeding period within a warm, protected niche with abundant ideal food. After bud flush, they spend a relatively short period of time until pupation in exposed shoots where the risk of mortality is great; overall survival of this cohort of budworm is high (Fig. 10). Larvae which emerge from overwintering at a time close to bud flush spend relatively more of their feeding and development time in the open shoots exposed to high mortality, and survival to pupation is poor. Therefore, there is a narrow 'window of maximum survival' available where bud and insect development are synchronized to allow for high larval survival (Shepherd, 1992). R.K. Lawrence (personal communication, 1992) independently found a similar relationship with populations of *C. fumiferana* caged onto trees with different degrees of synchronization, and termed the most favoured period a 'window of opportunity'. The budworm has a wide emergence period, which in most years ensures a reasonable degree of synchronization for part of the population, but occasionally the weather pattern may be unusual enough to result in asynchrony between bud development and larval emergence, resulting in an abrupt drop in population survival.

The spatial and temporal dynamics of the populations in mountainous situations is not completely understood but observations have indicated that defoliation by western spruce

budworm in the coastal mountains often appears as a midslope elevational band presumably where the window of maximum survival has occurred. Each spring, the weather varies and the defoliated band may be of different widths and appear at different elevations. This implies that, although many stands become infested through dispersal of moths and larvae, defoliation becomes prevalent only in those where the climate is suitable for good larval survival.

The defoliation bands vary in location each year but, over the years, occur more frequently at specific elevations; this indicates that certain stands, because of their location, are more susceptible to outbreaks than others. This means that, under this scenario, location, relative to spring thermal layering, is of prime importance in determining climatic susceptibility. Thus, the distribution of outbreaks does not appear to be directly related to the dispersal pattern of the insect, the location of specific ecological habitats, or the vigour or vulnerability of the trees. Instead, it appears to be related to the frequency of occurrence of the window of maximum survival. Elevational temperature belts have been related to outbreaks of other forest insects (Stark, 1958, 1959; Shepherd, 1977; Baltensweiler, 1984) and the foundations for the theory on climatic susceptibility have been explained in detail by Andrewartha and Birch (1954) and Wellington (1965).

Populations often build over time and cause repeated defoliation of the same trees over many years. Mortality begins after a number of years of defoliation and continues after insect density has returned to endemic levels (Fig. 5). In contrast to the fast-cycling defoliators, intensity of defoliation by the sustained types of defoliators is less important than the duration of the outbreak, i.e. the number of years the trees have sustained moderate to severe defoliation. When mortality does occur, it is primarily within the intermediate and suppressed crown classes (Figs. 2 and 7) (Alfaro et al., 1982). This is not of concern if clearcut harvesting is utilized, but where selective or shelterwood systems are required to promote survival of regeneration the loss of the understorey can be critical.

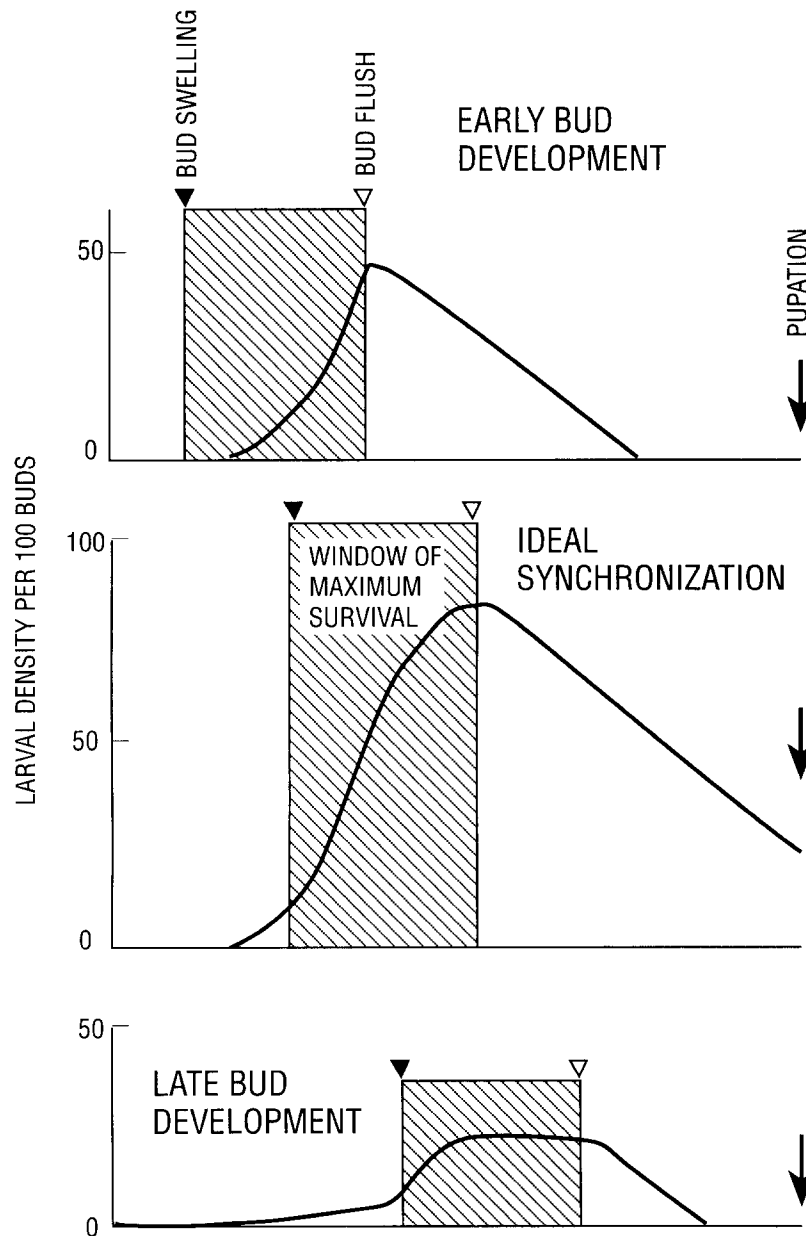


Fig. 10. Insect density of western spruce budworm from spring emergence to pupation as related to the synchronization between larval emergence and bud development (schematic; modified from Shepherd (1992)).

Other classifications of outbreak trends have been proposed. McNamee et al. (1981) described four classes of defoliating insects based essentially on theoretical considerations of processes which may affect populations. Similarly, Berryman et al. (1987) described three theoret-

ical patterns of population behaviour which could be expected depending on the role density-dependent or density-independent factors and negative or positive feedback processes could play at different times and in different environments. The population patterns described in this

paper are based on empirical field observations, and, in the case of the Douglas-fir tussock moth and western spruce budworm, the biological and climatic reasons for their specific patterns were subsequently investigated. The latter have been explained more fully by Shepherd (1977, 1985, 1992) and Shepherd et al. (1988a).

6. Selection of appropriate strategies

The objectives of a pest management programme must be clearly stated at the outset and related to the forest management objectives. The type of programme chosen will depend, in part, upon the costs, timing, and effectiveness of the programme and, in particular, the outbreak characteristics of the insect and the response of the populations to the treatment. A summary of the strategic steps for managing fast-cycling and sustained populations is given in Table 1.

An ideal strategy to avoid damage by fast-cycling insects is through changes in timing of forest management actions, as has been recommended for the black army cutworm in new plantations (Shepherd et al., 1992). Where this is not feasible, preventive actions should be initiated in areas of high populations the year before severe defoliation is expected, preferably with a biological insecticide or mating disruptant (Shepherd and Otvos, 1986).

Managing fast-cycling insects to prevent intolerable damage requires that an early detection system, such as a pheromone-trap monitoring and surveillance system, be in place for tracking endemic populations and signalling significant rises in densities (Shepherd et al., 1984a, 1985; Mason and Wickman, 1988). As densities approach damaging levels, other less variable survey techniques will be necessary to predict the degree of defoliation. The determination of potential outbreak zones is extremely useful to restrict the area requiring monitoring. Historical records, habitat, climatic or forest type mapping may be useful for this purpose (Shepherd and Otvos, 1986; Bejer, 1988; Shepherd et al., 1992). This strategy is now used operationally against Douglas-fir tussock moth in British Columbia

and has been recommended for nun moth management in Europe (Bejer, 1988). If populations rise to outbreak levels undetected, choices are reduced and a fast-acting insecticide may be needed to reduce populations before they cause significant damage. After the density of a fast-cycling insect is reduced through treatment, it is unlikely to rebound to damaging densities within the same cycle. This has been shown to be the case after virus treatment of Douglas-fir tussock moth (Shepherd et al., 1984b) but it needs to be checked for other species.

In sustained populations, tree mortality is not usually a severe problem and there is little threat to the ecosystem as the upper crown structure and species combinations do not change. Growth losses in a sustained insect outbreak can be severe but rarely justify the repeated treatments that would be necessary to maintain growth for the period of the outbreak. Selected high-value stands might be protected, but again they would probably have to be treated for several years because of reinvasion.

The outbreaks of sustained defoliators are often large in size, and high larval mortality is difficult to obtain consistently through aerial spraying. Alternative strategies of management should, therefore, be assessed which entail methods other than the direct application of insecticides or disruptants which provide benefits for only 1 year. Opportunities should be explored which create long-term changes in the susceptibility or vulnerability of the forest. Stands within areas of high climatic susceptibility which incur repeated defoliation could be identified and management systems employed to reduce population increases and related damage within the susceptible stands. Overlay mapping of annual defoliation patterns can provide an estimate of outbreak frequency for stands within different elevational climatic zones (Fig. 11). An extension of this climatic susceptibility theory is that the stands with high outbreak frequency may also act as epicentres and produce dispersing gravid females which spread to other stands with less favourable climates (Fig. 12). If so, a change of the highly susceptible stands to reduce insect rates of increase and/or survival would be even

Table 1
Strategic steps for managing forest insect defoliators

Required activity	Fast-cycling outbreaks	Sustained outbreaks
<i>Pre-outbreak plan</i>		
Habitat specificity	Determine habitat specificity of outbreaks and define susceptibility of stands	Map historically defoliated areas on climatic, ecological, or stand maps; define susceptibility of stands by frequency of defoliation
Determine objectives	Specify forest management objectives of susceptible stands; where damage is intolerable, reduce population densities below acceptable thresholds before significant damage occurs	Specify forest management objectives of susceptible stands; where warranted, reduce stand susceptibility of vulnerability in areas of high outbreak frequency; in high-value areas where significant foliage loss is not tolerable, treat annually
Monitoring requirements	Develop highly sensitive pheromone traps and place in all susceptible habitats to detect upwelling populations before damage occurs	Highly sensitive pheromone traps are used in high-value stands with low tolerance to defoliation; map all attacked stands by severity of defoliation
Predict damage	Develop sampling system for population density; determine predictive relationship between population density and damage levels	Develop sampling system for insect population density; determine damage levels as related to length and intensity of outbreaks
<i>Outbreak plan</i>		
Suggested courses of action	Avoid the problem through cultural techniques or, if necessary, treat with insecticide to reduce population density before damage occurs; when available, use specific low-intrusive materials such as virus, B.t. or pheromone	Develop or select trees of low insect survival or prolificacy and plant in areas of high outbreak frequency; where defoliation is not tolerable, treat with insecticide; when available, use specific low-intrusive materials such as virus, B.t. or pheromone

more important for the long-term reduction of damage by these insects.

The development of a technique capable of reducing population build-up is important to the management of the sustained populations. However, screening of hosts which support free-feeding defoliators has not yet found consistent evidence of a genetically based resistance, even though differences in compatibility with other insects, such as aphids, have shown distinct differences. Budworms appear able to detoxify monoterpenes, and there appeared to be little difference in survival of eastern spruce budworm when fed different provenances of white spruce (Mattson et al., 1988). McDonald (1985) obtained similar results with western spruce budworm on Douglas-fir, and again, Connor et al. (1982) reported no significant differences in susceptibility of 25 seed sources of white spruce

to yellow-headed spruce sawfly, *Pikonema alas-kensis* (Rohwer). However, the search needs to continue to find biologically active materials which occur or are induced in specific individuals and can be selected for or incorporated in planting stocks.

The outbreak areas of western spruce budworm in British Columbia are essentially monocultures of Douglas-fir where there is little opportunity to change to other species. At low elevations ponderosa pine may be planted and at higher elevations lodgepole pine may be useful. Observations over a great range of sites indicated little relationship between stand structure and damage levels, as in the *Abies-Picea* forests of the northern US Rocky Mountains. Therefore, silviculture treatments such as spacing and reduction of crown layers will probably have little significant effect on the susceptibility or vul-

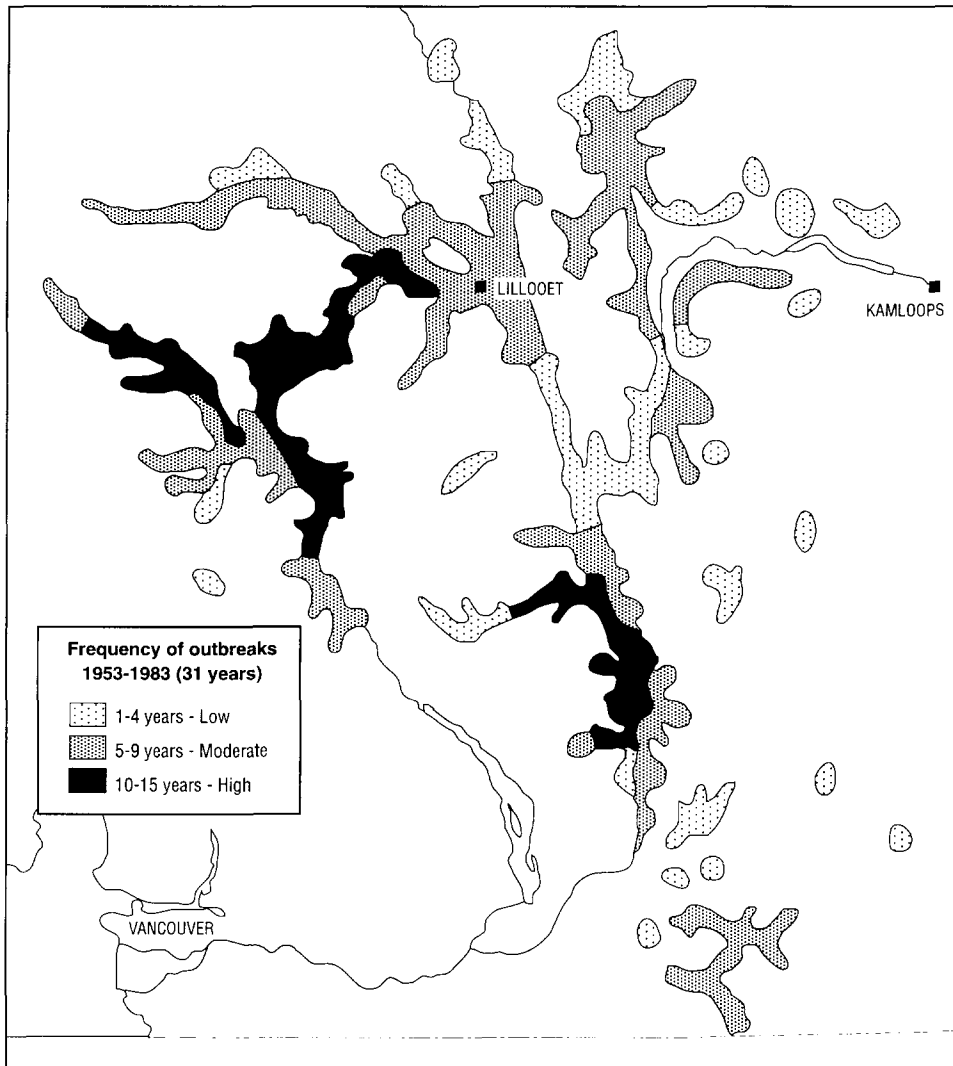


Fig. 11. Areas of British Columbia with different frequencies of outbreak of the western spruce budworm during the 31 year period 1953–1983 (from G.A. van Sickle, personal communication).

nerability of these stands to spruce budworm attack.

A promising technique for budworm management may be the selection of provenances of Douglas-fir trees with asynchronous phenology. Early flushing or late-flushing provenances could be planted in the areas of climatic susceptibility, which will decrease the rate of build-up of populations in these stands. Small changes in the synchronization between flush and emergence dates may be sufficient to shift the ratio of fa-

vourable years from 20/28 to less than 14/28 and this, in turn, may reduce defoliation to tolerable levels.

The selection of provenances for asynchronous bud flush would probably be more successful than breeding for this characteristic (Blum, 1988) as Douglas-fir already has a variation of about 42 days in date of flush between individuals (Griffith, 1968), which consistently remain in the same relative order of flush from year to year. The mixing of the highly mobile budworm

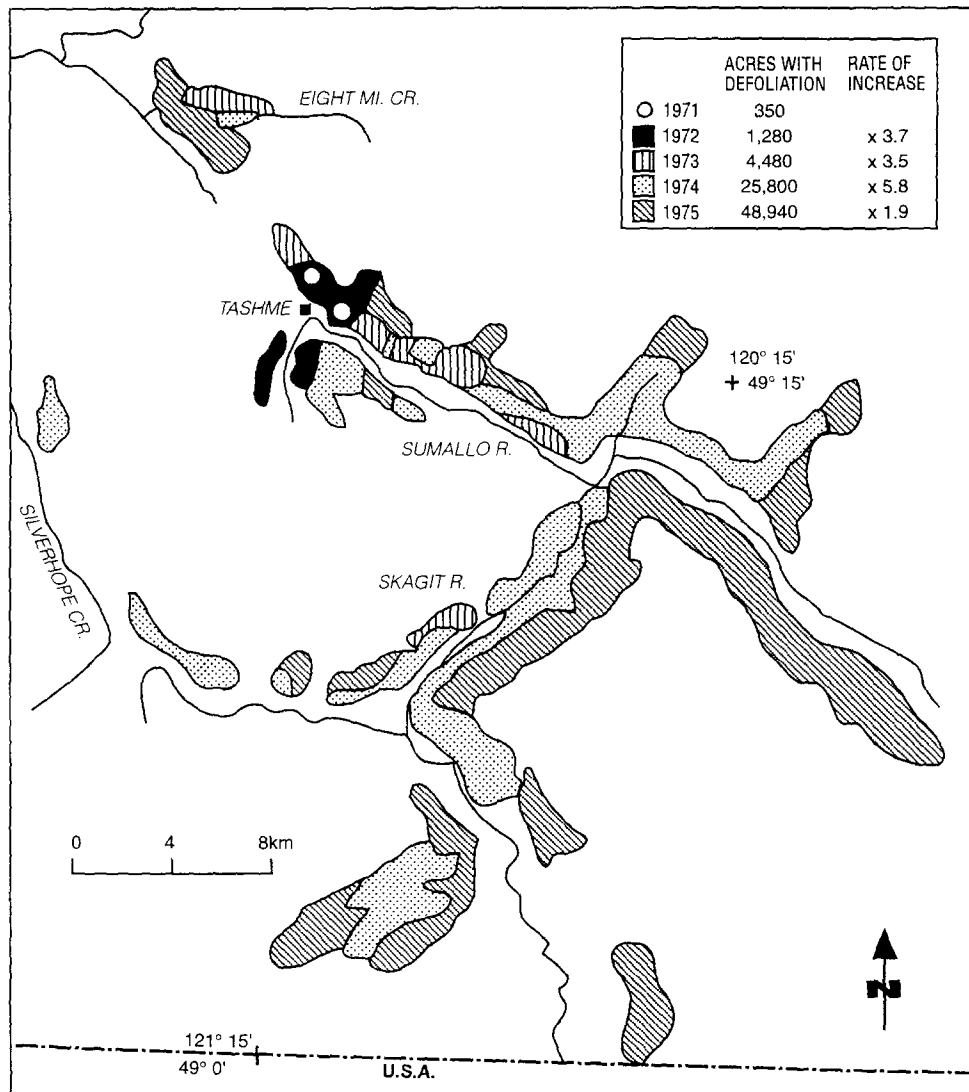


Fig. 12. Map of spread in an outbreak of western spruce budworm in a typical mountainous area between 1971 and 1975 (from Shepherd, 1977).

populations from adjacent non-treated stands with those surviving on the selected provenances should prevent genetic selection of an early flushing or late-emerging cohort of budworm. Bejer (1988) also noted that synchronization between emerging larvae and flush dates of Norway spruce were important for survival of nun moth, and suggested that the planting of late-

flushing Norway spruce could be useful in reducing outbreaks. One difficulty with this approach could be the assessment of selected trees in the field because the mobility of the insect results in all trees being reinfested repeatedly and inter-tree differences becoming obliterated. Plantations would have to be large to buffer against this effect.

7. Examples of the strategic steps for managing defoliating pests

The steps necessary to manage defoliators are outlined in Table 1. Two examples of fast-cycling insects follow which entail different problems.

7.1. Douglas-fir tussock moth

Defoliation by this pest occurs in the hottest and driest portion of the range of Douglas-fir, occurring in discrete spots of defoliation which enlarge during the second and third year of an outbreak. Outbreaks are cyclic, occurring every 8–14 years somewhere within the susceptible forest. The area of defoliation increases for 2–4 years as new spots appear before the outbreak collapses and the caterpillars disappear. A naturally occurring virus is the usual cause of the collapse. Damage is severe the first year defoliation appears in any stand; mortality and dieback are common. Details have been given by Shepherd and Otvos (1986) and Mason and Wickman (1988).

Pre-outbreak plan

(1) Identify the susceptible stands which have a significant component of Douglas-fir and which occur within the susceptible habitat, which is the PPBGa and -b and IDFa and -c biogeoclimatic zones.

(2) Determine the forest management objectives for these stands and define levels of acceptable damage. Derive from these damage levels the related insect density thresholds. Where unacceptable damage is expected, the objective of the pest management action should be to reduce insect densities before acceptable thresholds are exceeded, i.e. to prevent the outbreak.

(3) Select representative permanent monitoring sites in each watershed or at least at intervals of 40–50 km and deploy standardized highly sensitive pheromone monitoring traps at the same locations each year to obtain population trends and detect upwelling populations.

(4) When populations at permanent monitoring sites have increased for 3 years and reached

moth trap densities of 8–10, an outbreak may be 2 years away and future outbreak spots must be located. This can be aided by deploying in the subsequent year auxiliary traps every kilometre along all access roads throughout the area. Where trap moth density has reached 25 or more, nearby stands should be ground surveyed and the foliage scanned for egg masses. When a population centre is found, a lower-branch sequential egg-mass survey can be conducted to determine subsequent larval density and predict tree damage. Map all areas of predicted unacceptable defoliation.

Outbreak plan

The most acceptable treatment of threatening populations is the application of NPV virus via aerial or ground sprays. This is a naturally occurring pathogen which normally infects this pest and causes outbreaks to collapse. However, the collapse usually occurs after 2 or 3 years of defoliation when the damage has already occurred. To prevent damage, the virus must be applied the year before defoliation occurs, i.e. the virus epizootic is moved forward in time to reduce populations effectively before defoliation occurs rather than afterwards. Early detection and timing is critical for the use of the virus. After application, the caterpillars continue to feed for a number of weeks before the virus develops sufficiently to kill them. During this incubation period defoliation will occur, but not to a level where mortality or dieback will occur. If, however, populations were not detected and defoliation is present from the previous year, or insect densities have increased to high levels or Douglas-fir bark beetles are in the stand, significant tree damage can occur. In this case, a fast-acting insecticide will be required to prevent damage. Another viable option is to harvest the stand and burn the branches before egg hatch in the spring.

7.2. Black army cutworm

This insect is a pest of seedlings planted in areas burned by slash or wild fires. It is adapted to a mobile survival strategy and occupies a site in large numbers for only 1 year. Moths disperse

into a site in July and August and lay eggs. Larvae appear early next spring as seedlings are being planted and consume most green vegetation resprouting on the burned site, including the foliage of the seedlings. Insect densities are high but occur only during one growth season.

Interactions with site are important. Defoliated seedlings redirect their remaining photosynthetic resources into the formation of new buds for the following year rather than establishing new rootlets. If soil moisture remains adequate, the defoliated seedlings can probably survive on the basis of their current roots, but, if the site dries in summer and the seedlings have been unable to send new rootlets into the surrounding soil to make contact with the soil moisture and nutrients, mortality may be high. If seedlings have established a root system through a year's growth before defoliation occurs the seedlings usually survive and can regrow their crowns. Outbreaks appear suddenly in interior spruce and cedar hemlock sites the year after a moth flight into sites which have been burned within the previous 12 months. Details have been given by Shepherd et al. (1992).

Pre-outbreak plan

(1) Each year before 1 July, identify susceptible habitats which occur in the ESSF, SBS, MS and ICH biogeoclimatic zones, are prone to drought, and were burned within the last 12 months.

(2) Determine the forest management objectives for these sites and the requirements for maintaining stocking levels of seedlings. Where mortality of seedlings is unacceptable, the objective should be to avoid losses by shifting planting dates of seedlings in infested sites away from the period of that year in which the cutworm feeds. Feeding will be negligible in subsequent years.

(3) Deploy pheromone traps in susceptible sites for the moth flight period (1 July–15 September) and determine the total catch for that period.

(4) If 1200 or more moths are caught during the moth flight season, serious damage can be expected if seedlings are planted on this site the following spring. If fewer than 350 moths are

caught, significant damage is unlikely and planting should proceed. If the number of moths caught is between 350 and 1200, larval populations the next spring will be variable and further checking will be required. In the spring, shortly after snow melt, preferred plant species growing on the proposed planting site should be inspected for feeding damage. If no damage is found, repeat the examination a week later. If there is evidence of feeding on either occasion, then planting on that site should be avoided until the cutworm has completed its feeding.

Outbreak plan

Time constraints usually make it difficult to protect newly planted seedlings in remote areas with insecticide. It is usually more practical and less costly to adjust planting schedules to avoid the problem.

Where a fire occurs after the moth flight (i.e. after mid-September), every effort should be made to plant the site in the following year. An invasion by moths cannot occur until the following summer and damage by larvae would be two springs after the time of the burn. Even if seedlings are defoliated, they will have had a year to establish a root system and most will recover. This timing sequence results in little impact by cutworm on final stocking densities.

Where outbreaks occur on good growing sites that are not prone to drought, planting should proceed normally. However, special care should be taken to place the roots properly, as inhibition of root growth because of poor planting will also lead to mortality of defoliated seedlings. If well-planted seedlings on moist sites are defoliated, they generally survive, set new buds, and regain their growth rates in the next year.

On sites that will dry out if a summer drought occurs, seedlings are most vulnerable. If more than 60% of the foliage is lost or if terminal buds are killed, significant mortality and height growth loss will occur. If site conditions and seedling availability permit, it is best to delay planting in infested areas on dry sites. Damage will be minimal if planting can be delayed until the middle of June at low elevations or later at higher elevations. If planting cannot be delayed for a few

weeks, then postponement for a year should be considered. Immediate planting would result in significant damage and growth rates would remain depressed for several years. Again, it is important to maintain high planting quality.

If feeding on newly planted seedlings does occur unexpectedly on a dry site, areas of severe feeding should be delineated and assessed after bud flush the following year. Dead seedlings, seedlings defoliated more than 60%, and seedlings with dead terminals should be replaced. Surveys of sites where replanting may be necessary or sites where planting has been postponed will provide the information necessary to organize planting stock reallocations and to estimate future sowing requirements.

In this paper, I have attempted to keep the discussion as simple as possible by describing only two types of outbreaks. Other species may follow different patterns of population fluctuations, and it is important to select strategies which work best within the dynamics of each particular insect and forest environment.

Acknowledgements

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