FRST 497

The Spruce Beetle and Climate Change: Ecological Implications for Forest Management and Responses for Forest Managers in Western Canada

by

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A GRADUATING ESSAY SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

BACHELOR OF SCIENCE

In

The Faculty of Forestry

Forest Resources Management

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

April 11th, 2012

Abstract

Over the past two decades, unprecedented spruce beetle outbreaks have been observed throughout cordilleran North America. In contrast to historic spruce beetle outbreaks, recent outbreaks have not stemmed from clear, stand-level abiotic disturbance events, and instead, have been attributed to the progressive onset of climate change. With the continued influence of climate change, spruce beetle outbreak probabilities are expected to increase throughout the 21st century.

To provide insight for forest managers, this report summarizes the effect of climate change on spruce beetle ecology, population dynamics, and disturbance regimes. It also addresses the ecological forest management implications of altered spruce beetle disturbance regimes, and provides potential management responses for those managing spruce forests in a changing climate.

Spruce beetle disturbance is influenced both directly and indirectly by climate through changes in developmental timing, temperature-mediated population mortality, host-tree resistance, and trophic-level interactions. Spruce beetle outbreaks alter a suite of ecological forest values, and increased disturbance stands to fundamentally change the scope of these values in spruce-prevalent landscapes. Spruce beetle disturbance can influence stand structure and succession, wildfire, hydrology and aquatic ecosystems, wildlife, and forest carbon dynamics.

Direct and indirect control treatments used in conjunction with current forest inventories, effective spruce beetle monitoring programs, and strategic access development, provide forest managers with effective means to respond to increased spruce beetle disturbance within an integrated management framework. These treatments, however, are limited by economic, operational, and policy-driven constraints. Additionally, there are a number of harvesting considerations for spruce beetle that forest managers can incorporate into harvest planning

KEYWORDS

Climate Change, spruce beetle, forest management

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1. Introduction

The spruce beetle (***Figure 1***) (*Dendroctonus rufipennis* (Kirby), Coleoptera: Scolytinae) is a primary bark beetle native to spruce forests across North America (Safranyik et al., 1990). While all spruce species (*Picea spp.)* are suitable hosts in western Canada, its primary hosts are white spruce (*P. glauca* Voss), Engelmann spruce (*P. engelmanni* Parry), and their respective hybrids (Safranyik, 2011). The beetle acts as the most significant disturbance agent in mature, spruce-dominated forests and plays an important role in maintaining ecosystem diversity, triggering succession, and contributing to fire and soil nutrient cycles (Humphreys & Safranyik, 1993; Lewis & Lindgren, 2002; Carroll, 2010a).

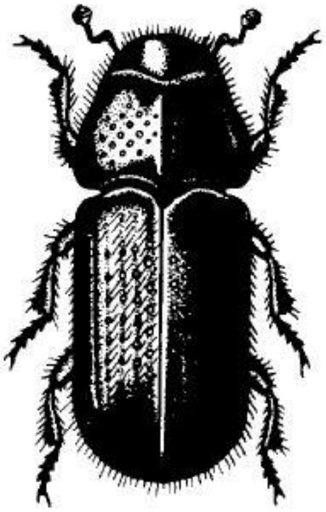

Figure 1: Adult spruce beetle (*Dendroctonus rufipennis* Kirby) (Humphreys & Safranyik, 1993)

Endemic spruce beetle populations persist for the most part in stumps, large-diameter slash, and in stressed, damaged, and recently killed trees. Mature spruce forests usually only provide enough host material to support small and scattered beetle populations. The physiological defences of healthy spruce trees keep scattered endemic beetle populations at bay; but when spruce beetle populations become eruptive, healthy trees can succumb to attack (Garbutt, et al., 2006). Periodic abiotic disturbance events that cause widespread stress or death in spruce trees, such as drought, windthrow, fire, right-of-way clearing, and harvest, increase host material volume. This increase in host material is favourable for beetle reproduction and can push populations from endemic to epidemic levels (Berg, et al., 2006).

Over the past two decades, unprecedented spruce beetle outbreaks have been observed throughout cordilleran North America. These outbreaks have caused significant and long-term alterations to a suite of forest functions and values. In some cases, these alterations may have surpassed historical resilience boundaries, resulting in irreversible changes across forested landscapes (Bentz et al., 2010). Unlike previous outbreaks, the recent epidemic populations have not stemmed from obvious, stand-level abiotic disturbance events (Berg et al., 2006). The recent outbreaks have been attributed to a progressive onset of climatic conditions conducive to beetle development (Garbutt et al., 2006). Spruce beetle fecundity, mortality, and host availability are all responsive to climatic shifts (Sherriff et al., 2011). Spruce beetle fecundity is enhanced by warmer growing season temperatures due to changes in larval developmental timing (Hansen et al., 2011). Warmer climatic regimes decrease spruce beetle mortality due to reduced cold temperature exposure (Bentz et al., 2010). Climatic events that cause widespread reductions in spruce tree vigour, such as drought, increase numbers of trees available for spruce beetle colonization (Garbutt et al., 2006). The dry and warm climatic conditions in western North America through the 1990's resulted in the culmination of several key factors that worked to accelerate the development of spruce beetle populations (Berg et al., 2006).

With climatic influences driving the recent unprecedented spruce beetle outbreaks, climate change raises particular concern for forest managers. Projections from current climate models indicate an increased probability of spruce beetle population outbreak throughout North America (Bentz et al., 2010). It is important for forest managers to understand the implications of climate change on spruce beetle disturbance and how our decisions today, carry forward to the future. It is also important for forest managers to understand the range of management options available to them to promote healthy, resilient ecosystems. This report summarizes the effect of climate change on spruce beetle ecology, population dynamics, and disturbance regimes. It will also address the forest management implications of altered spruce beetle disturbance regimes, and will provide potential management responses for those managing spruce forests in a changing climate.

2. Background

i. The Spruce Beetle

The spruce beetle is a widely distributed primary bark beetle native to spruce forests across North America. It can be considered a native ubiquitous species, present throughout its hosts' entire distribution (***Figure 2***) (Carroll, 2010b). All native spruce species are susceptible to spruce beetle infestation. During epidemics, spruce beetles may also attack non-host tree species, particularly *Pinus* spp (Holsten et al., 1999; Safranyik, 2011).

Figure 2: Spruce beetle distribution throughout North America (Holsten, Thier, Munson, & Gibson, 1999)

The spruce beetle exhibits facultative and obligatory diapauses (arrested stages of development) with a varying 1- to 3-year lifecycle (Carroll, 2010b). Diapause allows larvae and beetles to endure unfavourable conditions that may arise throughout development (Stark, 1982). Facultative diapause is triggered by environmental cues; for example, shorter day length or cold temperatures (Hansen et al., 2011). Obligatory diapause is genetically controlled and not influenced by environmental conditions (Stark, 1982). Broods that develop in one year after oviposition forgo facultative diapause, and are known as *univoltine*; whereas broods that develop in more than one year, exhibit facultative diapause, and are referred to as *semivoltine* (Carroll, 2010b). All adult spruce beetles must spend a winter in obligatory diapause prior to emergence the following spring (Humphreys & Safranyik, 1993). The presence of facultative diapause is the determining factor in the voltinism of spruce beetle broods. Individual broods can develop at different rates depending on solar radiation exposure. For example, a portion of a predominantly semivoltine brood may emerge from a host tree one year after oviposition, due to increased solar radiation occurring on portions of the infested bark (Humphreys & Safranyik, 1993).

Adult spruce beetles generally emerge from trees and attack new host material between late May and early July (Humphreys & Safranyik, 1993). Under-bark temperature generally reaches 14°C before adult flight occurs (Werner et al., 2006). After emergence, adult spruce beetles begin attacking new host material. Female beetles initiate the attack by boring through host bark and into the phloem tissue of suitable host material (MOFR, n.d.). Together with host volatile compounds, aggregating pheromones emitted by attacking female beetles, initiate mass beetle attack (Safranyik et al., 1990; MOFR, 1995). Upon entering the host material, female beetles begin excavating an egg gallery in the phloem where they are soon joined by a male. After mating with the female, the male remains in the egg gallery and assists with excavation (Humphreys & Safranyik, 1993). Following gallery completion, the female lays eggs in clusters along the two sides of the egg gallery and packs the gallery entrance with boring dust (Humphreys & Safranyik, 1993). ***Figure 3*** shows spruce beetle egg and feeding galleries in spruce phloem tissue.

Figure 3: Egg and feeding galleries in phloem (Humphreys & Safranyik, 1993)

Between 2 and 4 weeks after oviposition (by August), eggs hatch and first instar (larval stage) larvae begin to move away from their parent gallery and feed as a group on phloem tissue (Holsten et al., 1999). Once the larvae have reached their third instar, they leave their cohort and form their own individual feeding galleries (Humphreys & Safranyik, 1993; Holsten et al., 1999). Typical 2-year semivoltine broods exhibit facultative diapause and overwinter as early instar larvae or as second-year adults. To prepare for winter, larvae and young overwintering adults, drain and replace water from their cells with glycerol, an anti-freeze compound (Werner et al., 2006). The cellular anti-freeze compound allows beetles and larvae to withstand ambient temperatures of -26^{o}C. Beetles and larvae generally cannot tolerate sustained periods of -35^{o}C (one week or more), and will succumb to the cold temperatures (Werner et al., 2006).

In the following spring and summer, overwintered larvae finish their development and pupate between May and July, approximately one year after the initial attack. Pupation occurs at the end of larval feeding galleries and generally lasts two weeks. Teneral (young adult) beetles remain in the host material for the remainder of the season. In standing trees, some adults overwinter in their pupal chambers; whereas the majority emerge, and bore into the bark near the root collar. By overwintering at the base of the host tree, adult beetles can avoid predation and gain insulation from extreme temperatures. In downed host material, most beetles overwinter in their pupal chambers. The following spring, adult beetles emerge and begin their attack on new host material (Holsten et al., 1999).

Relatively high summer temperatures increase the probability of univoltine brood development. A mean 16.5°C phloem temperature during first and second larval instars has been associated with the development of univoltine broods (Werner et al., 2006). Univoltine broods reach maturity in the same season as the initial attack. Teneral adults overwinter and attack new host material the following spring (Humphreys & Safranyik, 1993). A shift to univoltine development marks a significantly higher probability of spruce beetle outbreak the following year (Hansen, et al., 2011).

Spruce beetle adults carry pathogenic blue-stain fungi that facilitate host colonization. Of several species, the most notable is *Leptographium abietinum* (Werner & Illman, 1994; Werner et al., 2006). Blue stain fungal spores are picked up by adult spruce beetles from host tissue prior to beetle emergence in spring. Blue-stain fungi colonize cells in both xylem and phloem tissues and are transmitted to the host via larval feeding (Safranyik et al., 1990). Fungal colonization of vascular tissues inhibits host water transport and production of resinous defense compounds. The inhibition of these processes promotes both brood establishment and survival (Safranyik et al., 1990; Werner et al., 2006). Host trees are killed when nutrient, food, and water flow is interrupted. While a combination of spruce beetle larval feeding and blue stain fungal infection usually results in the girdling and death of a host tree, a blue-stain fungal colonization alone, can kill the tree (Safranyik et al., 1990; MOFR, 1994).

Spruce trees have several lines of defense in response to spruce beetle attack. Upon initial attack, trees may excrete resin from boring wounds (Figure 4). This resin flow works to physically prevent infestation through entrapment of attacking beetles and serves as a primary defense mechanism; however, when tree vigour is depressed, resin production may not be sufficient to prevent spruce beetle colonization (Safranyik et al., 1990). Healthy conifer defense systems are very effective. To successfully colonize healthy trees, large numbers of beetles are required, attacking in unison (Stark, 1982). Only when a critical number (depending on host-tree vigour) of beetles are recruited to a tree can defenses be overcome (Bentz et al., 2010). This mass attack can overwhelm the resin defenses of vigorous, healthy trees (Safranyik et al., 1990). If primary resinous defenses are overcome by attacking beetles, spruce trees increase production of monoterpene and antimicrobial stilbenes in the phloem tissues. Monoterpenes are toxic to beetles and stilbenes inhibit the growth of blue-stain fungi (Werner et al, 2006).

Figure 4: Spruce resin emitted as a physiological defence against spruce beetle attack (Rod Garbutt, Canadian Forest Service)

The spruce beetle acts as an important agent of change in spruce-dominated ecosystems. At low population levels, scattered endemic populations target severely stressed trees (drought, advanced age, high stand density, defoliation, disease) or downed material (windthrow, logging residue, fire-damage) (Humphreys & Safranyik, 1993). These populations maintain stand diversity and complexity, contribute to fire and soil nutrient cycles, and work to trigger succession. In wetter ecosystems where fire disturbance is rare, spruce beetle infestation acts as an important local disturbance agent (Lewis & Lindgren, 2002; Carroll, 2010a). Normal mature forest ecological processes usually provide only enough host material to support scattered endemic populations. Normal physiological tree defences are sufficient in mitigating spruce beetle damage at these low levels. Only when spruce beetle populations become eruptive, is there widespread mortality of healthy spruce from mass attack (Garbutt et al., 2006).

Historically, spruce beetle populations have become eruptive at 30- to 50-year intervals (Werner et al., 2006). Eruptive populations have traditionally resulted from periodic disturbance events that create large influxes of host material (Garbutt, et al., 2006). Disturbance can be natural (drought, flooding, windthrow, fire), or anthropogenic (poor logging sanitation, mechanical damage) (Werner et al., 2006). Increases in host material are favourable for beetle reproduction and can push populations from endemic to epidemic levels (Berg et al., 2006). Additionally, climatic conditions leading to the development of univoltine broods also increase the likelihood of population outbreaks (Hansen et al., 2011). Over time, outbreak populations can kill the majority (up to 90%) of spruce trees over extensive areas (Veblen, Hadley, Reid, & Rebertus, 1991; Humphreys & Safranyik, 1993).

Figure 5: Stand damage from epidemic spruce beetle population (Rod Garbutt, Canadian Forest Service)

ii. Climate change and the Spruce beetle

The mean annual global temperature is expected to rise between 1.8 and 4.0°C throughout the 21st century (Bentz et al., 2010). The rise in temperature is expected to be greater in North America, particularly in areas of high elevation and high latitudes. Extreme weather events are also predicted to become more frequent along with extended dry seasons and increased likelihood of drought (Bentz et al., 2010). Expected temperature and precipitation changes in North America throughout the 21st century are displayed in Figures 6 and 7 respectively.

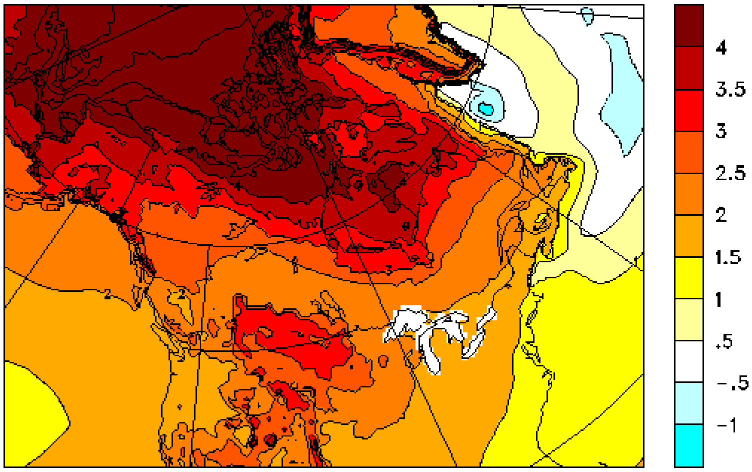

Figure 6: Projected change in mean annual temperature (°C) in 2041-2060 relative to 1971-1990 for North America simulated by the Canadian Regional Climate Model 3.6.1 (Environment Canada, 2012).

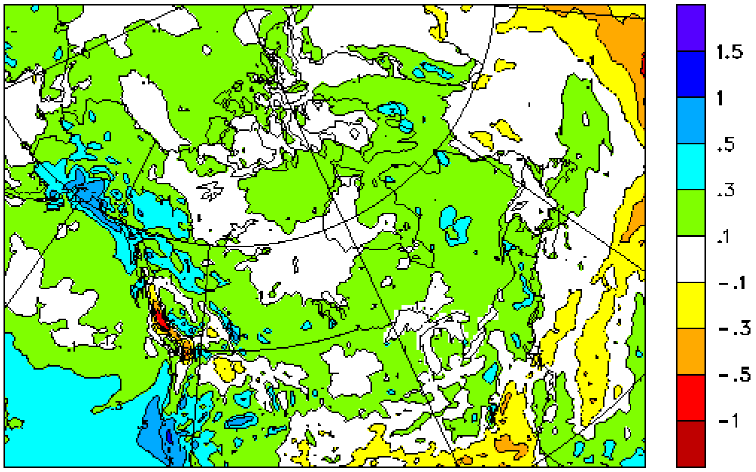

Figure 7: Projected change in mean annual precipitation rates (mm/day) in 2041-2060 relative to 1971-1990 for North America simulated by the Canadian Regional Climate Model 3.6.1 (Environment Canada, 2012).

Climate is a direct driver of phytophagous insect disturbance. Temperature and precipitation influence insect populations, pathogen abundance and tree responses (Bentz et al., 2010). Changes in climatic regimes can have significant impacts on the characteristics of insect disturbances. With regard to insect disturbance, climate change can result in:

- Altered outbreak frequencies and duration,
- New host-species interactions,
- Modified herbivory and damage rates, and
- Insect range expansion or contraction.

(Adapted from Carroll, 2010b)

Species, and host characteristics, in addition to competitor and natural enemy relationships and anthropogenic actions influence the extent of these climate change impacts on phytophagous insect disturbance. With regard to the spruce beetle, climate change may influence outbreak frequencies and duration, as well as herbivory and damage rates (Carroll, 2010b).

Spruce beetle disturbance may be both directly and indirectly influenced by climate. Climate influences spruce beetle populations directly through changes to developmental timing and through temperature-mediated population mortality. Climate influences populations indirectly through impacts to host-tree resistance, and host abundance (Bentz et al., 2010). Climate change may also indirectly affect spruce beetle populations through alterations to spruce beetle predator, parasitoid, competitor, and symbiotic relationships (Bentz et al., 2010; Carroll 2010b).. Recent spruce beetle outbreaks have resulted from a number of changes in climatic effects (Berg et al., 2006). The direct and indirect effects of climate change on spruce beetle disturbances are outlined below. The effects of climate change on the dynamics of spruce beetles and their community associates are not well understood, and will not be discussed in this paper.

Developmental Timing

The dynamic nature of spruce beetle developmental timing is directly related to growing season temperatures (Hansen et al., 2011). Increased growing season temperatures accompanying climate change will increase the frequency of univoltine brood development. Increased frequencies of univoltine brood development are indicative of increased spruce beetle outbreak probability (Bentz et al., 2010; Hansen et al., 2011). The developmental timing and synchrony of spruce beetles have evolved in part, with seasonality and climate (Bentz et al., 2010). Climate-related asynchrony attributed to changing climatic regimes could cause brood mortality (Carroll, 2010b).

Temperature-Mediated Population Mortality

Cold temperature-induced mortality is considered a key factor in spruce beetle population dynamics. The occurrence of frost events, prior to cold-hardening in the fall or after catabolism in the spring, is a significant cause of spruce beetle mortality. Elevated spring and fall temperatures associated with climate change result in decreased rates of cold-induced mortality (Bentz et al., 2010). Additionally, high winter temperatures ensure increased overwinter brood survival and increased emergent populations (Werner et al., 2006).

Host Resistance

Spruce beetle outbreaks are facilitated by sufficient quantities of host material – dead, dying or stressed trees. In western Canada, climate models indicate warmer mean annual temperatures, and increased annual precipitation (Figures 6 and 7) (Environment Canada, 2012). Increases in precipitation are expected to occur mostly in the winter months; whereas increases are negligible in the summer months (IPCC, 2007). Summer temperature increase without a relative precipitation increase may result in more severe and more frequent drought events (Barber et al., 2000). Widespread drought-related moisture stress can provide endemic spruce beetle populations with sufficient host material to grow to epidemic levels (Berg, et al., 2006).

Host Abundance

The spruce beetle is a native ubiquitous insect and therefore, is found throughout the entire range of spruce species in North America. Climate change does not provide the spruce beetle with the opportunity to expand its range. Spruce distribution (and consequently spruce beetle distribution), may migrate in response to warming climate conditions as new habitats become climatically suitable. This change in distribution may result in altered patterns of host material across the landscape and may change population and outbreak dynamics (Bentz et al., 2010).

A study by Bentz et al. (2010) predicted the probability of univoltine spruce beetle development throughout its range in North America. Their model simulated past and future climates from 1961 through 2100 using the Canadian Regional Climate Model. They predicted substantial increases in spruce forest area and markedly higher univoltine brood development probabilities (and therefore increased probabilities of population outbreak) throughout the 21st century. They noted the significant temporal and spatial variability within their findings, and emphasised that temperature regime changes may not necessarily enhance all aspects of spruce beetle population development (Bentz et al., 2010). Figure 8 shows the predicted probability of univoltine spruce beetle development in North America.

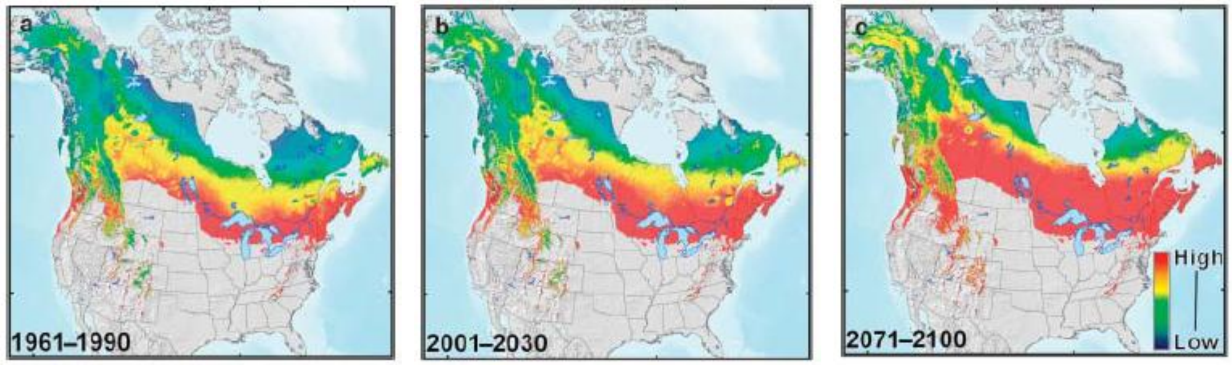

Figure 8: Predicted probability of univoltine spruce beetle development in North America during three climate normal periods: (a) 1961-1990, (b) 2001 -2030, and (c) 2071-2100 (Adapted from Bentz et al., 2010).

3. Ecological Implications for Forest Management

Spruce beetle disturbance influences a suite of ecological and socio-economic forest values. Alterations to spruce beetle disturbance regimes stand to fundamentally change the scope of these values in spruce-prevalent landscapes. With spruce beetle outbreak probabilities increasing in conjunction with changing climatic regimes, the severity and scale of outbreak implications can be expected to increase. The ecological implications of climate change and altered spruce beetle disturbance regimes are identified and discussed below.

Stand Structure and Succession

Impacts to stand structure and succession following spruce beetle disturbance are highly variable. The wide variation in stand structure and successional response to spruce beetle disturbance is a function of inter-related factors. Site condition, initial forest composition, and infestation severity dictate the resulting stand structure and successional pathway following infestation (Boucher & Mead, 2006). Mortality is variable and can range from several scattered trees to 90% overstory removal (Humphreys & Safranyik, 1993).

Initial forest composition influences post-disturbance vegetation succession and stand structure (Boucher & Mead, 2006). Mixed-species stands with spruce components become more homogenous as spruce populations dwindle following spruce beetle disturbance (Allen et al., 2006). As stand density decreases, residual trees are released from competition with spruce in the dominant and co-dominant canopy layers. This can constitute a major stand composition shift to shade-tolerant species as suppressed trees are released in the understory (Veblen, et al., 1991). Mixed deciduous-spruce stands have shown diminished or insignificant vegetation composition shifts following infestation. Infestations in continuous, spruce stands, or stands with majority spruce components, can invoke a major shift towards early successional herbaceous-shrub-woodland complexes (Boucher & Mead, 2006).

Post-disturbance spruce seedling re-establishment is limited. Successful establishment requires exposed tracts of mineral soil. Spruce beetle disturbance tends not to disturb the forest floor and create the sites necessary for seedling establishment. Without subsequent disturbances such as windthrow or wildfire, the seedbeds necessary for natural spruce regeneration are rare (Ross et al., 2001). Thick humus layers and vigorous vegetation competition (due to increased light levels) further inhibit seedling establishment following infestation. These factors can cause significant delays in stands returning to pre-disturbance states and facilitate the shift to woodland complexes (Allen et al., 2006).

By attacking older, large-diameter trees, spruce beetle infestation reduces average stand diameter, height, density, and age (Ross et al., 2001; Allen et al. 2006). This can also result in shifting basal area dominance to co-dominant species (Veblen et al., 1991). The targeting of larger spruce trees, also leads to a reduction in stand structural complexity and shift to earlier successional stages (Allen, et al., 2006).

Wildfire

Wildfire can act as an important secondary disturbance agent in spruce beetle-killed stands and has far reaching implications for almost all ecological values of spruce forests. Impacts to ecological values from wildfire will vary with respect to fire intensity, size, and frequency. Spruce beetle infestation can significantly increase fire hazard across spruce-prevalent landscapes by increasing surface and crown fuel loads (Garbutt et al., 2006). Slow decay, characteristic of many spruce stands, can ensure that elevated fire hazard persists long into the future. Studies in the Yukon in dry, continental climates showed that it can take up to 70 years for all dead stems to fall to the ground post spruce beetle infestation (Garbutt et al., 2006). This timeframe is reduced in more temperate climates, where decomposition rates are markedly higher, although there can still be significant delays (Garbutt et al., 2006). In a study in Colorado, up to 85% of spruce stems remained standing 25 years post-spruce beetle infestation (Ross et al., 2001). For this time, vertical continuity in the fuel structure is maintained and the likelihood of fast-spreading crown fire is increased (Garbutt et al., 2006).

Wildfire risk in spruce beetle-killed stands is a function of tree mortality, time since infestation, and site conditions (Ross, 2001). Fine fuels slowly accumulate on the forest floor post-infestation as needles and branchlets are shed. As beetle-killed crowns thin post-infestation, woody surface fuels increase substantially, and wildfire hazard increases accordingly (Garbutt et al., 2006). Eventually, vertical fuel continuity is decreased to the point where it limits the wildfire hazard of further surface fuel accumulations. At this point, intense post-infestation wildfire hazard will begin to decline (Garbutt et al., 2006). With increased drought predicted for western Canada due to climate change, wildfire disturbance post-spruce beetle infestation may become increasingly important in forest management (Amiro & Flannigan, 2004).

Hydrology and Aquatic Ecosystems

Alterations in vegetation coverage following spruce beetle disturbance have significant implications on forest hydrological processes. Streamflows are markedly higher following spruce beetle infestation due to reductions in interception and evapotranspiration. This increase in streamflow varies based on watershed characteristics but can persist up to 25 years (Bethlahmy, 1975). Decreased canopy interception following infestation can lead to increased snow accumulation and in turn, earlier and larger run-off peakflows (Ross et al., 2001). This effect may be lessened or negligible in stands with dense branch networks, typical of slow growing spruce stands due to residual branch network interception (Garbutt et al., 2006).

Stream ecosystems are directly affected by alterations in forest stand structure and composition. The course of succession following spruce beetle disturbance dictates the magnitude and duration of these changes (Ross et al., 2001). Alterations in riparian vegetation can affect both the physical and biological characteristics of riparian ecosystems (Beschta, 1998). Litterfall is the primary energy source in low order streams. Changes in riparian vegetation composition and structure resulting in altered litterfall can influence entire aquatic energy and nutrient regimes. Changes in aquatic energy flows can have significant effects and can affect adjacent and downstream ecosystems (Ross et al., 2001). Additionally, changes in riparian vegetation structure can affect a number of channel properties through alterations in coarse woody debris accumulations (Sedell et al., 1988). Channel pattern, pool characteristics, sediment accumulation, and energy dissipation are all influenced by these accumulations (Ross et al., 2001).

Wildlife

Stand structure and composition changes following spruce beetle disturbance can have a wide range of effects on wildlife species. These effects are highly variable and depend on species' specific habitat requirements, the infestation characteristics, and the successional processes that follow the disturbance. The successional progression and disturbance patterns post-infestation will dictate the subsequent duration and magnitude of changes in wildlife populations (Ross et al., 2001). Studies in Alaska following a major spruce beetle outbreak have demonstrated that diverse wildlife communities can be maintained in beetle-killed stands (Werner et al., 2006).

Mortality of mature spruce following spruce beetle disturbance can result in understory response of forage species. This flush of forage can benefit ungulates and other wildlife species dependent on abundant browse; whereas, species that depend on continuous mature spruce stands or clumped spruce distributions, may struggle to have their habitat requirements met (Holsten et al., 1999). Species that use white spruce for food or for nesting are the most significantly impacted following spruce beetle disturbance (Werner et al., 2006). Small mammal populations have been shown to decrease following spruce beetle disturbance due to declines in spruce seed abundance (Ross et al., 2001; Werner et al., 2006). In contrast, species that forage on grasses and herbs may flourish post-outbreak, if successional processes trend towards herbaceous-woodland complexes (Ross et al., 2001). Woodpecker abundance may increase during spruce beetle outbreaks due to the readily available beetle prey; however, populations will decline with decreasing food stocks as the outbreak runs its course (Ross et al. 2001).

Climate Change Feed-Back

Insect disturbance is one of the main factors influencing forest carbon budgets in North America. Significant changes in insect disturbance regimes may significantly reduce the ability of forests to sequester atmospheric carbon (Kurz et al., 2008). The current mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic has shifted western North American pine forests from net carbon sinks to net carbon sources (Kurz et al., 2008). Like spruce beetle disturbance, the current mountain pine beetle outbreak has been facilitated, in part, by climate change (Carroll et al., 2004).

With respect to forest carbon dynamics, implications arising from increased spruce beetle disturbance as a result of climate change, may be equally important to the implications of increased mountain pine beetle disturbance. Climate change has already facilitated increased spruce beetle fecundity and spruce herbivory with continued increases in spruce beetle outbreak expected throughout the 21st century (Berg et al., 2006; Bentz et al., 2010). If increased spruce beetle disturbance limits forests' capabilities to sequester carbon, forest carbon budgets will be impacted. In conjunction with wildfire, spruce beetle infestations could work to shift spruce forests from net carbon sinks to net carbon sources. This impact to the global carbon cycle could create positive feedback in climate systems and further contribute to climate change (Kurz et al., 2008).

4. Responses for Forest Managers

Spruce beetle disturbance is a natural and important part of forest ecosystem dynamics in forests with spruce components. Climate change is occurring, and with it, spruce beetle disturbance is expected to become more prevalent. A suite of ecological and socio-economic impacts accompany spruce beetle disturbance, the scale of their impacts varying with respect to disturbance frequency, severity, and spatial characteristics (Bentz et al., 2010). But climate change stands to change much more than just forest disturbance regimes. With dramatic changes on the horizon for all forested landscapes in western Canada, it is difficult to discern what the best course of action is for forest management as a whole. Do we embrace the changing climate and let it take its course? Cling to what we have and manage to retain our current forests and values? Or do we pursue some sort middle ground? Regardless of where forest management is headed, more research is necessary to gain insight on the implications of climate change on forests. And regardless of where forest management is headed, forest managers will need to cope with the issues that arise along the way; one of them being altered forest insect disturbance regimes. The following section provides an overview of the tools and strategies that forest managers have at their disposal to effectively manage spruce beetle disturbance.

Forest managers are tasked with mitigating the ecological and socio-economic impacts of changing spruce beetle disturbance regimes in response to climate change. Treatments that reduce spruce beetle populations or reduce the susceptibility of stands to infestation can be used to control spruce beetle outbreak dynamics. Treatments that achieve these objectives can be categorized as direct controls, or indirect controls, respectively (Carroll, et al., 2006). These treatments in conjunction with effective monitoring, current forest inventories, and strategic access development can form the basis of effective, integrated landscape-level infestation prevention (Shore et al., 2006). Direct and indirect control principles are summarized below in addition to the integrated approach necessary to effectively manage spruce beetle disturbance across the landscape. Additionally, a number of forest development considerations applicable to harvest planning in spruce-prevalent stands to minimize the likelihood of outbreak development are also discussed.

Direct Control

Direct control methods work to temporarily reduce insect populations to limit significant damage to forest stands in the short-term. Direct control methods limit population growth by directly killing target species. If enough mortality is introduced into the population, the rate of population increase can be limited. Ideally, direct control treatments will shift epidemic populations back to their endemic phase (Carroll et al., 2006). Direct controls are reactive and treat spruce beetle populations in the short-term and at the stand level.

Mechanical, semiochemical, and chemical (rare) treatments are employed as direct controls and include operations such as:

- Sanitation harvesting and processing,
- Felling and destroying (fall-and-burn),
- Conventional and lethal trap trees, and
- Pheromone baiting.

(Humphreys & Safranyik, 1993; Carroll, 2010c)

Sanitation harvesting and processing is the most common direct control tactic (Humphreys & Safranyik, 1993). Where economically feasible, infested individual trees, group of trees, or stands, are harvested, transported to mills, and processed. Processing in mills must occur prior to brood emergence and dispersal. Sanitation harvest treatments are limited by access, tenure, non-timber forest values, and economic constraints (McMullen et al., 1986). Where harvesting and processing is not economically or operationally feasible, felling and destroying infested stems may be a viable option. Infested stems can be felled, bucked and burned on site to kill beetle broods (Humphreys & Safranyik, 1993). High-intensity fire is required to cause sufficient brood mortality; this requirement reduces treatment feasibility. Where high-intensity burning is impractical, felled trees may be debarked to kill broods (Carroll et al., 2006). Debarking trees is labour intensive limiting its implementation feasibility (Carroll et al., 2006).

Semiochemical treatments, such as trap trees and pheromone baiting, are often used in conjunction with sanitation harvest or fall-and-burn operations. Trap trees are useful in treating areas with light infestations or in “mopping-up” spruce beetle populations post-harvest (Humphreys & Safranyik, 1993). To create conventional trap trees, green spruce are felled prior to beetle emergence and dispersal. Felled spruce are more desirable to attacking beetles and can host up to 6 times the beetle population relative to standing green trees (Humphreys & Safranyik, 1993). Conventional trap trees are then removed or destroyed following attack. Lethal trap trees are injected with insecticide and felled 10-14 days later (prior to beetle flight) (Humphreys & Safranyik, 1993). Aggregation pheromone baiting may be used to concentrate spruce beetle attack in previously infested areas or areas slated for harvest or treatment. Anti-aggregation pheromone treatments can also deter imminent spruce beetle attack from high value stands (Carroll et al., 2006).

Direct control methods require specific information on spruce beetle population dynamics. For direct control to be effective, beetle mortality must outweigh reproduction. Direct control treatment intensity must therefore vary in accordance with local population dynamics. It is also imperative that direct control treatments are applied in a thorough and timely manner with regular post-treatment monitoring and follow-up treatments (if necessary). When populations are small (endemic) and detectable, direct controls can prove effective permitting the scale of treatment is logistically possible. Initial outbreaks are also treatable with direct control methods if affected areas and incipient populations remain relatively small (Carroll et al., 2006). The efficacy of direct control treatments on landscape-level outbreak population dynamics is negligible due to the relative outbreak population numbers and the logistics of implementing a direct control treatment regime across the landscape in a timely manner. Limited access to remote stands and budgetary restrictions are major constraints on direct control treatment feasibility (Whitehead et al., 2006; Shore et al., 2006).

Indirect Control

The risk of spruce beetle infestation is a function of the susceptibility of stands, the arrangement of stands on the landscape, and the size, dynamics, and location of incipient populations. Indirect controls address stand susceptibility and arrangement; whereas, direct controls address beetle population-specific concerns. Indirect controls are considered proactive in that they work to stop, or to lessen the impacts of spruce beetle infestation prior to an actual outbreak occurring (Shore, et al., 2006). Strategic application of indirect control treatments at the stand level can work to reduce landscape-level susceptibility, and in turn limit likelihood of the landscape-level outbreaks we have witnessed in past decades. Indirect controls require well-planned and consistent management practices over long-term planning horizons to be effective (Whitehead et al., 2006). Recommendations made by Hopping and Mathers (1945) and reiterated by Carroll et al (2006) for the mountain pine beetle, are relevant to the importance of indirect control and disturbance by the spruce beetle:

- 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.

(Adapted from Carroll et al., 2006)

Indirect control strategies depend on two main components to limit landscape-level spruce beetle infestation: landscape planning and silvicultural intervention (Whitehead et al., 2006).

Landscape Planning

Landscape planning involves a detailed analysis and ranking of the relative susceptibility of spruce stands across the landscape. This process relies on current forest inventories and effective monitoring programs to properly identify, analyze, and rank stands. Access development priorities should also be determined at this level with consideration of both direct and indirect control treatments (Whitehead et al., 2006). Stand replacement is the most effective management action in lowering landscape spruce beetle susceptibility (Whitehead et al., 2006). Within the landscape planning framework, after high-ranking susceptible stands are identified, stand replacement planning can begin.

Stand replacement is the complete or partial removal of susceptible spruce stands and the re-establishment of stands in accordance with landscape management objectives. When replacing stands, managers should strive for mixed age-class distributions, and increased tree species diversity in the resulting stands. At the landscape level, stand replacement should occur in a manner that works to disrupt continuous areas of mature spruce and increase landscape vegetation variability (MOFR, n.d.). Age and species mosaics with generally younger and more widely separated spruce components are favourable in the mitigation of landscape-level spruce beetle outbreak (MOFR, n.d.; Whitehead et al., 2006).

Silvicultural Intervention

Silvicultural intervention can be employed in the management of susceptible stands and in the management of replacement stands to limit conditions encouraging spruce beetle outbreak. Silvicultural intervention is an important component of landscape-level spruce beetle management and should emphasize stand vigour and hygiene while promoting tree species diversity (Whitehead et al., 2006). A number of silvicultural treatments can contribute to these objectives, including:

- Host material removal to limit epidemic population development,
- Density management (thinning, partial harvest) to increase stand vigour and spruce resistance,
- Promotion of alternative tree species compositions to limit the relative impacts of future spruce beetle disturbance (with climate change in mind),
- Shortening harvest rotations to decrease the extent of old, susceptible stands across the landscape, and
- Diameter-limit and single-tree selection harvests to decrease the abundance of susceptible host trees.

(MOFR, n.d.; Humphreys & Safranyik, 1993; Whitehead et al., 2006)

Integrated Management Approach

Alone, direct and indirect controls are insufficient in mitigating landscape-level spruce beetle outbreaks. Direct and indirect controls, instead, should be used in conjunction under strategic landscape-level plans to limit the likelihood of large-scale infestations. Strategic landscape-level plans can incorporate spruce beetle disturbance management into overarching forest values such as biodiversity, wildlife, water quality, recreation, fire hazard, and aesthetics. Current forest inventories, effective spruce beetle monitoring programs, and strategic access development are crucial in ensuring the efficacy of landscape-level infestation prevention programs. These activities facilitate the effective implementation of direct and indirect control treatments in a timely and consistent manner. It is imperative to maintain these management activities when beetle populations are endemic and not necessarily in outbreak. In endemic periods, management focus on spruce beetle disturbance may shift and be lessened, only to escalate when epidemics occur. This can result in futile treatment efforts during epidemic phases, with no real improvement of landscape susceptibility in the interim. This approach should also be viewed through a socio-economic lens. Management usually incorporates a broad range of resource objectives and values. These objectives and values should be taken into consideration accordingly (Shore et al., 2006).

Forest Development Considerations

A number of considerations are applicable when planning development in spruce-prevalent stands. Anthropogenic disturbances can result in the development of epidemic spruce beetle populations without proper consideration of on-the-ground operational practices. Activities that increase on-site host material volume or that decrease residual tree vigour encourage post-operation spruce beetle infestation should be avoided. To limit the likelihood of spruce beetle infestation stemming from forest operations, actions should be taken at all opportunities to avoid:

- Accumulations of host material,
- Soil disturbance that impacts hydrological function and residual tree vigour,
- Mechanical damage to residual stems, and
- Cut-block layouts that result in windthrow hazard for residual stems.

(Humphreys & Safranyik, 1993)

These recommendations are based on minimizing on-site host material and avoiding damage that reduces the vigour of residual trees. By avoiding host material accumulations, endemic spruce beetle populations are less likely to grow to epidemic sizes, and by maintaining residual tree vigour, future infestation may be avoided (Berg, et al., 2006; Whitehead et al., 2006). Monitoring should occur for two years post-harvest, to determine the presence of infestation in residual trees and adjacent stands so the necessity of direct control treatments can be assessed (Humphreys & Safranyik, 1993).

5. Conclusion

Through changes in developmental timing, temperature-mediated population mortality, and host resistance, climate change stands to significantly alter spruce beetle disturbance regimes throughout western Canada. Projections from current climate models indicate an increased probability of spruce beetle population outbreak across North America. Increased spruce beetle disturbance may alter a suite of forest functions and values long into the future. In some cases, these alterations may surpass historical resilience boundaries, resulting in irreversible ecological changes in stand structure and succession, wildfire, hydrology and aquatic ecosystems, wildlife, and forest carbon dynamics in spruce-prevalent landscapes.

Direct and indirect control treatments used in conjunction with current forest inventories, effective spruce beetle monitoring programs, and strategic access development, provide forest managers with effective means to respond to increased spruce beetle disturbance within an integrated management framework. These treatments however, are limited by economic, operational, and policy-driven constraints. Additionally, there are a number of harvesting considerations for spruce beetle that forest managers should incorporate into harvest planning.

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