



Swedish University of
Agricultural Sciences

Population dynamics of tree-killing bark beetles - a comparison of the European spruce bark beetle and the North American mountain pine beetle

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Ips typographus



Dendroctonus ponderosae

Introductory Research Essay
Department of Ecology
SLU

No 10

Uppsala 2010

Introductory Research Essays

Department of Ecology, SLU,

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Abstract

During outbreak periods, the European spruce bark beetle and the North American mountain pine beetle are able to kill millions of coniferous trees. Throughout the 20th century, six outbreaks have occurred in Sweden and four in British Columbia, with about 20-year intervals in both regions. The outbreaks of the mountain pine beetles seem to grow much larger and last longer compared to the outbreaks of the spruce bark beetles. Over the years, the mountain pine beetle has killed about 60 million ha forest or 550 million m³ trees in British Columbia, which is at least one hundred times more than for the Spruce bark beetle in Sweden. Damages of both species have increased markedly in the last forty years. About 750 spruce bark beetles per m² are necessary to kill a healthy spruce, whereas seven times fewer, i.e., about 110 mountain pine beetles per m², are needed to kill a healthy pine. Furthermore, twice as many offspring per m² bark are produced by the spruce bark beetle compared to the mountain pine beetle. An explanation for the large differences in population dynamics between these two beetle species may spring from differences in (1) the availability of host trees, (2) number of specimens required to kill a tree, and (3) reproductive success. The latter is in turn affected by the intraspecific competition, nutrient content, and occurrence of fungi.

Introduction

Bark beetles (Curculionidae, Scolytinae) include at least 6000 species, distributed all over the world (Wood, 2007). A few of these species are able to colonise and kill living trees and thus are economically important species. Two such species are the European spruce bark beetle (SBB, *Ips typographus* L.) and the North American mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopk.), which are able to kill mature conifer trees (Amman, 1977; Wermelinger, 2004). The major host tree species utilized by the SBB in Europe is Norway spruce (*Picea abies* L. Karst.) whereas the MPB generally is associated with lodgepole pine (*Pinus contorta* Dougl.), even though it also attacks western white pine (*P. monticola* Dougl.), ponderosa pine (*P. ponderosa* Dougl.) and white bark pine (*P. albicaulis* Engelm.) occasionally (Wood and Unger, 1996). During endemic periods (i.e., when the population densities are low) both species breeds in wind-felled and weakened trees. However, during epidemic periods (i.e., when the population densities are high), both species breed in living trees that are killed in large numbers. In the following text this situation is referred to as an outbreak. In comparison, the MPB caused tree mortality in more than 13 million ha of conifer forests of western Canada between 1999 and 2005 (Raffa et al., 2008). Furthermore, in 2008 alone, the area affected by the MPB increased to 14 million ha in British Columbia and Alberta (Lindgren, 2009). The SBB is estimated to have attacked more than 3 million ha of spruce forest in Europe, resulting in more than 32 million m³ of killed trees, between 1990 and 2001 (Grégoire and Evans, 2004). In addition to causing economic losses, bark beetle outbreaks change forest structure and composition.

In recent years, the magnitude of bark beetle outbreaks has increased, and have also expanded into locations that previously have only rarely been affected, maybe as a result

of climate change (Raffa et al., 2008). Thus, it is important to understand the causes behind outbreaks, which factors that influence outbreak magnitude and why the populations collapse. In this review I compile the most recent knowledge about population dynamics of the SBB and the MPB. The aim is to analyze and gain a better understanding of the underlying causes of differences in outbreak patterns between the two species.

The review consists of the following parts: (1) a description of the life cycles of the two species, (2) basic theory on population dynamics, (3) a compilation of outbreak histories, and analyses of outbreak patterns, of the SBB in Sweden and the MPB in British Columbia in Canada, and (4) an analysis of differences in population dynamics between the two species.

Life cycles

Many aspects of the biology of the SBB and the MPB have been known for a long time (for reviews see e.g., Christiansen and Bakke, 1988; Safranyik et al. 2006). Here follows a short summary of the life histories of the two species.

The first spring-flight by the SBB occurs when air temperatures rise to about 20 °C (Christiansen and Bakke, 1988). The lowest flight temperature for the MPB is about the same as for the SBB, i.e., 19 °C -21 °C (Safranyik and Wilson, 2006). But, one important difference between the species is that the flight period of the MPB starts much later in the summer. At endemic population levels, the beetles are unable to colonise healthy trees and therefore they are restricted to recently killed or dying trees such as wind throws, which are commonly used by the SBB, or trees affected by drought, rain or struck by lightning which are preferred by the MPB (Berryman, 1999). When finding a suitable tree, males of the SBB and females of the MPB bore an entrance hole through the outer bark into the phloem layer under the bark. The inner bark is food for the larvae.

In a first step the SBB distinguish their host trees through chemical compounds released from the trees, so-called kairomones, and in a second step, males release several pheromone components that strongly attract both males and females (Schlyter et al., 1987; Paynter et al., 1990). Also the MPB has aggregation pheromones that attract both sexes. In this species, females are the pioneer colonizers, locating the host trees and when found, produce pheromone components that are mainly attractive for males (Aukema et al., 2008). The males have also pheromones, and they attract mainly females (Safranyik and Wilson, 2006). These aggregation pheromones can attract thousands of beetles to a tree. When the tree is almost completely colonized, the beetles can instead produce anti-aggregation pheromones which reduces attraction and thus intraspecific competition (Wermelinger, 2004).

When beetles attack healthy trees, they have to struggle against the tree defence. Apart from the constitutive defence in the form of resin, the trees also respond with induced defences as increasing flow of resin, containing toxic monoterpenes, diterpenes acids and

stilbene phenolics. Concentrations of these compounds rise in response to attack, and can vastly exceed the tolerance of the beetles (Raffa et al., 2008). If the beetles exhaust the host defensive response, the tree will die and beetle reproduction will be initiated. Accordingly, there are two factors that are determining whether the attacks are successful or not. First, it is the tree vigour (strength of constitutive and induced defence), and second, the number of beetles attacking the tree.

An important factor for the tree killing ability derives from the mutualistic relationship between the bark beetles and several species of blue stain fungi. In the MPB, fungal spores are inoculated from cuticular structures (termed mycangia) on the elytra, in which spores are carried into the trees when beetles bore through the bark. The MPB benefits from the association with fungi by feeding on it and by that the fungi contribute to the death of the host tree (Paine et al., 1997). The importance of fungi as a food resource is less known in the SBB. The SBB is however, known to carry at least four blue stain fungi species of the genus *Ophiostoma*, *Grosmannia* and *Ceratocytis*, of which *C. polonica* is able to kill healthy trees (Christiansen and Bakke, 1988; Persson et al., 2009), whereas the MPB is known to carry at least four species of the genus *Ophiostoma* of which some have been demonstrated to kill trees if inoculated (Paine et al., 1997).

Under the bark, the adults make nuptial chambers where the mating takes place. After mating, the females construct galleries where they deposit their eggs (Fig. 7). The SBB is polygamous with one to three or occasionally even more females per male. Each SBB female can lay up to 80 eggs per gallery (Wermelinger, 2004), but usually fewer during outbreaks as a result of higher attack densities and thus shorter egg galleries (Figure 7). The MPB is monogamous (one female per male), and the females can lay up to 60 eggs per gallery (Safranyik and Wilson, 2006). The number of deposited eggs per female depends on the length of the egg-galleries and is thus dependent on the rate of intraspecific competition (Anderbrant, 1988). Successful breeding of both species in living trees is dependent on the death of all or part of the trees.

The development time from egg to adult depends on temperature. In a study of the SBB, the average time from egg to adult beetle was 46 days in 20 °C (Wermelinger and Seifert, 1998). Consequently, if the SBB lays their eggs in May, which is the most common start of the flight period in Sweden, the new generation of beetles should start to emerge in late June or early July. The SBB hibernates as adults in the autumn, either under bark or into litter at the base of the tree.

Due to the MPB's late summer flights, there is not enough time for the larvae to develop to adults before winter. Therefore, the MPB hibernates as larvae under bark. As an adaptation to this trait, the larval stage of the MPB is the most cold-tolerant stage in the life-cycle (Safranyik and Wilson, 2006). Depending on temperature, and thus geographic area, both species can produce one or more generations per year.

Basic theory on population dynamics

The most commonly used definition of a population is “a group of individuals of the same species that live together in the same place” (Berryman, 1999). The factors that affect the population size are birth and death, and emigration and immigration. Consequently, a stable population should have a balance between birth, death and migrations. When dealing with populations spread over geographic areas larger than the mean dispersal distances, the emigrations and immigrations could be assumed to balance each other. Thus, in this review I will exclude migration as a factor influencing the population dynamics of bark beetles (even though it might be important at a smaller scale).

Conditions influencing population dynamics can be divided into exogenous and endogenous factors. Exogenous factors affect the population size but are not, in turn, affected by it (i.e., population density independent). The exogenous factors may occur randomly, such as storms, precipitations and earthquakes, or non-randomly, such as, for instance, seasonality. Endogenous factors, in contrast, are dependent on population densities, such as, e.g., intraspecific competition and natural enemies (Figure 1). Endogenous factors act by population feedbacks. A negative feedback implies that the population growth declines when the population increases. For example, the number of predators can increase (numeric response) or shift to a certain prey (functional response) due to the population increase, which may lead to a population growth rate decline. There may also be positive feedbacks (Figure 1). For example, several thousand bark beetles may co-operate by attack and overcome the defense of their host tree. Feedbacks can occur with a time lag. A first-order feedback acts more or less immediately, whereas a second-order feedback acts with delay. The differences between the first- and second-order feedbacks are distinguished by whether the time lag is less or greater than the generation time. A well-known second-order negative feedback is when predators limit the population growth of a prey.

The reasons why populations not grow in eternity differ among organisms. One cause is resource limitations, such as for instance space, nests or food. If these causes are the main factors limiting population growth, the population is “bottom-up” controlled, i.e., there is not space, nests or food for everyone (Figure 1). “Top-down”-control mean that the population is regulated by a higher trophic level (e.g. by predators or herbivores). A good example of a negative feedback and “top-down” regulation is successful biological control.

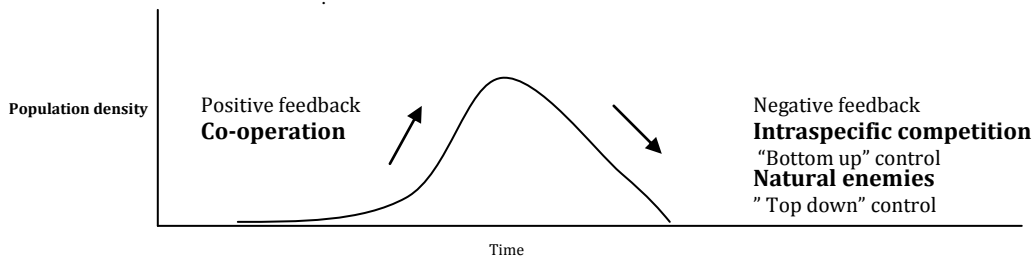


Figure 1. Endogenous (density dependent) factors. If population size increases from a low level, it can get affected by a positive feedback such as co-operation. When population density increases, it can be affected by negative feedback, such as for instance intraspecific competition or enemies.

Outbreak history of the spruce bark beetle in Sweden and the mountain pine beetle in British Columbia

For a comparison with the SBB outbreaks in Sweden, British Columbia was chosen due to the large amount of information available about the tree mortality caused by the MPB. In addition, the two regions are about equal in size, have a temperate climate, and a large proportions of coniferous forests.

Data of outbreaks from Sweden and British Columbia were generally compiled from government reports, mainly from the Forest Insect and Disease Survey, Canadian Forestry Service, Natural Resources Canada, British Columbia Ministry of Forests, and reports from the Swedish Forest Agency. These data are based on ground field estimates and in recent times also on surveys conducted from aircrafts. Outbreak data in Sweden are in general expressed as volumes (m^3) of killed trees, whereas data of distinct outbreak periods from British Columbia usually are expressed in hectares (ha) of forests with tree mortality. For the MPB, these attacked areas are classified due to severity of damage ranging from trace ($<1\%$ tree mortality) to very severe ($>50\%$ tree mortality) (Tim Ebata - Forest Health Initiatives Officer in British Columbia, personal comm.). Volume data of tree mortality in British Columbia are also available but not used to a great extent, due to the complex and somewhat difficult task of converting the areal estimations to volume. To make it possible to compare the outbreaks of Sweden and Canada, data of volumes are used in general, but also areal data for the MPB.

To get an overview of temporal trends of outbreak history, data were grouped in four time periods: 1910-1940, 1940-1970, 1970-2000 and 2000-2009. Data from the outbreaks are compiled in table 1 and 2 and figure 2-6.

- 1910-1940

For Sweden an outbreak was reported 1911-1912, but few data exist from this outbreak. It was suggested that this outbreak, with a size of about 50 000 m³, could have been caused by drought and high snow pressure in the previous year (Lekander, 1950). In the 1930's, outbreaks progressed more or less simultaneously in Sweden and British Columbia. The Swedish outbreak was following after three storms in 1931 and 1932 which resulted in 5.5 million of wind-throws (Trägårdh, 1935; Lekander, 1972). Subsequently, the SBB killed about 48 000 m³ of trees during the three following years (1933 to 1935) (Butovitsch, 1941). In British Columbia a long drought period in the 20's was the probable reason for the later outbreak (Trzcinski and Reid, 2009). This outbreak between 1930 and 1936 resulted in a lodgepole pine area of 650 000 ha with killed trees (Wood and Unger, 1996). For the volume of killed forest however, data are not available, except for 1931-1932 and 1935. However, probably more than 3 000 000 m³ trees were killed in British Columbia during this period (Forest Insect and Disease Survey, Canadian Forestry Service, Natural Resources Canada through Tim Ebata - Forest Health Initiatives Officer in BC, personal comm.; Wood and Unger, 1996).

- 1940-1970

A SBB outbreak started in 1947 and continued until 1952 after a storm hit central Sweden in the end of 1945. This time, the SBB killed about 120 000 m³ of spruce forests (Lekander, 1950). A few years later, in 1955-1965, 135 000 ha of white pines (*Pinus strobus*) were killed by the MPB on the Vancouver Island in British Columbia (Wood and Unger, 1996). Other sources estimate the volume of killed forest in British Columbia over the same period to about 1 500 000 m³ (Forest Insect and Disease Survey, Canadian Forestry Service, Natural Resources Canada through Tim Ebata - Forest Health Initiatives Officer in BC, personal comm.). Compared to other outbreaks in the Canadian province, this outbreak was relatively small, but anyway at least ten times larger than the outbreak in Sweden over the same period. This outbreak in British Columbia lasted for more than 10 years, i.e., two times longer than the Swedish outbreak (Table 1 and 2).

- 1970-2000

In the fall of 1969, both Sweden and Norway were struck by a heavy storm. About 35 million m³ spruces and pines were storm-felled in Sweden (Eidmann, 1983). In addition, the forest was weakened due to snow damages in the previous year (Löyttyniemi *et al.*, 1979). There were also enhanced population levels of bark beetles due to bad forest hygiene in the 60's (Bo Långström, pers. comm.). These factors initiated the largest Swedish outbreak documented so far. During eleven years of outbreak (1971-1981) the SBB killed more than about 4.5 millions m³ trees (Eidmann, 1983). About the same amount of trees were also killed in Norway during same period (Økland and Bjørnstad, 2006). Another extensive outbreak in Sweden begun in 1996 and ended up in 1998, with

an amount of about 500 000 m³ killed trees per year. No storm initiated this outbreak and it is not known why this outbreak started (Samuelsson, 2001).

In British Columbia, enhanced population levels in the 70's are contributed to the outbreak in 1984. In this outbreak, over 483 000 ha killed trees. This was nearly three times the area harvested of all conifer species in British Columbia in 1982-1983 (Wood and Unger, 1996). The outbreak declined in 1985 as a result of -40°C or more in the wintertime which killed most of the overwintering brood. Furthermore, it continued to decline slowly until 1990 when the infestations were down to 41 300 ha (Wood and Unger, 1996) The total amount of killed forest during this outbreak period was about 1.2 million ha or 42.7 million m³ (Forest Insect and Disease Survey, Canadian Forestry Service, Natural Resources Canada, through Tim Ebata - Forest Health Initiatives Officer in BC, personal comm.).

- 2000-2009

Sweden has suffered from the largest tree mortality caused by the SBB per year in this period. In January 2005 the storm Gudrun felled about 70 million m³ forest (Svensson, 2007) and an outbreak initiated in the summer of 2006. This summer was warmer than normal and therefore a second brood occurred, which led to the highest tree mortality in a single year in Sweden. More than 1.5 million m³ trees were killed during 2006 (Svensson, 2007) compared to the two followed years when the beetles killed about 700 000 – 800 000 m³ each year (Anonymous, 2008). In 2009 the mortality rate decreased to 214 000 m³ (Lennart Svensson, pers. comm.). Thus, the total amount of killed trees is about 3.2 million m³.

The largest outbreak of the MPB so far initiated in British Columbia in 2001 (Figure 3 and 4). In the first two years, about 1.4 million ha of conifer trees were killed per year. In 2003 to 2005, the average raised up to 6.6 million ha per year (calculated from Taylor and Carroll, 2003; Safranyik and Wilson, 2006; Nikiforuk, 2007; Ebata, pers. comm.). In volume however, the average estimation of killed trees per year was about 55 million m³, with the extreme year of 2004 when about 130 million m³ trees were killed (Figure 3). The estimated volume killed trees in 2009 i.e., 46 million m³ (Figure 3) is based on a projection from 2008 by the British Columbia Forest service.

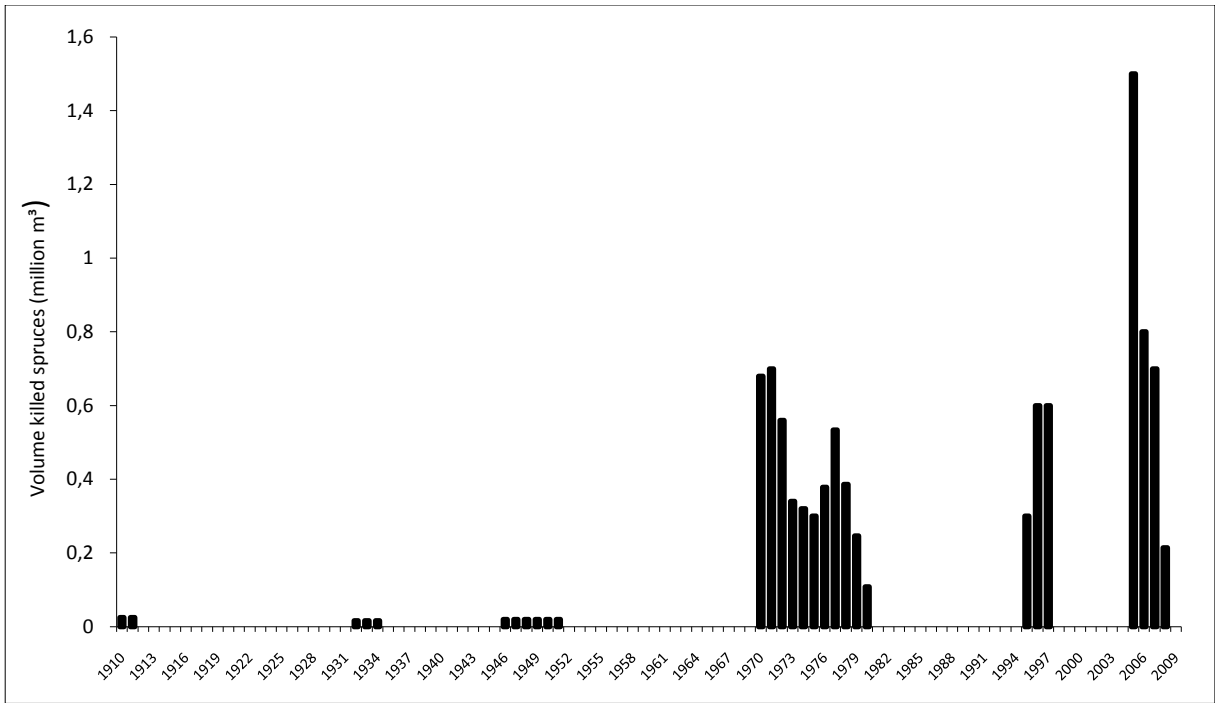


Figure 2. Estimates of tree mortality in volume caused by the spruce bark beetle during outbreaks in Sweden. Observe the increase of outbreak magnitudes in the second half of the 20th century. For the first three outbreak periods only data of the total amount of killed spruces are available. Hence, these data are divided by the number of outbreak years, to get an estimate per year.

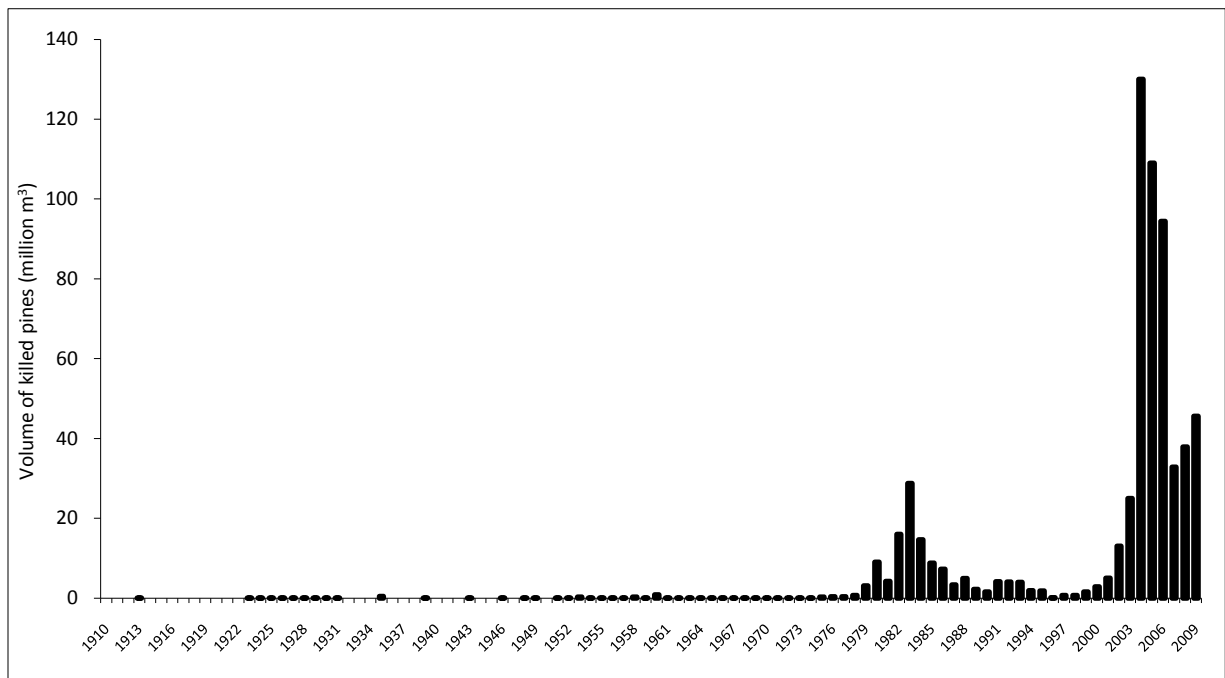


Figure 3. Estimates of tree mortality in volume caused by the mountain pine beetle during outbreaks in British Columbia. Observe the increase of outbreak magnitudes in the second half of the 20th century.

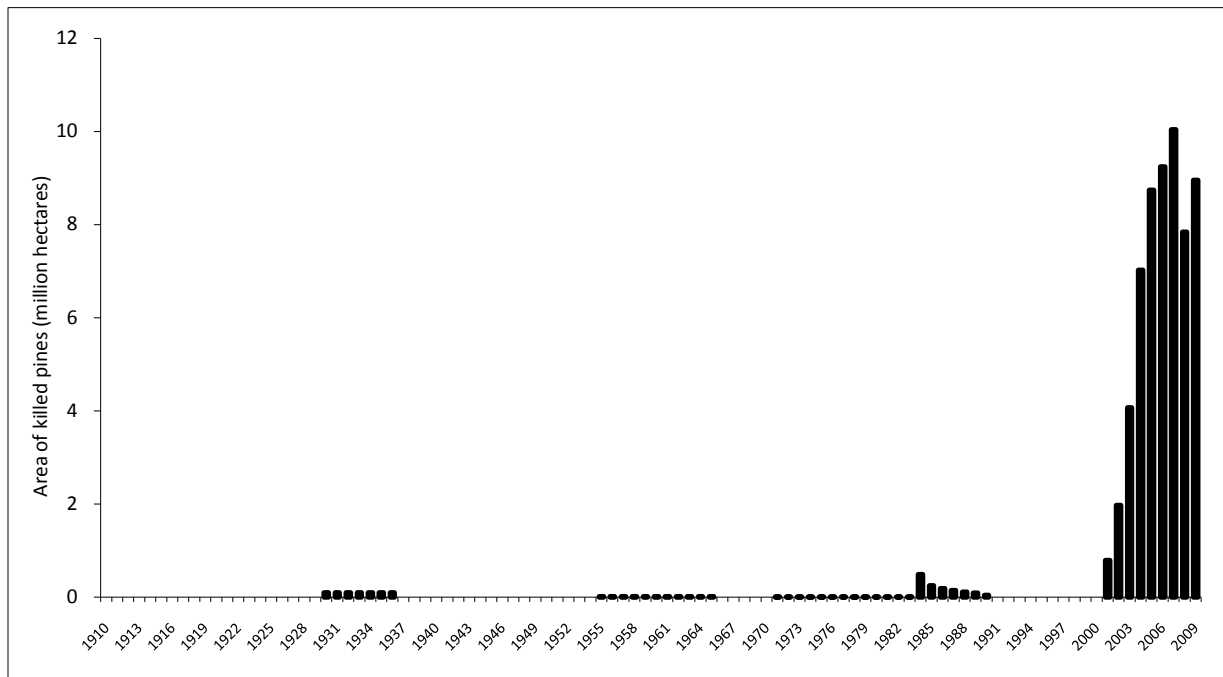


Figure 4. Estimates of tree mortality in area caused by the mountain pine beetle during outbreaks in British Columbia with four distinct outbreak periods. The infested pines in the 70's are not considered as an outbreak, but a large endemic population opening for the outbreak in the 80's. Observe the increase of outbreak magnitudes in the end of the 20th century and the extreme increase in the beginning of the 21th century. For the first three outbreak periods only data of the total area of killed pines are available. Hence, these data are divided by the number of outbreak years, to get an estimate per year.

Table 1. Spruce bark beetle outbreak periods, total volume of killed trees, mean volume of killed trees per year and outbreak durations and periodicity in Sweden (calculated as number of years between the first years of the outbreaks).

Outbreak period	References	Volume killed trees (m ³)	Volume killed per yr	Outbreak duration	Outbreak periodicity
1911-1912	Lekander 1950	50000	25000	2	
	Trädgårdh 1935;				
1933-1935	Lekander 1972	48000	16000	3	22
1947-1952	Lekander 1950	120000	20000	6	14
1971-1981	Eidmann 1983	4500000	409091	11	24
1996-1998	Samuelsson 2001	1500000	500000	3	25
	Svensson 2007;				
	Anonymous 2008				
2006-2009	Svensson, pers.com.	3200000	800000	≥4	10
Sum		9418000		29	
Average		1569667	25000	5.0	19.0

Table 2. Mountain pine beetle outbreak periods, total area of killed trees, total volume of killed trees, mean volume of killed trees per year and outbreak durations and periodicity (calculated as number of years between the first years of the outbreaks). The column of references refers to the column of area, whereas the reference of volume originates from Forest Insect and Disease Survey, Canadian Forestry Service, Natural Resources Canada and Province of British Columbia, Ministry of Forests and Province of British Columbia, Ministry of Forests through Tim Ebata pers. comm. but is to some extent revised by the other references.

Outbreak period	References	Area (ha) killed trees	Volume killed trees (m ³)	Volume killed per yr	Outbreak duration	Outbreak periodicity
1930-1936	Wood & Unger 1996	650000	3000000	428571	7	
1955-1965	Wood & Unger 1996	135000	1460000	132727	11	25
1984-1990	Wood & Unger 1996	1200000	42700000	6100000	7	29
2001-2009	Taylor & Carroll 2003; Safranyik & Wilson 2006; Nikifuruk 2007 Ebata, pers.com.	58700000	500 000 000	55555556	>9	17
Sum		60685000	547160000		>34	
Average		15171250	136058000	2081004	8.3	23.7

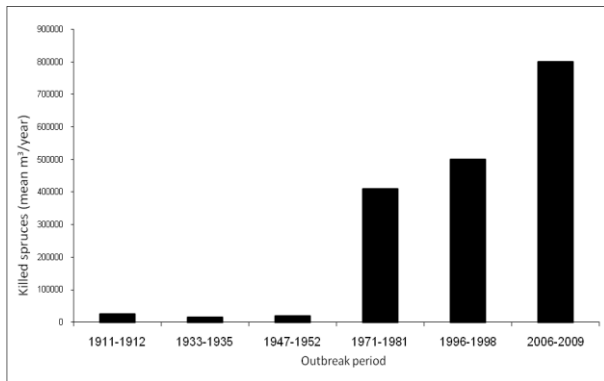


Figure 5. The outbreak periods of Spruce bark beetle in Sweden and the average volume of killed trees per year for each outbreak.

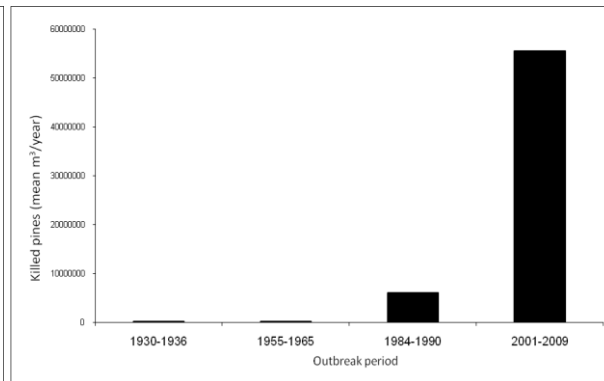


Figure 6. The outbreak periods of Mountain pine beetle in British Columbia and the average volume of killed trees per year for each outbreak.

General outbreak patterns

From the literature compiled in table 1 and 2, and figure 2 and 4, it is possible to discern six outbreaks in Sweden and four in British Columbia. Within the last one hundred years, outbreaks have been recorded for a total of 29 years in Sweden and more than 34 years in British Columbia (Table 1 and 2).

The outbreak patterns of the two species of bark beetles appear to differ from each other. Durations of outbreaks by the SBB are in average shorter than outbreaks by the MPB

(Table 1 and 2). The average duration of the SBB outbreaks is 5.0 years (Table 1), which is in accordance with populations in central Europe where outbreaks are suggested to last for three to six years (Wermelinger, 2004). This review suggests that outbreak durations of the SBB have been fairly constant over the years (two to six years), except from the outbreak in the 70's, which lasted for eleven years. The average when excluding this outlier is 3.6 years. The present outbreak in Sweden is now declining severely and will most probable be recorded as a four or possibly a five year period (Figure 2). In this review, the average duration of the MPB outbreaks, excluding the present outbreak, is 8.3 years (Table 2.) which also goes in line with the records of MPB outbreaks in British Columbia, where the literature suggest that a normal duration is five to ten years (Safranyik and Wilson, 2006). The shortest outbreak in Canada lasted seven years, and the longest eleven years. However, the present outbreak is so severe that it may continue even for longer.

The periodicity of outbreaks is similar for the SBB and the MPB in the two regions. Outbreaks roughly occur every 20 years for both species (Table 1 and 2). The different outbreaks were, however, not always located in the same geographical areas, which means that it is probably much longer periods between outbreaks at a local scale.

Outbreaks by the MPB are much larger compared to the SBB outbreak. In comparison with the MPB in British Columbia which has killed in total about 550 million m³ of pine forests, the SBB has killed about 1-2% of the quantity of killed forest in British Columbia. If comparing the ongoing outbreaks in Sweden and British Columbia, the ratio is not even 1%.

To conclude, the MPB has longer and much larger outbreaks compared to the SBB. Common for both species is that the outbreaks generally occur every 20th years at the national level and have increased markedly in magnitude during the last decades.

Future patterns

Tree mortality caused by both the SBB and the MPB to increase markedly during the last forty years, probably due to the changed climate conditions. In the future, different models predict even more storms and increasing temperatures (McMichael et al., 2006), which may result in even more stressed host trees and larger damages.

Factors influencing population dynamics

Availability of suitable host trees

One explanation for the much larger damages caused by the MPB, could be differences in forest structure between Sweden and British Columbia. Sweden has a history of a intensive forest management and an even forest age structure. In contrast, forest

management has been totally absent in some areas in British Columbia as a result of the underdeveloped road system (Lindgren, 2009). In addition, the age structure is uneven with a dominance of old stands that are susceptible for MPB attacks. This is mainly due to an efficient fire control, and that large-scale logging of logdepole pine did not occur until the 60's (Safranyik and Wilson, 2006). This has led to large areas of homogenous mature pines and a surplus of resources for the MPB populations.

Co-operation

Both the SBB and the MPB take advantages of co-operation when killing trees. A higher density of attacks by the SBB seems to be needed to kill a spruce, in comparison with the density of the MPB to kill a pine. During outbreaks, the SBB usually has about 500 egg galleries per m² in standing trees (Lekander, 1972; Weslien and Regnander, 1990), whereas the MPB usually has between 40 to 70 galleries per m² (Raffa and Berryman, 1983) (Figure 7). Using this data, and the assumption that the most common ratio are two females per male per egg gallery in SBB (Birgersson et al., 1984) and one male per female per egg gallery in the MPB, the number of attacking beetles per m² is about 750 SBBs and about 110 (median of 80 – 140) MPBs. Thus, it seems that the SBB need about seven times more beetles to kill a tree compared to the MPB.

Reproductive success

In standing trees during outbreaks, the SBB has a much lower reproductive success than the MPB. For the SBB, the mean numbers of daughters per female has been reported to be 0.77 (0.20- 1.75) (Lekander, 1972), and 1.18 (0.60 -1.75) (based on Weslien and Regnander, 1990). The reproductive success is decreasing vastly at the end of an outbreak. In comparison, the ratio of offspring per female in the MPB is about 10.3 (Latty and Reid, 2009), which corresponds to 6.8 daughters per female, since two-thirds of the MPB offspring are females (Safranyik and Wilson, 2006). Thus, the reproductive success seems to be one of the most important factors that differ between the SBB and the MPB.

Output of beetles

The SBB has a higher production of beetles per area bark in comparison to the MPB. A calculation from reproduction success of 0.97 daughters per females of the SBB (average of 0.77 and 1.18, of the SBB reproduction success, see above) and 6.8 daughters per female of the MPB times the number of egg galleries per m², i.e., 500 galleries for the SBB and 55 galleries (median of 40-70) for the MPB, gives a reproduction of 485 daughters per m² in the SBB and 308 daughters per m² in the MPB; or in total 970 (SBB sex ratio: 1:1 → 485 F + 485 M) beetles per m² and 462 (MPB sex ratio 2:3 → 308 F + 154 M) beetles per m², respectively. In other words, the SBB produces more than twice as many offspring per area than the MPB.

Some factors that may influence the reproduction success of the two species are intraspecific competition, interspecific competition, and natural enemies. In the following text the importance of each one of these factors will be discussed.

Intraspecific competition

For both the SBB and the MPB there is a negative correlation between attack density and reproductive success in successfully attacked trees (Raffa and Berryman, 1983; Anderbrant *et al.*, 1985). At lower attack densities, this translates into longer egg galleries (which means that more eggs are laid per gallery) and less competition between larvae, and thus, the population can grow rapidly (Figure 7). Forest disturbance may provide the SBB and the MPB with a sudden surplus of resources with weak defences that can be exploited by endemic populations that consequently are relaxed from intraspecific competition. For the SBB, droughts and storms with wind-felled trees result in sudden surpluses of breeding material. For the MPB, tree drought and stroke of lightning are the most common reason for weakened trees, resulting in relaxation from intraspecific competition. In the following summer, the beetle density may be high enough to overcome the defense of living trees, i.e., a co-operation that could result in an outbreak. Higher attack density in living trees leads, however to a higher degree of intraspecific competition.

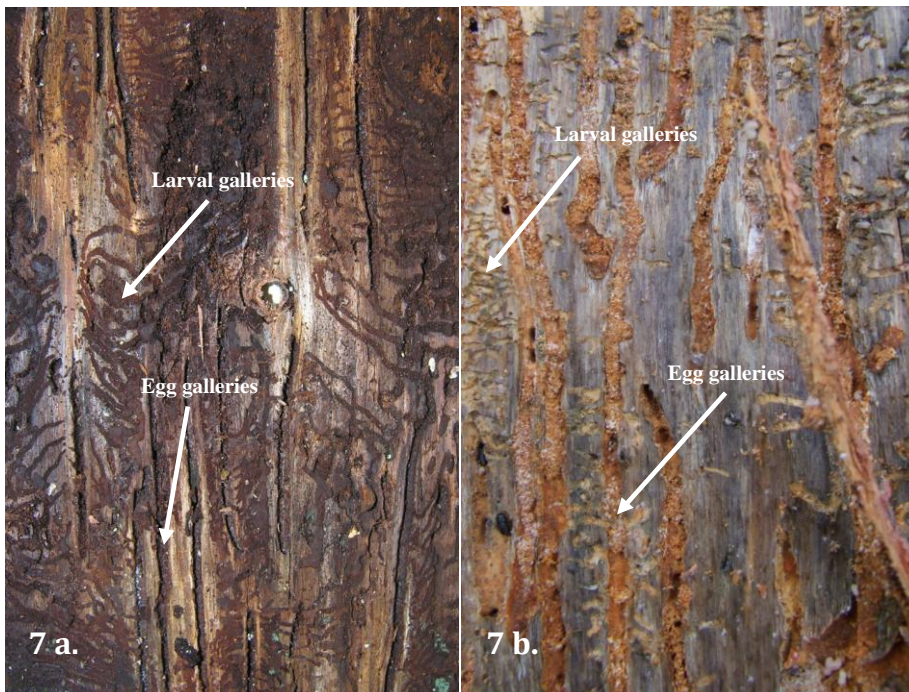


Figure 7. Egg galleries and larval galleries under the bark of the host trees of the Spruce bark beetle (7 a.) and the Mountain pine beetle (7 b.).

Also differences in nutrient quality between the tree hosts may contribute to the differences in reproductive success between the SBB and the MPB. There are indications of a higher nitrogen ratio in lodgepole pine compared to Norway spruce (Ingestad and Kähr, 1985). In addition, it may be that the MPB larvae have access to the host resources stored in the sapwood through the fungi (Sala and Lahr, 2009).

An outbreak may result in depletion of suitable host trees (Raffa and Berryman, 1983; Økland and Berryman, 2004) and the beetles are then forced to breed in trees with reduced nutritional quality or increased resistance which may negatively influence the reproductive success (Safranyik and Wilson, 2006). Depletion of suitable trees might be more important for the SBB compared with the MPB, due to the more efficient feature for the MPB to kill a suitable host tree. The importance of host tree depletion might be a more important factor the greater the outbreak is. At the most extreme, a total depletion of host trees may occur in certain circumstances. This seems to happen with the lodgepole pine in some parts of British Columbia during the ongoing outbreak and thus will end the outbreak. Because of the larger and longer outbreaks in the MPB, it is more likely that the MPB will suffer more by depletion of host trees compared to the SBB. This confirms the common theory that the number of susceptible host trees is one of the most important limiting factors of the size of bark beetle populations (Berryman, 1999).

Interspecific competition

Interspecific competition may in many cases be avoided as a result of different species using different parts of the tree trunk. However, negative effects on reproduction success as a result of competition between different bark beetle species have been reported (Schlyter and Anderbrant, 1993 and references therein). Interactions between the SBB and the double-spined bark beetle (*Ips duplicates*) resulted in lower reproduction and smaller body size in both species (Schlyter and Anderbrant, 1993). The six-spined spruce bark beetle (*Pityogenes chalcographus*) may also compete with the SBB. This species avoids trees with higher densities of the SBB, in order to reduce interspecific competition (Byers, 1993), even if they in lower densities can breed sympatric.

During outbreaks none of the species seem to be much effected by competitors because of their relative unique niche in live trees. However, the MPB seem to be somewhat less affected by interspecific competition during the epidemic conditions compared to the SBB, because the unique tolerance level it has for high tree defense (Safranyik and Wilson, 2006) and therefore the infested bark area is often fully colonized by the MPB (Berryman, 1976). However, during endemic condition the MPB might suffer a bit more than the SBB, due to their later flight period when the low-defence host trees already can be occupied by other species, e.g., by the pine engraver beetle *Ips pini* (Safranyik and Wilson, 2006).

Natural enemies

Bark beetles are used as food by a diverse group of natural enemies, including both woodpeckers and insects. The most common enemies associated with the SBB are predatory clerid beetles (*Thanasimus formicarius* and *T. femoralis*), flies (*Dolichopodidae*, e.g., *Medetera sp.*) and parasitic wasps (especially from the *Pteromalidae* and *Braconidae* family) (Weslien and Regnander, 1992; Wermelinger, 2004). The adult clerid beetles mainly feed on adult bark beetles, whereas the clerid larvae feed on immature bark beetles under the bark. Weslien and Regnander (1992) showed that *T. formicarius* may reduce the productivity of the SBB with almost 50%. One *Medetera spp.* larva can during its development kill 5-10 bark beetle offsprings (Weslien and Regnander, 1992).

The natural enemies of the MPB are closely related with the enemies of the SBB, and have the same niches. One of the most common enemies of MPB eggs and larvae is *Medetera aldrichii*. In certain situations this species can consume up to 50 % of the MPB eggs and it requires 5-15 MPB larvae to complete its development (Safranyik and Wilson, 2006), i.e., about the same number as a *Medetera spp.* can consume of the SBB (see above). As for the SBB, clerid beetles are important enemies on adults and larvae of the MPB, especially *T. undalatus* and *Enoclerus sphegeus*. Furthermore, a parasitic wasp of the *Braconidae* family (*Coeloides dendroctoni*) is considered as the most important parasitoid of the MPB (Safranyik et al. 2006 and references therein). This enemy preferentially parasitizes late instar MPB larvae and is more abundant in older established mountain pine beetle infestations (Safranyik and Wilson, 2006).

In both species of bark beetles, woodpeckers can consume large numbers of larvae, pupae and adults, and they may indirectly destroy many more by decreasing the reproduction area, by chipping away and reducing the thickness of the bark (Safranyik and Wilson, 2006). Compared with investigations on how the insect enemies affect bark beetle populations, woodpeckers are much less studied.

It is still under debate to what extent natural enemies influences outbreak dynamics in the SBB and the MPB (e.g. Reeve and Turchin, 2002; Wermelinger, 2004; Økland and Berryman, 2004). In the early phases of outbreaks, relaxation from the enemy impact may contribute to a rapid population increase of bark beetles. The SBB in outbreak areas is less affected by natural enemies compared to the SBB in an endemic stage. A lag time of three years seems to occur until outbreak populations reach the same magnitude of enemy impact as in endemic stage (Schroeder, 2007). At least the first years, this may be interpreted as the larger an outbreak gets, the less is the enemy pressure. It is unlikely that enemies are the main factor ending outbreaks of the SBB and the MPB. However, they may contribute when the outbreaks already have started to decline for other reasons.

Acknowledgement

I thank my supervisors Martin Schroeder and Thomas Ranius for useful suggestions and critical reading of the essay. I am also grateful to Tim Ebata (Forest Practices Branch, BC Min. of Forests), Bo Långström and Åke Lindelöw, which provided historical data on outbreaks of the two species of bark beetles.

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