Chapter 6

Direct Control: Theory and Practice

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Abstract

Direct control programs intended to minimize the impacts of epidemic mountain pine beetle (*Dendroctonus ponderosae* Hopk. [Coleoptera: Scolytidae]) populations began 100 years ago. Since then, many tactics have been developed that are capable of introducing significant mortality into a beetle population. These tactics include cultural and mechanical treatments, chemical insecticides and semiochemical manipulation of populations. This chapter reviews the suite of operational tactics that have been, and are currently, used to control mountain pine beetle populations. Based upon simple population processes, a framework for successful control is also presented. This framework is considered within the larger context of control programs over large landscapes where multiple objectives may be desired. Finally, previous attempts at mitigating mountain pine beetle impacts are assessed in relation to the direct control framework. A successful direct control program requires prompt and thorough application of the most appropriate treatments at a magnitude dictated by the population size and rate of increase.

Résumé

Les programmes de lutte directe destinés à atténuer les effets des épidémies de dendroctones du pin ponderosa (*Dendroctonus ponderosae* Hopk. [Coleoptera: Scolytidae]) ont débuté il y a cent ans. Depuis, on a mis au point de nombreuses tactiques permettant de décimer les populations de ce ravageur. Ces moyens comprennent des traitements mécaniques et culturaux, l'application d'insecticides chimiques et la manipulation des populations à l'aide de substances sémiochimiques. Le présent chapitre examine la série de tactiques opérationnelles qui ont été utilisées et celles auxquelles on a recours à l'heure actuelle pour lutter contre le dendroctone du pin ponderosa. On y présente également un cadre de lutte efficace fondé sur des processus démographiques simples. Puis ce cadre est pris en considération dans le contexte plus vaste des programmes de lutte à l'échelle des grands paysages pouvant comporter plusieurs objectifs. Enfin, on y évalue les interventions passées destinées à réduire l'impact du ravageur en relation avec le cadre de lutte directe. Le succès d'un programme de lutte directe repose sur l'application rapide et rigoureuse des traitements les plus appropriés dans une proportion qui dépend de la taille et de la rapidité de croissance de la population de ravageurs.

Introduction

Mountain pine beetle (*Dendroctonus ponderosae* Hopk. [Coleoptera: Scolytidae]) outbreaks are periodic landscape-level disturbance events that occur in pine forests of western North America. Typically, they last from 3 to 20 years and invariably result in the destruction of large-diameter trees within affected stands (Safranyik et al. 1974). The potential for outbreaks to negatively affect timber supplies was recognized nearly 100 years ago (Mason 1915). As a consequence, during the past century many large-scale and costly programs aimed at mitigating the impacts of mountain pine beetle epidemics were undertaken in the USA and Canada (reviewed by Klein 1978).

A mountain pine beetle outbreak requires both a supply of susceptible host trees and a large population of beetles. Therefore, mitigating the impacts of an epidemic may be achieved theoretically through treatments aimed at limiting the amount of susceptible trees or reducing the number of beetles. The former is termed "indirect control" or "preventive management", whereas the latter is considered "direct control", the central topic of this chapter.

Between outbreaks, mountain pine beetle populations normally exist at very low endemic levels, constrained by biotic and abiotic mortality factors. Relaxation of the effects of these mortality factors allows populations to erupt into epidemics. The objective of a direct control program is to limit beetle epidemics to levels that do not cause economically important damage (McMullen et al. 1986). Biologically, this means that successful direct control tactics are those that can introduce sufficient mortality into an increasing population to limit its rate of increase, or ideally, return it to the endemic phase.

The first documented direct control program against the mountain pine beetle occurred between 1902 and 1903 in South Dakota, USA (Hopkins 1905). Since then, some level of control has been attempted against most significant infestations throughout the beetle's range. During the last several decades, exploitation of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) for forest products has increased tremendously (e.g., Taylor and Carroll 2004), and the necessity for more effective mountain pine beetle control programs in that forest type has increased accordingly.

The objectives of this chapter are as follows. First, a brief review of the direct control tactics that have been, and continue to be, employed against the mountain pine beetle in lodgepole pine forests will be presented. This review will mainly focus on tactics that have been used operationally; however, where necessary for a complete overview, some tactics still within the realm of research will be considered. Second, a theoretical framework for suppression of the mountain pine beetle using direct control tactics, derived from simple population processes, will be presented. Third, the framework will be considered within the larger context of control programs over large landscapes where multiple objectives may be desired. Finally, the theoretical framework will be used to critically assess previous efforts at direct control (insofar as the literature will permit).

Direct control past and present

The tactics associated with operational direct control programs can be grouped into three broad categories based upon their mode of action: cultural and mechanical treatments that entail killing beetles by destroying the bark of infested trees; chemical tactics that are based upon the application of insecticides either directly or as systemics; and semiochemicals involving the use of signal-bearing volatile compounds to manipulate beetle populations, most often in concert with other direct control efforts. To date, there are no biological control alternatives for the treatment of mountain pine beetle infestations (see Safranyik et al. 2002). Depending upon the logistics of their application, tactics may be applied to individual infested trees, or more broadly to whole stands or groups of stands.

Cultural and mechanical tactics

There are a variety of techniques available for the cultural and mechanical treatment of mountain pine beetle infested lodgepole pine trees; some more effective than others. Due to the time and effort associated with felling trees, many tactics have been developed for application to standing infested trees, whereas others were designed to be applied after trees have been felled.

Fire has been a common tool in the direct control of mountain pine beetle infestations, although its efficacy in many circumstances can be unsatisfactory. Early attempts to burn standing infested trees resulted in fires that were seldom hot enough to kill a significant proportion of the brood, even if the trees were sprayed first with fuel oil (Evenden 1927, 1929). Later, pressurized flame throwers were employed (Klein 1978; McMullen et al. 1986). Even though higher burn intensities and greater brood mortality were possible, this technique was limited by high fire hazard conditions and difficult access in dense stands and steep terrain (McMullen et al. 1986).

Fire has also been applied as prescribed or broadcast burns to control larger mountain pine beetle infestations. In these treatments, controlled fires are ignited in an infested stand or group of stands. Although a potentially valuable tactic in remote locations or areas where other treatment options are not permitted or feasible, appreciable mortality can only be attained with very high fire intensity (Stock and Gorley 1989; Safranyik et al. 2001). Given the difficulty of controlling high-intensity fires (e.g., Hirsch et al. 1998), prescribed fire to suppress beetle populations is unsuitable in most situations.

Perhaps the most effective means of ensuring significant mortality of broods is to remove the bark of infested trees before beetles complete their development. The first efforts at debarking standing trees involved the use of long-handled spuds to peel bark from the lower 3-4 m of the bole (Evenden 1927). Later, in an effort to establish a less labour-intensive treatment, several attempts were made to debark trees using explosive detonating cord wrapped around the stem (Adams 1926; Whitney et al. 1978). Notwithstanding the obvious risks associated with handling explosives, it was found that unless all of the bark was blown off the main stem, many beetles survived intact beneath the bark. More recently, a self-climbing mechanical tree pruning device known as a "tree monkey" was modified to peel the bark from standing infested trees (Whitney et al. 1978). Unfortunately, the variable morphology among the stems of trees rendered the device too unreliable.

In spite of the convenience of treating standing trees, felling infested trees prior to treatment remains the most dependable technique to ensure significant brood mortality. Under natural conditions during hot, dry weather, beetle broods may suffer extensive mortality due to drying. Patterson (1930) attempted to exploit this phenomenon by felling trees, removing their limbs and exposing them to direct sunlight. However, he found that bark temperatures above 43°C were required for several hours, and that the logs had to be rolled daily for several days to achieve significant mortality. Consequently, the tactic was considered too labour intensive and suitable only for the hottest periods of the summer in very warm regions.

Regardless of the many and varied attempts at developing alternative effective control techniques, felling and destroying or harvesting and processing trees remains the most common tactic for the control of mountain pine beetle populations (Klein 1978). This tactic can take the form of single tree treatments, which are used to deal with small isolated groups of infested trees, or stand level applications which are used for larger scale infestations.

The treatment of single trees can take one of several forms. Where it is economically feasible, individual infested trees may be harvested and transported to mills where beetle broods will be killed during processing. If individual or small groups of infested trees are uneconomic to harvest and process, they may be felled, cut into manageable pieces, piled up over the stump and burned. As outlined above, however, achieving a thorough, high-intensity burn is essential to kill the beetles due to the insulating properties of bark. Often, fuel oil is used to increase the intensity of the fire, particularly when the bark is moist (McMullen et al. 1986). When it is impractical to remove or burn infested trees, they may be debarked after felling. However, this treatment is much more laborious than the preceding alternatives, and therefore, less desirable.

Where infestations encompass whole stands or groups of stands, block harvesting may be used to control populations in a tactic known as "sanitation logging". This is the most commonly utilized tactic for dealing with larger groups of infested trees. It can be effective in reducing beetle populations, but is limited by the availability of road access to stand(s), land tenure considerations, non-timber forest values (e.g., riparian/wildlife habitats) and timber markets (McMullen et al. 1986). In spite of these limitations, sanitation logging is more cost-effective than individual tree treatments and is often the only method suitable for treating large infestations (McMullen et al. 1986).

Sanitation logging in itself will not kill a significant proportion of mountain pine beetles. Since beetle broods can complete their development in trees that have been felled and decked in a mill yard, infested logs must be milled before new adults emerge and disperse. The restricted window during which harvesting and processing (thereby debarking) can be effective against developing beetles may, in some circumstances, limit the value of this direct control tactic. However, treatments have been developed that are capable of removing this constraint. McMullen and Betts (1982) found that by sprinkling log decks with water, the survival of beetle broods was reduced to 5% compared to 93% in controls. Similarly, Safranyik and Linton (1982) found that submersion of infested logs in water for 6 weeks will cause 100% mortality of developing bark beetles.

Chemical tactics

Given that the mountain pine beetle spends all but a very brief part of its life cycle beneath the bark of its host trees, it is not amenable to the application of broadcast insecticides in the way that many other forest insect pests, such as defoliators, have been. Nonetheless, pesticides became popular for the direct control of beetle populations during the middle of the last century, and considerable research efforts were devoted to identifying the most effective chemical, carrier and application method (reviewed by Klein 1978). Based upon their method of application, two broad categories of insecticides have been developed; chemicals designed to be applied to the bark over the bole of the tree, and those injected into trees as systemics.

Insecticides applied to the bole have been used both to kill mountain pine beetle broods within infested trees by penetrating the bark, and to prevent attacks of susceptible trees by killing the beetles as they attack. The earliest penetrating chemical formulation comprised naphthalene in an oil carrier (Salman 1938; Gibson 1943). Although this mixture proved to be effective at killing beetle broods, it was difficult to use due to the relative insolubility of the naphthalene (Gibson 1943). Orthodichlorobenzene (Gibson 1941, 1943), or ethylene dibromide (Massey et al. 1953; Kinghorn 1955), in diesel oil were also found to be effective penetrating insecticide formulations, and the former became one of the most common direct control tactics applied during the 1940s and 1950s in the USA (Klein 1978). Since oil solutions are expensive, unpleasant to use, and associated with skin irritation, research was conducted to develop water-based formulations of bark penetrants. Ethylene dibromide in water was found to be very effective in killing mountain pine beetle broods (Stevens 1957, 1959), and therefore, became the standard chemical tactic for controlling infestations during the 1960s and 1970s (Klein 1978).

Interest in protecting trees from attack, rather than treating them after infestation, stimulated the development of preventive insecticides. Formulations of lindane or carbaryl in fuel oil were found to give excellent levels of protection from mountain pine beetle attacks (Smith 1970; Gibson 1977; Smith et al. 1977). However, the oil-based carriers were often found to kill the very trees they were intended to protect (Rogers 1976). Lindane or carbaryl formulated with water as a carrier also worked well at preventing attacks under a variety of conditions (Gibson 1977; Smith et al. 1977) and were both widely used in the USA and Canada.

Due to their ease of application, preventive or penetrating insecticides sprayed on the bole of trees were favoured by forest managers. However, the subcortical habits of the mountain pine beetle suggest that systemic insecticides should be more effective at killing brood beetles. Nevertheless, the number of systemic pesticides used as operational direct control tactics against the mountain pine beetle has been relatively small. Copper sulfate applied to a shallow axe frill cut into the sapwood of newly infested trees was found to be effective (Bedard 1938). Much later, monosodium methanearsonate (MSMA), also applied to an axe frill, was determined to be successful in killing beetle broods (Maclauchlan et al. 1988). MSMA is an arsenical herbicide with insecticidal properties that has been widely used to control a variety of bark beetle species (e.g., O'Callaghan and Fairhurst 1983; Holsten 1985).

Systemic formulations have advantages over other insecticides in that impacts to non-target species can be minimized. Unfortunately, the attack dynamics of the mountain pine beetle renders successful application of systemics somewhat problematic. Tunneling by the beetles and their offspring in the phloem tissue beneath the bark, combined with the colonization of the sapwood by the blue stain fungi that beetles introduce, severely impairs the ability of trees to translocate. Therefore, application of systemic insecticides too long after beetles colonize trees will be largely ineffectual since the formulation will not move up the stem and come into contact with the beetles. Indeed, for this reason it is recommended that systemics such as MSMA are applied within three weeks of initial attacks (McMullen et al. 1986; Maclauchlan et al. 1988).

In spite of the efficacy of chemical tactics for direct control, their toxicity to the environment and workers has led to the discontinuation of their use in virtually all operational direct control programs (although in some jurisdictions, several insecticides may be available for use on private lands). Currently, MSMA is the only registered pesticide that is widely used against the mountain pine beetle in Canada, and its continued use is in jeopardy due to limitations of supply and environmental challenges.

Semiochemical tactics

Semiochemicals are signal-bearing chemicals involved in interactions among organisms. There are several different types depending upon the "message" contained in the semiochemical and/or the behaviour it evokes in the recipient (e.g., Nordlund 1981). For example, pheromones are substances emitted by an organism that cause a specific reaction in a receiving organism of the same species, whereas kairomones are substances that evoke in the receiver a reaction that favours the receiver but not the emitter. The mountain pine beetle employs a complex suite of pheromones and kairomones to mediate its attack behaviour (e.g., Borden et al. 1987).

As the semiochemical system employed by the mountain pine beetle has been elucidated, two broad strategies have emerged to exploit it in direct control programs. The first is based upon the beetle's aggregation behaviour during mass attacks, the second is derived from its use of antiaggregation pheromones to terminate mass attacks and minimize intraspecific competition (Borden 1989). The primary semiochemical constituents of the aggregation response of mountain pine beetles in lodgepole pine forests are the pheromones *trans*-verbenol and *exo*-brevicomin, and the host-tree produced kairomone myrcene (Conn et al. 1983; Borden et al. 1983a, 1987). The antiaggregation response is largely a function of the pheromone verbenone (Ryker and Yandell 1983; Borden et al. 1987). These compounds have been developed into commercial devices intended to either focus or concentrate (i.e., aggregate) beetle populations in stands, or deter or redirect (i.e., antiaggregate) them from stands (Borden 1995).

Since the application of semiochemicals does not directly cause the mortality of beetles, they are normally used in conjunction with the cultural/mechanical or chemical tactics described above. For example, in treating isolated small infestations where falling and burning/peeling is impractical, infested trees may be treated with an insecticide [e.g., sprayed with carbaryl or injected with MSMA (Borden and Lindgren 1989; Borden 1995)] to kill brood beetles. Trees around the infestation would then be baited with the synthetic aggregation semiochemicals to induce any beetles that survived the initial treatment to attack nearby trees (i.e., not disperse), after which those trees would be treated with insecticides.

Aggregation semiochemicals are often used in conjunction with sanitation logging of larger infestations in a treatment known as “post-logging mop-up” (Borden et al. 1983b). Since it is difficult to remove every infested stem in a sanitation logging treatment when infestations become reasonably large, aggregation semiochemicals are often applied to residual susceptible trees in the vicinity to ensure that remaining beetles do not disperse and can be easily located for follow-up treatments. This tactic can be quite successful when applied over several years, and is common in western Canada (Borden 1995).

The mountain pine beetle’s aggregation response has also been exploited to extend the utility of direct control efforts during widespread increases of infestations over the landscape. During these periods, the number of infestations often exceeds the capacity of forest managers to treat them before the beetles emerge and disperse, causing existing infestations to grow and new ones to establish, frequently at significant distances from the original infestation. In a tactic known as “containment and concentration”, infested stands are inundated with synthetic aggregation semiochemicals, allowing infestations to intensify without expanding, thereby facilitating sanitation logging during the subsequent season (Borden et al. 1983c). This has proven to be an effective means of slowing the spread of mountain pine beetle infestations (Gray and Borden 1989), and has been employed operationally in western Canada since the early 1980s (Borden and Lacey 1985).

Exploitation of the antiaggregation pheromones of the mountain pine beetle still lies in the realm of research. However, several trials (e.g., Amman et al. 1989; Lindgren et al. 1989) have shown that when verbenone release devices are placed in an infested stand, the number of attacked trees can be reduced relative to control stands. Borden (1995) has proposed that the most operationally feasible use of antiaggregation pheromones would be to deploy them in one stand while using aggregation pheromones in another to push beetles from high-value areas and draw them into adjacent trees slated for treatment.

A Population-based Framework for Successful Control

Knowledge of the basic population processes associated with the mountain pine beetle is essential to effective control efforts. In populations where conditions have changed such that reproduction outweighs mortality, unless a sufficient amount of additional mortality is introduced, the infestation will expand. From the above review of direct control tactics, it is clear that an array of alternatives is available for the treatment of mountain pine beetle infestations. The relative success of these tactics, however, is dependent upon the state of the beetle population.

Since, on average, female mountain pine beetles produce 60 eggs and two-thirds of offspring (i.e., 40) are female (Reid 1962), then given that only one female offspring needs to survive to achieve replacement, approximately 97.5% generation mortality (i.e., 39/40) is required to keep populations static. Interestingly, only a small rise in survival is required for populations to increase dramatically. For example, if generation mortality declines from 97.5% to 95.0%, then populations have the potential to double in size.

Initially, mountain pine beetle populations appear to grow relatively slowly. As an illustration, consider a stand with one infested tree and a population where the generation mortality has declined slightly to allow it to double each year (i.e., a rate of increase, $R = 2$). After 10 years, only 512 trees would be killed (Fig. 1). This represents less than 2% of the trees within a 20 ha stand, and therefore the population may escape detection or concern for a number of years (e.g., Shore and Safranyik 2004). If the infestation was detected and, in an effort to control it, 37.5% of the infested trees were treated during the fourth year, 194 fewer trees would be killed by year 10, but the population would continue to expand (Fig. 1). From this example, the question arises: What level of mortality must be added and how often, to slow or stop an increasing population?

The general concept is straightforward. Assuming that the number of infested trees is a good index of beetle population size (a reasonable assumption for increasing populations [e.g., Safranyik 1988]), then, to maintain a static population, a proportion of infested trees (P) must be treated in each year equivalent to:

$$P = 1-1/R \qquad [1]$$

where R is the yearly rate of increase in the population. In other words, if the population is expected to triple yearly ($R = 3$), then two-thirds of all infested trees would have to be treated before the flight period each year. Obviously, if population reduction is the goal, then treatment rates must exceed two-thirds. The concept is presented graphically in Figure 2. For any measured rate of increase, unless sufficient mortality is introduced into a population that equals or exceeds the yearly growth in a population, it will continue to increase.

With the above framework in mind, control efforts must be considered in light of the size of the beetle population. When populations are very small (i.e., endemic), their rates of increase are usually constrained to unity. This is the point at which management efforts can have their greatest impact. Beetles are usually restricted to a few weakened or damaged trees within a stand, so relative to the potential rate of increase and the number of trees involved, removal of any of the infested stems would suppress the population, and perhaps even cause local extinction (Fig. 2). Thus, provided they can be detected, endemic populations are highly amenable to direct control.

Larger incipient-epidemic, or "spot" infestations, by virtue of their size and more obvious impacts, are much easier to detect. Because they have gained access, through mass attack, to healthy, large-diameter trees, their rates of increase are often between two- and fourfold yearly. Typically, when these populations are first detected, the number of trees involved is still relatively small (<500), and the area they occupy is well defined and often much less than a whole stand. To limit the potential for increase if $R = 4$, then ≥75% of the infested trees must be treated every year (Fig. 2). If 500 trees were found, then at least 375 stems must be treated that season, and a similar proportion in subsequent seasons provided R remains constant. If there is ready access to the infestation, it is highly amenable to many of the available direct control tactics.

An incipient-epidemic population may take only 2 to 3 years to develop into a full outbreak if left untreated and rates of increase remain high. During an outbreak, the number of trees killed annually is often in the millions and may encompass hundreds of thousands of hectares. The rate of increase may not be more than that of an incipient population, but its size renders most management tactics useless. As an example, if an outbreak is spread across 300 000 ha and $R = 2$ (a conservative rate during peak outbreak years), then 150 000 ha of infested trees must be harvested in each year just to keep the infestation static. Logistically, detection and removal of such a vast number of infested trees is impossible.

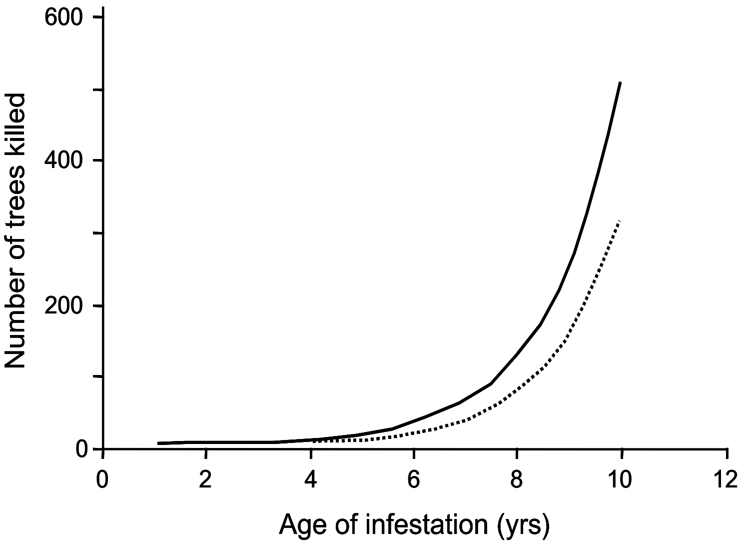

Figure 1. Number of trees killed by mountain pine beetle versus age of infestation for a population doubling in size yearly [i.e., the yearly rate of increase R = 2 (solid line)]. The broken line represents the same population with the removal of 37.5% of the population (i.e., 3 of 8 infested trees) during year 4.

Interestingly, even if a proportion of a mountain pine beetle infestation in excess of the threshold derived by equation 1 (Fig. 2) can be treated with direct control tactics, it may not be sufficient in an operational context to suppress a population if its initial size and/or rate of increase is large. During a direct control program, the number of trees infested (N) in any given year will be a function of the number of trees initially infested (N_o), the yearly rate of increase (R), the proportion of trees treated each year (P) and the number of years (t), such that:

$$N = N_o[R(1\text{-}P)]^t \qquad [2]$$

If the objective of the control effort is suppression (i.e., where $N = 1$), then the number of years (t) of continuous direct control can be determined given knowledge of R and P, provided $P > 1\text{-}1/R$ (see Fig. 2). This concept is illustrated in Figure 3. If direct control tactics were employed against a mountain pine beetle infestation involving 10,000 infested trees, doubling yearly, such that 80% of infested trees were treated each year, then it would take 10 years to reduce the infestation to a single infested tree (Fig. 3a). If that population was tripling or quadrupling yearly, then it would take 18 or 41 years, respectively, of continuous 80% treatment to suppress it. Obviously, if a greater proportion of trees could be detected and treated, then suppression would be possible in a shorter time. For example, if it was possible to detect and treat 90% of infested trees each year, then it would require either 6, 8 or 10 years of continuous effort to suppress a population initially infesting 10,000 trees and increasing at a rate of two, three or four times yearly, respectively (Fig. 3a). If an infestation was allowed to increase by an order of magnitude to 100,000 infested trees

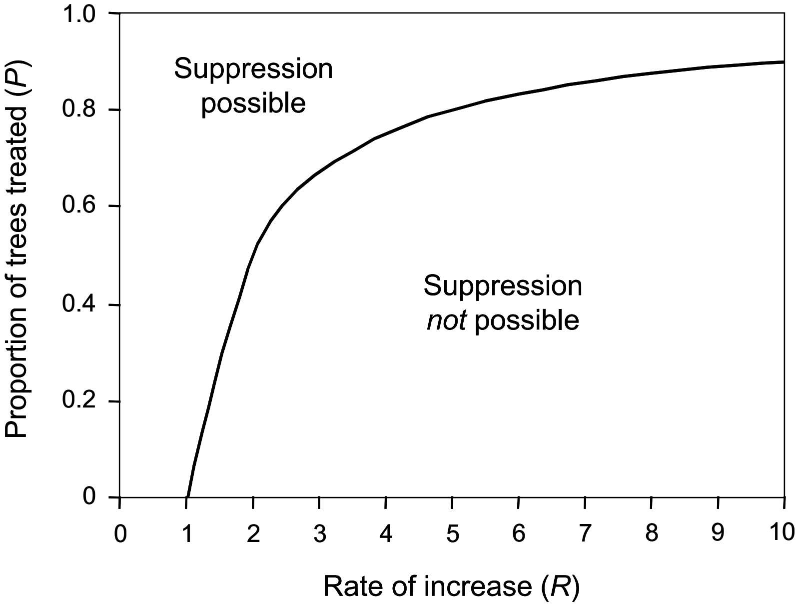

Figure 2. Graphical representation of the proportion of a mountain pine beetle population (P) that must be removed in relation to the yearly rate of increase (R) to suppress population growth ($P = 1\text{-}1/R$). The area below the curve represents treatment levels where suppression is not possible, treatment levels above the curve (applied yearly) will suppress populations. See text for details.

without intervention, then the time to suppression increases, even if the same proportion of trees are detected and treated. In the case of 80% treatment, where $R = 2$, 3 or 4, continuous control efforts would be required for 13, 23 or 52 years to achieve suppression (Fig. 3b). If 90% detection and treatment were possible in this circumstance, then 7, 10 or 13 years would be needed.

In each of the theoretical scenarios just described, the proportion of trees treated was within the "suppression possible" zone indicated in Figure 2. However, suppression would be operationally intractable in virtually all of the scenarios due either to the number of years of continuous treatment necessitated, or the level of detection and treatment required. In most cases, a consistent direct control program lasting 10 years against a single infestation would be difficult to maintain, let alone one requiring 40 to 50 years (assuming there is sufficient mature pine to sustain an infestation for that duration). Moreover, whereas the detection and treatment of 80% of infested trees may, in some cases, be possible, given the challenges associated with detecting mountain pine beetle infestations, identification and treatment of a greater proportion of a population in a single season is unlikely.

From the preceding discussion, there emerges three points that cannot be overemphasized if direct control is to be effective in the management of mountain pine beetle populations. First, growing infestations must be detected as early as possible. Second, aggressive direct control tactics must be applied promptly and thoroughly. Third, control programs must be continuous until the desired population level is achieved. If small incipient-epidemic populations are allowed to grow, either through lack of detection or as a consequence of intermittent control interventions, the probability of successful suppression will decline dramatically, often within only a few years.

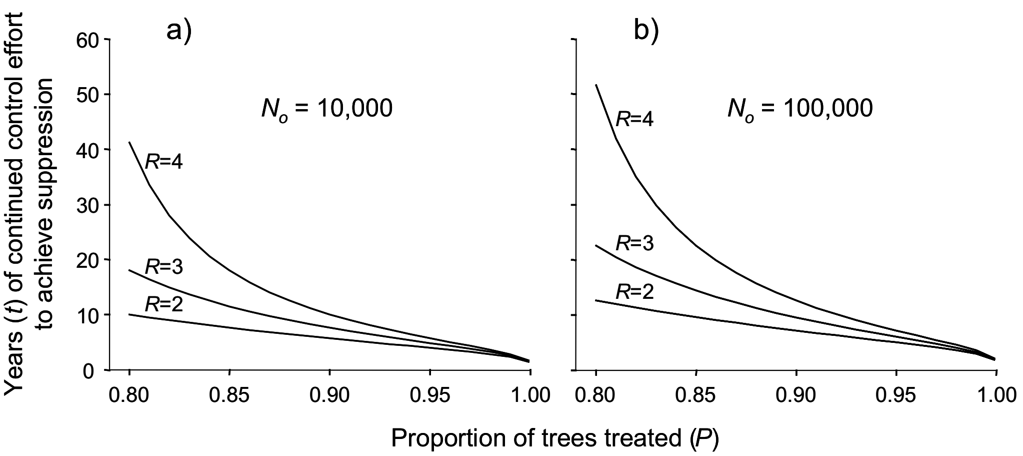

Figure 3. Graphical representation of the number of years (t) of continued control effort to achieve suppression (number of infested trees, $N = 1$) given a proportion of trees (P) treated yearly and a yearly rate of increase (R) based upon (a) 10,000 or (b) 100,000 trees infested initially (N_o). $N = N_o[R(1\text{-}P)]^t$ where $P > 1\text{-}1/R$.

Direct control over landscapes

The preceding discussion of direct control has centred upon the application of tactics for the suppression of individual infestations. However, when mountain pine beetle populations increase to epidemics, they often do so synchronously over very large areas (Taylor and Carroll 2004). Widespread, synchronous increases in population levels may exceed the capacity of forest managers to implement suppression activities over a large area. Furthermore, the strategy of suppression may not meet the objectives of all jurisdictions associated with forest management, such as parks and protected areas where natural disturbance events are important components of forest ecosystems. Therefore, alternative strategies for the application of direct control tactics may be required for the management of mountain pine beetle impacts across large and varied landscapes.

Perhaps the most comprehensive example of the application of alternative strategies for the direct control of mountain pine beetle populations over large areas is found in British Columbia, Canada, where two outbreak events during the previous three decades, involving millions of hectares of forests, have challenged the sustainability of forestry in lodgepole pine-dominated landscapes. A series of strategies, based upon the application of relevant direct control tactics, were developed to encompass a complex mix of land uses, tenures, ecosystems and economic circumstances (Hall 2004). The four main strategies are: (i) suppression/prevention, where aggressive direct control tactics are applied to reduce populations to endemic levels within a few years; (ii) holding, where control efforts are aimed at maintaining population levels at no more than current levels, often until more resources become available or until the underlying cause of the infestation subsides; (iii) salvage, where aggressive options are deemed unlikely to succeed and, therefore, efforts are diverted to recovering dead timber while it still retains value; and (iv) monitor, where the preceding strategies are inappropriate, such as in inaccessible or inoperable regions, parks and protected areas (Hall 2004). Obviously, the strategies of "suppression/prevention" and "holding" require the application of some or all of the direct control tactics previously described. Provided these strategies are implemented within the population-based framework for successful control, the probability of realizing their objectives remains high.

Evaluation of a selected strategy for a portion of a larger landscape (e.g., management unit) must consider the resource objectives, the number of infested trees, the risk to surrounding resources, the financial and physical resources available to apply to the strategy, and the potential for success. Each year these factors need to be re-evaluated to determine if a shift in strategy is required. Decision support tools (Shore and Safranyik 1992) are available to facilitate the process of strategy selection and application.

Trials and errors: lessons from the past

Lodgepole pine forests occur over approximately 160 million ha of western North America. The mountain pine beetle is a ubiquitous component of mature stands over much of this area. Despite the vastness of the region in which mountain pine beetle populations exist, epidemics normally initiate and spread from well defined epicenters (Aukema et al., 2006). Therefore, direct control tactics aimed at controlling developing epicenters in the incipient-epidemic phase are theoretically amenable to a suppression strategy.

Despite many significant efforts at direct control of mountain pine beetle populations during the previous century, suppression was seldom, if ever, achieved and, at best, the rate of tree mortality was reduced only marginally (Craighead et al.1931; Amman and Baker 1972; Klein 1978; Amman and Logan 1998). A brief examination of historical control activities in light of the framework proposed above reveals three major shortcomings. First, most efforts targeted treatment of infested trees as either a fixed percentage of the total or of the area involved (e.g., Klein 1978, and references therein). Without assessments of the yearly rate of population increase, the treatment levels were most often insufficient. Second, even when a sufficient proportion of a population was removed in one year, the efforts frequently did not persist in subsequent years (e.g., Craighead et al. 1931). Since building populations often have very high rates of increase, and conditions amenable for increase typically persist for more than a single year, a single aggressive intervention may slow the development of an epidemic, but not prevent it (see Fig. 1). Finally, early control programs suffered from the inability to accurately detect and delimit increasing populations. As a consequence, they were often abandoned when populations erupted in adjacent unsurveyed jurisdictions (e.g., Evenden 1944). In recent years, detailed systematic aerial survey techniques have been applied, and remote sensing techniques are being developed to provide accurate, real-time quantification of the abundance, distribution and rates of increase of the mountain pine beetle over the landscape.

Interestingly, there is one documented example of successful suppression of a mountain pine beetle population. During the early 1940s, an incipient epidemic was detected near Banff, Alberta, Canada. Every tree in the vicinity of the infestation was checked over two years, and any tree with evidence of mountain pine beetle attack was felled and burned. During the third year, no beetles could be found (Hopping and Mathers 1945; Hopping 1946). Although rates of increase were not considered, it is not surprising that such an aggressive and consistent intervention was successful.

More general issues may also be at the root of failures to manage mountain pine beetle populations using direct control tactics. For example, where drought has caused the reduction of host resistance over relatively large areas, the increase in beetle populations may be more widespread than initially recognized. Combined with the difficulties of early detection of scattered infested trees, the sudden eruption of infestations over the landscape can quickly outstrip the resources available for treatment. Moreover, improperly applied treatments such as low-intensity fires that were not hot enough to kill the developing brood under the bark, incomplete peeling of the bark, or poorly timed application of systemic insecticides, can mislead the forest manager into thinking an area has been successfully treated when it has not. Therefore, the meagre historical record of direct control in reducing beetle epidemics may be more a result of poor execution than poor theory.

Conclusions

There exists a large suite of tactics for direct control of mountain pine beetle populations. Many of the tactics are highly complementary and can be applied in an integrated management program. However, it cannot be overemphasized that for direct control to work, there must be prompt and thorough application of the most appropriate treatments at a magnitude dictated by the population size and rate of increase. Furthermore, direct control tactics must include a persistent follow-up; possibly the most important, yet most neglected aspect of mountain pine beetle management (Whitney et al. 1978).

Efforts to mitigate the impacts of mountain pine beetle outbreaks have been ongoing for nearly 100 years. During that time, options for direct control have come and gone, but the potential efficacy of the current toolbox is unparalleled. Interestingly, many of the basic requirements for successful direct control were recognized many years ago. Indeed, some of the recommendations, listed below, of Hopping and Mathers (1945) are particularly noteworthy given the preceding discussion:

- Control work must be started when the first signs of abnormal bark beetle increase become apparent.
- Control work must be continued as long as the underlying causes of the infestation are operative.
- The objective must be to treat every infested tree, over the entire area.
- As long as the character of the stand remains the same, future outbreaks may be expected whenever tree vigour is seriously reduced.
- The only permanent solution to the problem in high-hazard areas is to change the composition of the stands on the landscape.

It is important to realize that any successful direct control program is by its very nature only temporary. Any stand of lodgepole pine within the range of mountain pine beetle that reaches maturity will very likely contain a large proportion of trees that are susceptible to beetle attacks. Therefore, retention of lodgepole pine on the landscape for future harvesting will require future direct control of mountain pine beetle populations.

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