

# Spruce Beetle

## A Synthesis of Biology, Ecology, and Management in Canada

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### Spruce Beetle

#### A Synthesis of Biology, Ecology, and Management in Canada

This book presents a synthesis of published information on the biology, ecology, and management of spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae), in Canada. It is intended as a reference for forest practitioners, researchers, and students. The volume is divided into two sections: history, biology, and ecology; and management and decision support systems. There are six chapters, which cover the following areas: taxonomy and outbreak history, biology and population dynamics, host finding and communication, ecological interactions, management, and decision support systems.

### Dendroctone de l'épinette

#### Une synthèse de la biologie, de l'écologie et de la gestion au Canada

Ce livre présente une synthèse des informations publiées sur la biologie, l'écologie et la gestion du dendroctone de l'épinette, *Dendroctonus rufipennis* (Kirby) (Coleoptera : Curculionidae), au Canada. Il s'agit d'un ouvrage de référence pour les praticiens de la forêt, les chercheurs et les étudiants. Le volume est divisé en deux sections : histoire, biologie et écologie ; et gestion et systèmes d'aide à la décision. Les six chapitres couvrent les domaines suivants : taxonomie et histoire des épidémies, biologie et dynamique des populations, recherche d'hôtes et communication, interactions écologiques, gestion et systèmes d'aide à la décision.

Front cover: Spruce beetle outbreak in Manning Park corridor, southern British Columbia. Photo: L. Maclauchlan.

Back cover: Adult spruce beetle. Photo: G. Smith

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## Preface

This book is dedicated to the biology, ecology, and management of spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae), in Canada. This volume would not exist without the foresight of Drs. Les Safranyik and Terry Shore, scientists with the Canadian Forest Service, Pacific Forestry Centre, who saw the need for such a synthesis more than 20 years ago. We are grateful to these scientists for their encouragement and contributions.

Historically, spruce beetle has impacted coniferous forests across Canada, from the Atlantic to the Pacific coasts. Outbreaks stimulated several seminal works on spruce beetle over the last 100 years. In the late 1800s and early 1900s, outbreaks in eastern Canada spurred two early works on spruce beetle biology and control by Swaine (1924) and Watson (1928). An outbreak in the 1940s in the western United States was extensively studied, leading to a comprehensive publication on biology and management in Colorado by Massey and Wygant (1954). The significance of Massey and Wygant's detailed biological observations and studies on spruce beetle is shown in Schmid and Frye's (1977) seminal review of spruce beetle in the southern Rocky Mountains in the United States, later augmented by Jenkins et al. (2014). Recent and on-going outbreaks in western North America over the last 50 years have further fuelled research and highlighted the need for a synthesis to serve forest practitioners, managers, and researchers in Canada.

This synthesis is divided into two parts: history, biology, and ecology; and management and decision support systems. The six chapters that comprise this volume cover spruce beetle taxonomy and outbreak history, biology and population dynamics, host finding and communication, ecological interactions, management, and decision support systems.

Katherine Bleiker, 25 March 2021

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#### **CHAPTER 1**

## Taxonomy and Outbreak History

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The insect we know today as spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae), was described in 1837 from specimens collected during Sir John Franklin's second overland journey to the Arctic Ocean. Spruce beetle was known by various names, largely differentiated by region and host, until 1969. The beetle is native to spruce forests across North America, and it plays a key ecological role by promoting nutrient recycling and biodiversity and by driving successional pathways. In some regions, favourable conditions periodically lead to outbreaks that cause significant mortality of large-diameter spruce. The earliest documented reports of outbreaks date back to the 1830s in both eastern and western Canada. Harvesting and land use changes through the 1800s and early 1900s have reduced the amount of susceptible spruce in the east. However, extensive and severe spruce beetle outbreaks remain a common occurrence in British Columbia and the southern Yukon. This chapter reviews spruce beetle's confusing taxonomic past, as well as its distribution and outbreak history across Canada.

#### I.I. Taxonomic History and Phylogeny

The first recorded specimens of the species currently known as *Dendroctonus rufipennis* were collected during Sir John Franklin's second expedition (1825–1827) *en route* to the Arctic Ocean by John Richardson (Kirby 1837). Richardson served as naturalist and surgeon on the journey, and he eventually sent the specimens to the English entomologist William Kirby at the recommendation of William Jackson Hooker. Kirby first described *Hylurgus rufipennis* Kirby (red-winged *Hylurgus*) in 1837 based on the "Many specimens taken in the Journey from New York to Cumberland-house and in Lat. 65°" (Kirby 1837, p. 195). No further specifics regarding the location or host trees were reported, although most of the natural history specimens were from north of 49°N when the expedition was travelling during the warmer months of the year.

Hylurgus rufipennis, along with H. obesus Mannerheim, which was described in 1843, was moved to the genus Dendroctonus by LeConte in 1868 (LeConte 1868; Hopkins 1909; Wood 1963, 1969, 1982). Dendroctonus similis LeConte, which was described in 1860, was referred to D. obesus in 1868 by LeConte (LeConte 1868). In the early 1900s, D. engelmannii, D. piceaperda, and D. borealis were all described by Hopkins (1909), and in 1963, these three species, as well as D. rufipennis, were synonymized with D. obesus (Wood 1963). However, in 1969, the correct senior name of

*D. rufipennis* was recognized by Wood (1969). The accepted common name of *D. rufipennis* is spruce beetle. The confusion that seems to surround the taxonomy of *D. rufipennis* may be due to some combination of an overlap in size and morphological characters, in addition to potentially mislabelled specimens in collections upon which taxonomists have based their descriptions (Hopkins 1909; Wood 1963).

The aforementioned five species of spruce beetle recognized in Hopkins's (1909) seminal monograph on the genus Dendroctonus were most easily differentiated by their geographic distribution and host species. The range of D. piceaperda extended from Manitoba to the east coast, and its main hosts were Picea glauca (white spruce), P. rubens (red spruce), and P. mariana (black spruce). The range of D. engelmannii was limited to western North America with P. engelmannii (Engelmann spruce) and white spruce listed as hosts. The range of D. borealis extended through Alaska and into northern British Columbia and the Canadian Territories, where white spruce was the primary host. Dendroctonus obesus was restricted to attacking P. sitchensis (Sitka spruce) along the west coast. Hopkins (1909) used the common name, the red-winged pine beetle, for D. rufipennis and stated it was found attacking downed *Pinus strobus* (eastern white pine) around Lake Superior. He noted that little else was known about its habits even though it was one of the first species in the genus to be described from North America. Swaine (1918) reported eastern white pine and Pinus banksiana (jack pine) as the only hosts of D. rufipennis. No host was listed for H. rufipennis in Kirby's 1837 original description of the species. Mannerheim (1853) does not list the host for insects identified as H. rufipennis collected from the Kenai Peninsula, Alaska, but the most likely hosts would have been white or Sitka spruce or their hybrid P. × lutzii (Lutz spruce). No host was listed in LeConte (1868), but Peck's 1876 treatise on black spruce describes extensive mortality of spruce in northeastern North America caused by H. rufipennis. The pine hosts listed in Hopkins (1909) and Swaine (1918) may have been listed in error, perhaps in part due to the challenge of distinguishing D. rufipennis from D. murrayanae. The taxonomy of spruce beetle has remained stable since 1969, but there could be revisions in the future (see below).

Dendroctonus is one of 247 genera in the subfamily Scolytinae within the weevil family Curculionidae (Kirkendall et al. 2015). The genus was established by Erichson in 1836, based on the type specimen Bostrichus micans Kugelann (= D. micans [Kugelann]). Hopkins's (1909) monograph on Dendroctonus recognized 24 valid species, and Wood's (1982) monograph on Scolytidae recognized 19 species, with one species having two subspecies (Furniss 2001; Ruiz et al. 2009). Since 1982, D. mesoamericanus Armendáriz-Toledano has been described and D. barberi Hopkins has been removed from synonymy with D. brevicomis and reinstated (Armendáriz-Toledano et al. 2015; Valerio-Mendoza et al. 2019). This brings the total number of Dendroctonus species to 21 as of early 2021. All species, except for two Eurasian species, are native to North America, and all species feed under the bark of conifers (Wood 1982). Pine (Pinus) is the primary host for most species in the genus, although Picea (spruce), Larix (larch), and Pseudotsuga (Douglas-fir) are the primary hosts of some species.

Genetic and morphological analyses support five main species groups within *Dendroctonus* (Wood 1982; Kelley and Farrell 1998; Víctor and Zúñiga 2015; Godefroid et al. 2019). Three groups are exclusively *Pinus*-feeders, and two notorious tree-killers in the genus, *D. ponderosae* Hopkins (mountain pine beetle) and *D. frontalis* Zimmermann (southern pine beetle), belong to

two of these groups. Another group contains the Asian Pinus-feeding species D. armandi Tsai and Li (Chinese white pine beetle), which is the sister to all other species, and two very closely related North American species that attack Pseudotsuga and Larix (Wood 1982; Kelley and Farrell 1998; Víctor and Zúñiga 2015; Godefroid et al. 2019). Following isolation of the ancestors of Dendroctonus armandi, the main Dendroctonus lineages in North America diverged. Spruce beetle belongs to the "rufipennis" species group, which moved to specializing on Picea. In addition to spruce beetle, the "rufipennis" group consists of three other species: D. punctatus LeConte (boreal spruce beetle, which was formerly called the Allegheny spruce beetle) and the Eurasian D. micans (Kugelann) (great spruce bark beetle), both of which attack Picea; and D. murrayanae Hopkins (lodgepole pine beetle), which underwent a reverse host shift from Picea back to Pinus (Wood 1982; Víctor and Zúñiga 2015; Godefroid et al. 2019). The ancestor of the "rufipennis" group may have colonized Eurasia through Beringia in the genus's last intercontinental dispersal event (Furniss 1996; Godefroid et al. 2019).

Genetic variation within D. rufipennis indicates the potential for cryptic species (Maroja et al. 2007). The presence of cryptic species has been suggested for at least seven other species of Dendroctonus (Six and Bracewell 2015). The genetic population structure of spruce beetle across its range in North America points to two major haplotype groups in the north, which are broadly sympatric on white spruce from Alaska to Newfoundland and likely interbreed (Maroja et al. 2007). A barrier to gene flow apparently exists between the two northern populations and a third haplotype, which occurs on Engelmann spruce throughout the Rocky Mountains. Within the Rocky Mountain clade, spruce beetles from British Columbia, Washington, Montana, and Colorado are distant from populations in Utah and Arizona (Maroja et al. 2007). Spruce beetle may have spread from at least three glacial refugia: central and eastern United States, Beringia, and south of the Rocky Mountains or the Pacific Northwest (Maroja et al. 2007). Estimates of initial divergence support isolation for approximately one to two million years. Gene exchange during previous interglacial periods may have been limited by a lack of contact or intrinsic barriers. Barriers to genetic exchange could include habitat fragmentation, host specialization, or variation in pheromones (e.g., Kelley and Farrell 1998; Bracewell et al. 2010; Sullivan et al. 2012; Isitt et al. 2020). Possible differences in life history, host preference, pheromones, and behaviour that may exist among populations or cryptic species could potentially be exploited for management.

#### 1.2. Distribution and Host Trees

Spruce beetle occurs throughout the range of spruce in Canada and the United States. The distribution extends from Alaska and the west coast of British Columbia across Canada's boreal forest to the east coast of Newfoundland and Labrador (Figure 1.1). Spruce beetle has been reported as far north as 68 °N near Agiak Lake in Alaska, Old Crow in the Yukon, and Aklavik in the Northwest Territories (Furniss 2013). The distribution of spruce beetle extends into the United States, following the range of spruce along the Rocky Mountains in the west and the Appalachian Mountains in the east (Wood 1982).



**Figure 1.1.** The distribution of spruce beetle largely follows the range of *Picea* species in Canada and the United States (see text). Distribution of *Picea* is represented from percent cover data for Canada (Beaudoin et al. 2014) and from basal area data for the United States (www.fs.fed.us/foresthealth/applied-sciences/mapping-reporting/indiv-tree-parameter-maps.shtml). Map: G. Thandi.

All native species of spruce in Canada and their hybrids are susceptible to attack. Large-diameter, mature trees are preferred (see Chapter 2, Biology and Population Dynamics). The most common host depends on the region and the species present. White spruce is the main host in northern British Columbia and across the boreal forest, whereas Sitka spruce is the primary host along the west coast. Engelmann spruce is the most common host in southern British Columbia and the southern Rocky Mountains. White spruce is the main host in the east, although red spruce is also attacked (see section 1.3.2, Atlantic Canada). Black spruce is considered a rare host (e.g., Watson 1928; BC FLNRORD 2020); however, references from the 1800s recognize black spruce as a common host, and there are historical reports of extensive outbreaks in New England that killed large-diameter, old-growth black spruce growing on better sites (Peck 1876; Packard 1890; Fox 1895). Land use changes have reduced the distribution of large-diameter black spruce on upland sites in eastern North America over time. Much of the black spruce in Canada's boreal forest grows on wetter sites and is likely too small to be susceptible to spruce beetle.

Like other eruptive bark beetles, spruce beetle may attack a limited number of non-*Picea* species during outbreaks when they are close to spruce trees that are also being attacked. There is an arguable report of substantial mortality of lodgepole pine (*Pinus contorta*) by spruce beetle during the 1940s outbreak in Colorado (Massey and Wygant 1954). Wood (1982) states that all the preserved specimens collected from pine during the Massey and Wygant study (1954) were actually lodgepole pine beetle (*Dendroctonus murrayanae*); however, Massey, who examined numerous attacked lodgepole pine trees and who presumably based his identification on galleries, maintained the attacks were made by spruce beetle (personal communication cited in Schmid and Frye 1977). Many *Dendroctonus* species attack nonhost conifers during large outbreaks, but populations do not persist longterm in nonhosts. Although spruce beetle can successfully reproduce in lodgepole pine logs in the laboratory, attacks on non-*Picea* hosts are rare (Safranyik and Linton 1983).

#### I.3. Outbreak History

#### 1.3.1. Early reports and surveys

The earliest written account of significant and sudden mortality of mature spruce that was likely caused by a spruce beetle outbreak dates back to the early 1800s in eastern North America (Swaine 1924). An insect outbreak apparently killed every mature spruce tree in a large area of Maine around 1818 (Hough 1882; Packard 1890). Significant mortality in standing spruce was also recorded throughout that century in New England in the 1830s, 1850s, 1870s, and the late 1890s (Peck 1876; Packard 1890; Hopkins 1909). The 1870s outbreak was particularly notable: a "blight" or "scourge" reportedly killed one-half to one-third of the mature spruce throughout the region over a 10-year period (Fox 1895). Parts of eastern Canada were undoubtedly affected by large outbreaks that occurred through the 1800s (Swaine 1924). One report confirms impacts in New Brunswick from the 1870s outbreak: plans to cut 95 000 m<sup>3</sup> of spruce up the Nashwaak River in the winter of 1882–1883 were thwarted because half of the timber was killed by spruce beetle (Packard 1890). A large outbreak from 1897 to 1901 in New Brunswick and Maine resulted in an estimated loss of 2.4 million m<sup>3</sup> of "the finest spruce" (Swaine 1924). The cause of mortality in the 1870s was initially debated. Some forest workers felt the 250- to 300-year-old spruce were dying of old age, whereas others argued that excessively dry weather and damage due to agitation by high winds were to blame (Peck 1876; Fox 1895). However, it was noted that young spruce trees, as well as other species, were not afflicted. The descriptions provided of tree death, including foliage fade and needle drop, are consistent with spruce beetle attack. Spruce beetle (Hylurgus rufipennis) was eventually confirmed as the causal agent (Peck 1876; Fox 1895).

Records of insect infestations, including spruce beetle, have improved in Canada over the last century with the initiation and development of programs to monitor forest resources and with advancements in survey technologies. When the Entomology Branch of the Dominion of Canada's Department of Agriculture was organized in 1914, Dominion of Canada Entomologist Charles Gordon Hewitt established the Division of Forest Insects (Wallace 1990). James Malcolm Swaine was the first chief of the division. Swaine's 1918 book on Canadian bark beetles refers to spruce beetle (*D. piceaperda*) as one of the most destructive beetles in the genus, killing enormous

quantities of spruce in southwestern New Brunswick. Spruce beetle (*D. borealis*, *D. engelmannii*) was also listed as killing large amounts of white and Engelmann spruce, particularly in northern Alberta. Along the west coast, spruce beetle (*D. obesus*) was reported to prefer weakened Sitka spruce; however, it was described as a destructive mortality agent under the right conditions. Swaine (1918) reported *D. rufipennis* only from dying white and jack pine.

After the creation of the Division of Forest Insects, regional laboratories were created, scientific capacity was increased, and systematic forest health surveys that eventually employed aircraft were developed. As early as 1920, the first aerial sketch mapping records of insect infestations were published; however, aircraft were not consistently used for overview flights until the 1950s due to prohibitive costs and limited availability (Van Sickle et al. 2001). In 1936, the Forest Insect Survey was established by John J. de Gryse, Swaine's successor, to monitor populations of insects and support research across the country (Wallace 1990). The survey, which would later be known as the Forest Insect and Disease Survey (FIDS), ran until 1995, after which time the provinces assumed the roles and responsibilities, including the annual aerial overview survey (Van Sickle et al. 2001; see section 5.1.1, Aerial overview survey). Below is a brief description of spruce beetle infestations in Canada, by region, over the last 120 years, based on available accounts, reports, and aerial overview surveys.

#### 1.3.2. Atlantic Canada

Nova Scotia, New Brunswick, and Prince Edward Island have similar infestation histories, with notable spruce beetle outbreaks in approximately 1897-1901, 1915-1920, 1930-1934, and 1976–1984 (Swaine 1924; Balch 1931, 1942; Morris 1958; Ostaff and Newell 1981; Magasi 1985; Kondo and Moody 1987). The 1930s outbreak was attributed to populations building up in trees that had been weakened by defoliation by the European spruce sawfly (Gilpinia hercyniae; Morris 1958). Limited infestations occurred periodically in Nova Scotia between 1940 and the 1970s. The last outbreak, which started in 1976, was attributed to logging debris left on-site after harvesting from a recent spruce budworm outbreak (Choristoneura fumiferana); defoliation from budworm damage was also thought to have weakened trees, making them more susceptible to spruce beetle. However, excessive blowdown from a hurricane in 1974 was likely the main contributing factor (Renault and Ostaff 1980). By 1979, before the outbreak had ended, 48% of white spruce stands and 5% of red and black spruce stands examined across Nova Scotia had been impacted by spruce beetle (Ostaff and Newell 1981). On Cape Breton Island, which was hit hardest by the 1974 storm, more than half of the merchantable mature white spruce was killed by the end of the outbreak in the mid-1980s (Magasi 1986; Kondo and Moody 1987). The same outbreak killed one-third to one-half of the mature white spruce around the Bay of Fundy in New Brunswick and one-third of the merchantable white spruce on Prince Edward Island (Magasi 1983; Kondo and Taylor 1985; Moody 1989). Spruce beetle has also been noted as an agricultural problem in some Atlantic provinces, particularly Prince Edward Island, because it kills mature spruce trees in hedgerows and windbreaks (Kondo and Taylor 1985).

Since the mid-1980s, spruce beetle populations have remained relatively low in New Brunswick and on Prince Edward Island. In Atlantic Canada today, spruce beetle is most active in Nova Scotia, where it is considered a significant mortality agent of mature spruce in the province (Nova Scotia

Department of Natural Resources 2017). Even-aged stands of old-field white spruce growing on farmland abandoned in the first half of the twentieth century are common in Nova Scotia and are more susceptible to spruce beetle compared to white or red spruce growing on forested sites (McGrath 2018). There are periodic reports of significant localized mortality in red spruce, but most damage recorded to date has accrued in white spruce (e.g., Forbes et al. 1975; Magasi 1991; Hurley and Magasi 1996). Both species can grow to 60 cm in diameter, but white spruce is considered overmature at 60 to 80 years of age, whereas red spruce is not considered overmature until 100 years of age (McGrath 2018). White spruce may become susceptible to spruce beetle at an earlier age than red spruce because of their differences in physiological age.

Land use and harvesting history have undoubtedly changed the distribution and abundance of susceptible hosts on the landscape in eastern North America over the last two centuries and have altered the outbreak cycle of spruce beetle. In the 1800s, harvesting shifted from white pine to spruce. Considerable amounts of spruce was regenerated in the early- to mid-1900s, after extensive harvesting for the growing pulp and paper industry and to support Canada's effort in World War II. In fact, in 1942, Balch predicted that spruce beetle would be of importance only to parks and to those interested in growing full-sized trees and that the beetle would become a minor pest in much of Atlantic Canada as large stands of old spruce became increasingly scarce. Indeed, in eastern North America, spruce beetle outbreaks during the 1900s do not appear to have been as extensive and severe as those reported during the 1800s. Improved harvesting practices also may have played a role by reducing the size and amount of waste material left on-site after logging, which can serve as ideal breeding habitat. Scattered and notable spruce beetle-induced mortality of mature white spruce still occurs in Nova Scotia. Today, approximately 160 000 ha of white spruce within Nova Scotia's 4.2 million ha of forested lands are considered highly susceptible to spruce beetle (Nova Scotia Department of Natural Resources 2017).

Spruce beetle is also endemic in Newfoundland and Labrador. Extensive, severe outbreaks are relatively uncommon, but small outbreaks that result in localized mortality of white spruce are periodically reported. Swaine (1924) states that spruce beetle (D. piceaperda) killed an unknown quantity of spruce in Newfoundland in the early 1920s. Payette (2007) attributed significant mortality of mature white spruce that occurred near Napaktok Bay in northern Labrador between 1989 and 1991 to spruce beetle. Outbreaks in western Newfoundland in the 1970s occurred in stands that previously suffered defoliation by budworm (Sterner and Davidson 1981). Notable outbreaks also occurred in areas of Gros Morne National Park in the early 1990s (Bowers et al. 1993) and around Goose Bay in the 2000s and 2010s (Lavigne 2012, 2016). Infestations appear to be on the rise in a number of jurisdictions in recent years, and climate change has been cited as a potential contributing factor (Lavigne 2016). Scattered pockets of one to five attacked trees are often reported, indicating that spruce beetle is active and could potentially respond to favourable conditions in the future where susceptible hosts are present. Susceptible white spruce is common along the coast and in abandoned fields in Newfoundland and Labrador, but white spruce is not overly abundant in much of the interior. Black spruce is abundant in Newfoundland and Labrador, but it tends to grow on poor sites and often does not reach a sufficient size to be susceptible to spruce beetle.

#### 1.3.3. Central Canada

Québec, particularly the Gaspé Peninsula, was affected by the 1897–1901 spruce beetle outbreak that impacted Atlantic Canada and the northeastern United States (Swaine 1924). Additional notable outbreaks in the Gaspé region occurred between 1915 and 1920 and between 1930 and 1934 (Gobeil 1941; Martineau 1985). Recurrent infestations in the Gaspé Peninsula were attributed to the susceptibility of mature spruce forests in the region at the time and to frequent winter storms and logging operations that provided pulses of ideal breeding habitat (Swaine 1924; Morris 1958). After the mid-1930s, spruce beetle populations remained relatively low in Québec until 1984, when infestations were noted on Anticosti Island off the Gaspé Peninsula; these populations reached outbreak levels in the late 1990s, causing damage over 71 000 ha by 2001 (Ministère des Ressources naturelles 1997; Ministère des Ressources naturelles et de la Faune 2005). A small 1000-ha infestation was also reported on the adjacent mainland near Manche d'Épée in 2001 (Ministère des Ressources naturelles 2001). Small infestations by a bark beetle, potentially spruce beetle, have reportedly caused waves of white spruce mortality in the 1970s, 1980s, and 1990s near Kuujjuarapik on the eastern shore of Hudson Bay (Caccianiga et al. 2008). In Ontario, there was also a five-year outbreak starting in 1915 along the eastern shore of Lake Superior (Swaine 1924). The next, and last, notable spruce beetle outbreak in Ontario was reported around Lake Nipigon, north of Lake Superior, in the early 1950s (Belyea and Prebble 1951).

In both central and eastern Canada, it has been noted repeatedly that spruce beetle outbreaks seem to follow defoliation by the eastern spruce budworm or, in the case of the 1930s outbreaks, the European spruce sawfly. Spruce beetle prefers stressed trees, and defoliation stress was widely thought to have possibly triggered the spruce beetle outbreaks (e.g., Morris 1958, and references therein). However, in many cases, spruce beetle did not attack standing defoliated trees until after budworm populations collapsed. It is likely that, at least in some cases, spruce beetle populations built up in the larger tops and cull logs from harvesting associated with the budworm outbreaks. The beetle would have started attacking standing trees, which were defoliated, after they had run out of suitable logging residue. In addition to potential changes in the age and composition of eastern forests, improved logging practices may explain why spruce beetle populations have not increased in response to recent eastern spruce budworm outbreaks in eastern and central Canada, including the on-going large outbreak in Québec, which started around 2006.

#### 1.3.4. Prairie provinces, Northwest Territories, and Nunavut

Spruce beetle is found throughout west central Canada, although only the province of Alberta seems to experience significant, repeated outbreaks. Outbreaks were reported in northern Manitoba and northern Saskatchewan about a century ago, in the early- to mid-1920s (Swaine 1924). In southwestern Manitoba, spruce beetle has been reported attacking white spruce in plantations and in a farm shelterbelt in the Turtle Mountains, which is surrounded by agricultural land and prairie (Cerezke et al. 1991; Furniss 2013). No notable outbreaks have been reported in Nunavut or the Northwest Territories, except in Wood Buffalo National Park.

Parts of Wood Buffalo National Park, in northern Alberta and in the Northwest Territories, have experienced repeated light infestations. About 5% of the spruce was killed over 13 000 ha in the park in the early 1960s (Safranyik 1971), 8% to 10% of the spruce was killed along the Peace River

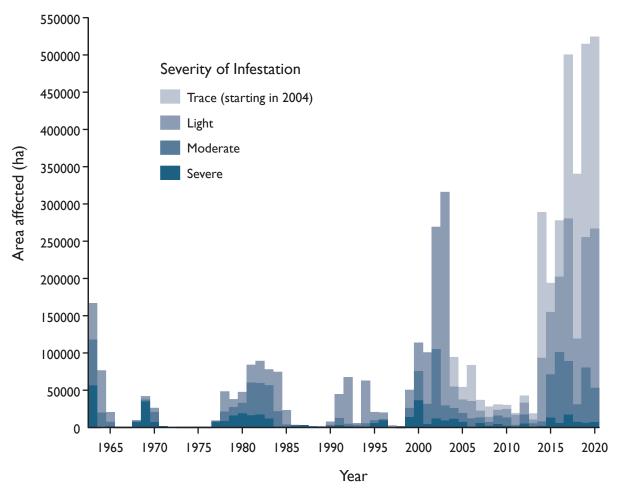
between Jackfish River and the park's western boundary in the early 1980s (Moody and Cerezke 1985), and scattered mortality was observed over 13655 ha near the confluence of the Peace and Slave Rivers and near Lake Claire in the early 1990s (Brandt 1995). Small scattered outbreaks are common in northern Alberta, and their combined impacts have been significant in some cases. For example, outbreaks scattered over more than 100000 ha in the Footner Lake and Peace River Forest Districts starting around 1977 and lasting through the early 1980s caused accumulated tree mortality ranging from 5% to 70%, with more than 80000 m³ of spruce killed (Moody and Cerezke 1984, 1985). Small but severe outbreaks also occurred near High Level and in other areas of northwestern Alberta in the mid-1980s and again in the mid-1990s, as well as near Wabasca-Desmarais (e.g., Moody and Cerezke 1984, 1985; Cerezke et al. 1991; Cerezke and Gates 1992; Cerezke and Brandt 1993; Brandt 1995).

In southwestern Alberta, localized outbreaks have also periodically caused severe mortality in mature spruce forests. Infestations are being reported with increasing frequency along the eastern slopes of the Rocky Mountains. A survey in 2016 mapped over 10 000 ha that had recently been affected by spruce beetle in Rocky Mountain House, Whitecourt, and Grande Prairie forest areas (Alberta Agriculture and Forestry 2018). Stands of Engelmann and white spruce over 120 years old have been most susceptible to outbreaks (Moody and Cerezke 1985). Most of the infestations to date in Alberta have been attributed to populations building up in large-diameter logging residue and rights-of-way logging or in windthrow and broken stems produced by storms.

#### 1.3.5. British Columbia and the Yukon

Western Canada has a long history with severe spruce beetle outbreaks. The first known written record comes from a Hudson's Bay Company fur trader named John McLean. McLean described dying trees in the forests around Prince George, British Columbia, in 1836: "unfortunately, however, the woods are decaying rapidly, particularly several varieties of fir, which are being destroyed by an insect that preys on the bark: when the country is denuded of this ornament, and its ridges have become bald, it will present a desolate appearance" (McLean 1849, p. 286). One of the varieties of "fir" he refers to was undoubtedly spruce, given the distribution of conifer species in the region. Dendrochronological studies support widespread mortality of spruce in the area around that time (Lindgren and Lewis 1997; Zhang et al. 1999).

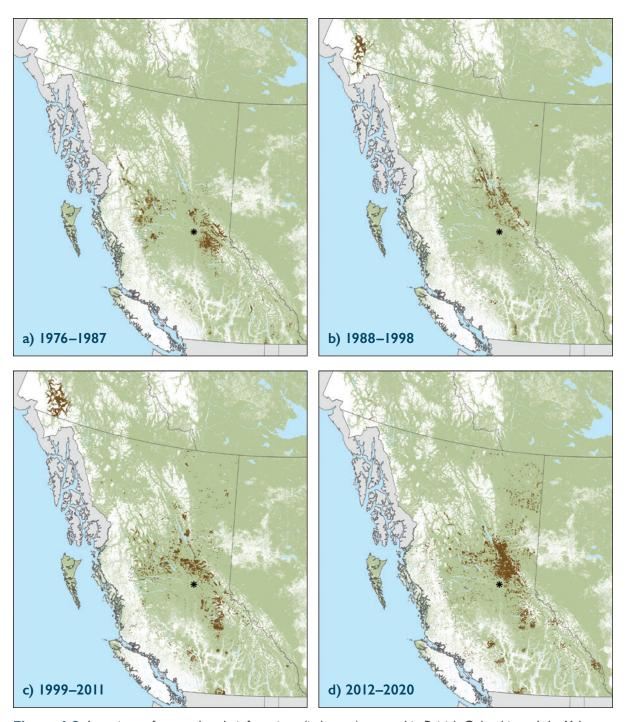
Notable spruce beetle outbreaks occur about every 10 years somewhere in western Canada. In the late 1930s and early 1940s, an outbreak in northwestern British Columbia and southwestern Yukon killed approximately 878 000 m³ of spruce over 50 000 ha; additional losses were accrued at the same time in the Nass River area of British Columbia (Humphreys and Safranyik 1993; Berg et al. 2006). An outbreak in the early 1950s in southeastern British Columbia killed 400 000 m³ of spruce, and smaller scattered outbreaks were common throughout much of the southern interior in the late 1960s (Humphreys and Safranyik 1993). A severe outbreak in central British Columbia in the Prince George and Prince Rupert Forest Regions occurred in the early 1960s and killed approximately 14 million m³ of spruce over 243 000 ha, whereas another outbreak in the late 1960s killed an additional 822 000 m³ of spruce in the Prince George region (Sterner and Davidson 1981; Humphreys and Safranyik 1993).



**Figure 1.2.** Area affected by spruce beetle annually in British Columbia. The intensity of the infestation in each polygon delineated during aerial surveys is classified according to the percentage of trees recently killed by spruce beetle: trace (< 1%); light (1% to 10%); moderate (11% to 29%); and severe (≥ 30%). Infestations classified as very severe (≥ 50%) were minimal, therefore, this category is combined with severe. The trace intensity class was added in 2004. Area affected by spruce beetle is based on annual aerial overview survey data from the Federal Insect and Disease Survey (1976–1998) and the provincial forest health survey (1999–2020; www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial\_Overview/; see text).

Since the outbreaks of the 1960s subsided, there have been a further four distinct periods when spruce beetle populations have increased in western Canada, based on annual aerial overview survey data: 1976–1987, 1988–1998, 1999–2011, and 2012–2019 (Figure 1.2). Figure 1.3 shows the area infested in each of these time periods. Infestations were scattered across much of British Columbia, with the exception of the west coast and some areas of the far north, in each time period; however, the largest and most severe outbreaks occurred and continue to occur in central British Columbia. The southwestern corner of the Yukon, in and around Kluane National Park, also experienced a major outbreak in the 1990s, which is discussed below.

The next and most infamous spruce beetle outbreak occurred from 1978–1984 in central British Columbia, in the Bowron River Valley, southeast of Prince George (Figures 1.2, 1.3a). Spruce beetle had killed over 2 million m³ of spruce in the Bowron area by 1982, resulting in substantial pressure from industry for the Province of British Columbia to take action to curb insect population growth and expected timber losses (Halleran 1992). Harvesting levels for 1981–1987 were elevated,



**Figure 1.3.** Locations of spruce beetle infestations (in brown) mapped in British Columbia and the Yukon since 1976. Infestations are plotted for four time periods during which distinct population increases were observed in British Columbia (Figure 1.2): (a) 1976–1987; (b) 1988–1998; (c) 1999–2011; and (d) 2012–2019. The 1994–2006 outbreak in the Yukon spans two periods (b and c). The city of Prince George in central British Columbia is marked with an asterisk (\*). The distribution of spruce (*Picea*) is shown in green. Area affected by spruce beetle is based on annual aerial overview survey data from the Federal Insect and Disease Survey (1976–1998) and the provincial forest health survey (1999–2020; www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial\_Overview/; see text). Maps: G. Thandi.

and at the peak of harvesting, 750 loaded logging trucks departed the Bowron every day for mills in Prince George (Figure 1.4). The memory of the losses incurred from the extensive 1960s outbreak likely spurred the aggressive harvesting response in the Bowron. Cutting that had been planned to occur over 25 to 30 years occurred in seven years (Halleran 1992). By the end of the outbreak, about 15 million m³ of wood had been harvested (Figure 1.5). The result was the largest—and most notorious—clearcut in the province's history, at around 50 000 ha, depending on how it is measured. Reforestation efforts were on-going for more than a decade afterward. The Bowron spruce beetle outbreak brought deforestation in British Columbia to the attention of the public, which led the provincial and federal governments to invest \$500 million in reforestation initiatives in British Columbia between 1985 and 1995 (Parfitt 2005).

The rapid and extensive harvesting in the Bowron also drew national and international criticism for its ecological impacts. Examples of notable articles and shows criticizing harvesting practices and policies in the Bowron include: "The Ancient Forest," by Catherine Caufield, published in *The New Yorker* on 14 May 1990 and reprinted as a series of articles in the *Vancouver Sun* in June 1990; "Canada's Troubled Trees," by William Stewart, published in the 8 July 1991 issue of *TIME* magazine; "Voices in the Forest," a documentary episode of the Canadian Broadcasting Corporation television series *The Nature of Things* that aired on 3 February 1991; *Paradise Despoiled*, a television presentation produced by Westdeutsche Rundfunk and aired in Germany on 4 March 1991; and "British Columbia's Big Cut," by Joel Connelly, published in the May/June 1991 issue of *Sierra Magazine*.



**Figure 1.4.** Logging trucks backed up in a clearcut in central British Columbia in February 1985. Harvesting was in response to the 1978–1984 spruce beetle outbreak in the Bowron River Valley (see text). Photo: F. Van Der Post (provided by R. Hodgkinson).

In the early 1990s, about 10 years after the Bowron outbreak subsided, spruce beetle populations increased again. Scattered infestations occurred over much of the southern interior of British Columbia, but the main outbreak was north of Prince George around Mackenzie and Williston Lake (Figure 1.3b). Also during this time, the southwestern Yukon experienced its largest outbreak in recorded history. Populations started increasing through the early 1990s along the Alsek River in Kluane National Park and near Bear Creek Summit just north of the park, but the infestations were not reported and mapped until 1994 because aerial surveys were infrequent in the area at that time (Wood and Van Sickle 1994; Garbutt et al. 2007; Yukon Ministry of Energy, Mines and Resources 2008). When the outbreak was first mapped, it covered 32 000 ha, and by the time it subsided in 2006, over half the mature spruce was killed over approximately 400 000 ha (Garbutt et al. 2007; Yukon Ministry of Energy, Mines and Resources 2019). Spruce beetle populations in the Yukon have remained relatively low since 2006; a small 1200 ha infestation was mapped east of Kluane National Park in 2018, but fecundity and survival were low (Yukon Ministry of Energy, Mines and Resources 2019).

In the early 2000s, numerous outbreaks were again reported over large regions of British Columbia, especially the central-interior region north of Prince George; tree mortality from this outbreak peaked in 2003 (Figure 1.3c). Impacts from spruce beetle in northeastern British Columbia, east of the Rocky Mountains, became apparent after 1999. From 2007 to 2012, tree mortality was relatively low in western Canada, although it was still higher compared to that recorded during intervals between previous outbreaks (Figure 1.2).



Figure 1.5. View overlooking part of the Bowron clearcut that resulted from harvesting associated with the 1978–1984 spruce beetle outbreak. Spruce beetle killed just over 2 million m³ of spruce in the area by 1982, but harvesting saw 15 million m³ of wood cut in response (see text). Photo: R. Hodgkinson.

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Populations began to rise again in British Columbia in 2013, and as of 2020, over 500 000 ha are infested to some degree in the latest and on-going outbreak (BC FLNRORD 2020). The hardest hit area is in the Omineca region, northeast of Prince George and along the western slopes of the Rocky Mountains (Figure 1.6). The current outbreak follows the recent extensive mountain pine beetle epidemic, which caused significant mortality of lodgepole pine in some of the same timber supply areas now being impacted by spruce beetle. Socio-economic considerations, including maintaining the mid-term timber supply, have put extreme pressure on the provincial government to actively manage spruce beetle. The province has developed specific guidelines, recommendations, and best practices for management and harvesting in ecosystems affected by spruce beetle, based on lessons learned from past outbreaks and scientific research (see Chapter 5, Management). However, there is significant concern about the level of compliance and enforcement (e.g., Cox 2019).

In western Canada, most large spruce beetle outbreaks to date appear to have been triggered by a sudden increase in large-diameter downed material produced by windthrow events, unsanitary logging practices, and right-of-way clearing for construction projects (Safranyik et al. 1983; see section 2.5, Population Dynamics). This increase in downed material has usually coincided with a period of favourable weather, which increases winter survival and shifts spruce beetle to a predominately one-year life cycle, and which also leads to moisture-stress in standing trees. For example, tree felling for the construction of the road to Haines, Alaska, likely contributed to the



**Figure 1.6.** Harvesting in the Omineca region, northeast of Prince George, in response to a spruce beetle outbreak that started in the region in 2013. Photo: J. Robert.

start of the late 1930s outbreak in southwestern Yukon and northwestern British Columbia (Berg et al. 2006), and construction of the Aishihik Power Project started a tiny 100-ha outbreak in 1977 about 110 km northwest of Whitehorse, Yukon (Garbutt et al. 2007). A significant windthrow event in 1958–1959, several hot summers, and moisture stress in standing trees likely triggered the extensive and severe outbreak in central British Columbia in the 1960s (Safranyik et al. 1983). The Bowron outbreak was attributed to a windthrow event in October 1975 and successive years of favourable weather for winter survival (e.g., Halleran 1992; Cozens 2004). Similarly, windthrow events in 2010 and 2011 and a period of warmer-than-average summer temperatures probably contributed to the current outbreak north of Prince George. The high susceptibility of central British Columbia to large spruce beetle outbreaks is likely due to several factors: the relatively high volume of spruce in the region's forests; frequent wind storms that periodically produce sudden increases in downed material; and the potential for concurrent periods of warm, dry weather that promote a one-year life cycle in the beetle and cause moisture stress in standing trees (also see section 2.5, Population Dynamics).

The large outbreak that started in the Yukon in the 1990s is significant because weather has been proposed as a main inciting factor (Garbutt et al. 2007; Yukon Ministry of Energy, Mines and Resources 2010). Large-scale outbreaks have likely been rare in this region for at least the last several hundred years, but climate change could be increasing the susceptibility of these northern forests (Berg et al. 2006). However, given the remote location and the time that lapsed before the 1990s outbreak was identified, a scattered windthrow event cannot be ruled out as a possible inciting factor.

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## CHAPTER 2 Biology and Population Dynamics

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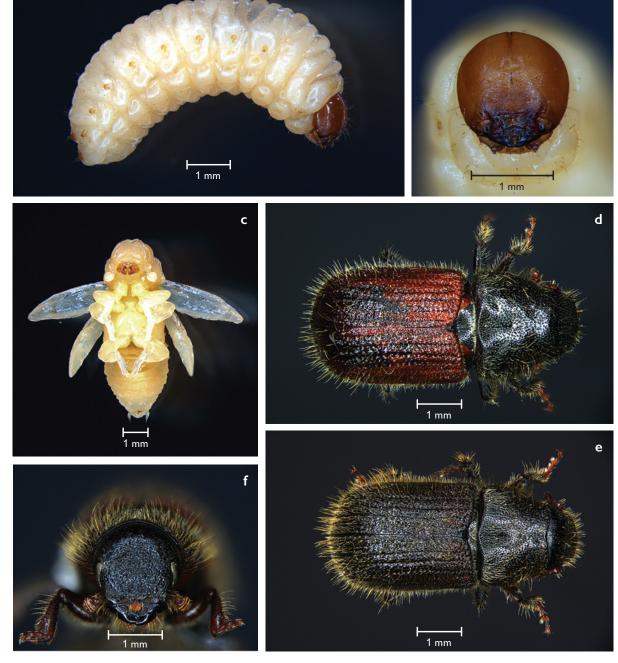
Inherent in the definition of an outbreak is that the high population levels cause some impact considered negative by humans. Few insect species are capable of explosive population growth, and only some of those species negatively impact human values. Spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae), is one of those species. Spruce beetle preferentially attacks recently downed or stressed large-diameter trees. Mature trees felled during late autumn or winter storms provide ideal breeding habitat because the phloem is still green and of good quality when adults disperse in search of new hosts in the spring. Outbreaks in living trees are often precipitated by a sudden abundance of downed or stressed trees, coupled with a period of favourable weather for reproduction and survival. Although populations can build to very high densities in downed trees, outbreaks are declared only when insects kill standing trees valued by humans.

Spruce beetle outbreaks were considered to be one of the greatest threats to Canada's forests when the Division of Forest Insects was first formed under the Department of Agriculture in the early 1900s (Swaine 1918, 1924). Competition between spruce beetle and humans for the same resource has led to extensive research on the insect's biology and population dynamics in an effort to develop control methods and to mitigate its impacts (see Chapter 5, Management). In this chapter, we synthesize our current understanding of spruce beetle biology and population dynamics, including factors affecting voltinism, reproduction, development, and survival. Interactions with host tree defences and other species, such as natural enemies, are covered as they pertain to the life history and population dynamics of spruce beetle, and more detailed discussions can be found in Chapter 3, Host Finding and Communication, and Chapter 4, Ecological Interactions.

#### 2.1. Life Cycle and Life History

#### 2.1.1. Life stages

Spruce beetle passes through four life stages in its holometabolous development: egg, larva, pupa, and adult (Figure 2.1). The general description of the life stages below is based on Massey and Wygant (1954), Wood (1982), personal observations, and other sources where noted. Eggs are pearly white, oblong, and 0.75 to 1.00 mm in length. The larvae are legless grubs that reach up



**Figure 2.1.** (a) A mature (fourth-instar) spruce beetle larva, lateral view; (b) close-up of head of a mature larvae, anterior view; (c) pupa, ventral view; (d) two-toned mature adult with reddish elytra and black pronotum, dorsal view; (e) all-black mature adult, dorsal view; and (f) close-up of head of mature adult, anterior view. Photos: G. Smith.

to 7 mm in length at maturity. The creamy white, somewhat translucent larvae can have a grey or reddish tint due to material passing through the digestive tract. The four larval instars can be differentiated based on head capsule width, which increases linearly with a mean growth factor of 1.37 (Patterson 1950; Hall and Dyer 1974). Pupae are about 6 mm long and white, becoming creamy white to tan near maturity. Pupae are exarate, with wings, legs, and antennae visible.

Adult beetles are often referred to as "robust" because they are larger than most, but not all, other species of *Dendroctonus*. Beetles of both sexes are similar in size and range in length from 4.4 to 7.0 mm, with most individuals 5.5 to 6.5 mm in length (Safranyik and Linton 1983, 1985; Sahota et al. 1987; Holsten and Werner 1990; Safranyik et al. 2010; Safranyik 2011). The pronotal width of adult beetles is approximately 0.4 times the length, or 2.3 mm on average. Adult size increases with development time and host quality, and it decreases with intraspecific competition (Safranyik and Linton 1983, 1985; Safranyik 2011). Based on both field and laboratory studies, the sex ratio of spruce beetle is slightly female-biased at about 56% (e.g., Watson 1928; Dyer 1973; Safranyik and Linton 1985; Safranyik 2011). Safranyik (2011) suggests that the sex ratio may be balanced for insects developing in one year; however, further investigation is needed.

Young adults turn from a light tan colour to a medium brown as the exoskeleton sclerotizes. Once fully hardened, the pronotum is black and the elytra are either black or reddish brown (Figure 2.1). Red elytra were originally thought to turn black with age, overwintering, or hibernation (Swaine 1924; Schmid and Beckwith 1975; Wood 1982); however, there are two colour morphs present in mature adults after overwintering, and experimental crosses indicate that colour is likely genetically controlled (Linton et al. 1984). The red-black colour morph appears to dominate. The all-black colour morph is rare in eastern Canada, but an average of 29% of spruce beetles are all black at some sites in central British Columbia, although this varies widely among sites.

#### 2.1.2. Emergence and dispersal

There are usually two emergence periods for spruce beetle adults: in the spring and early summer from late May to mid-July, and in the summer and autumn from July to October. The timing of emergence, and thus of the dispersal flight, depends on temperature. The first emergence period is mainly comprised of young adults. These are insects that eclosed to the adult stage the previous growing season, overwintered once as adults, but have not yet reproduced and are dispersing in search of a host tree to establish their first brood (see section, Young adults, below). The young adults may potentially be joined by some of their parents, which have been reported to live and reproduce for two growing seasons (Swaine 1924; Hansen and Bentz 2003). There is often a second wave of emergence that occurs several weeks or more after the first main emergence period and is comprised of the same beetles—the adults that dispersed in the spring, established one brood, and are now parents. Only a fraction of these new parent beetles can fly and disperse to new hosts at this time. These beetles usually re-attack the same tree higher on the bole, where there is suitable phloem in which they can establish a second brood, or move to the base of the tree to overwinter (Swaine 1924; Watson 1928; Massey and Wygant 1954; Lawko and Dyer 1974; see section, Parent beetles, below).

The later emergence begins in the spring, or the longer the cold period, the more rapid and synchronous the emergence period (McCambridge and Knight 1972; Bleiker and Meyers 2017; Dell and Davis 2019; Bleiker and Willsey 2020). Once emergence of young adults from the natal host tree begins, it progresses at a similar rate regardless of daily fluctuations in temperature (McCambridge and Knight 1972). More than one beetle may emerge through the same exit hole. For example, using cages on naturally attacked trees during an outbreak, Massey and Wygant (1954) determined that an average of seven beetles emerged from the same hole.

Snow may still be on the ground in some regions when the dispersal flight starts. The majority of dispersal occurs when shade temperatures exceed 16 °C in the stand, and the lower threshold for flight is estimated at around 13 °C (Dyer 1973; Werner and Holsten 1985; Safranyik and Linton 1987; Holsten and Hard 2001; Safranyik 2011). In much of British Columbia and interior Alaska, where spring temperatures are relatively warm, the emergence and flight of overwintered beetles starts in mid-May and peaks early in June (e.g., Beckwith 1972; Dyer 1973; Safranyik and Linton 1987; Holsten and Hard 2001; Safranyik 2011). On the Kenai Peninsula in Alaska and at high-elevation sites in the Rocky Mountains in British Columbia and the United States, where spring temperatures are cooler, the main emergence and flight period occurs in mid- to late-June or July (e.g., Massey and Wygant 1954; Knight 1961; Beckwith 1972; McCambridge and Knight 1972; Holsten and Hard 2001; Davis and Hansen 2017). In central Canada, emergence starts in June (Swaine 1924; Watson 1928). Flight can continue through late summer at some sites. There is a diurnal pattern to flight related to heat accumulation above 13 °C; flight starts mid-morning, peaks between 15:00 and 16:00 hours, and ceases around 20:00 hours (Safranyik and Linton 1987).

Overwintered beetles are ready to fly upon emergence and have a well-developed lateralis medius muscle (Chansler 1960; Gray and Dyer 1972). Strong winds and rain limit flight. Bark beetles avoid taking off in winds that exceed their maximum flight velocity, which is unknown for spruce beetle, but about 2 m/s for similarly large-sized scolytids (Rudinsky 1962; Meyer and Norris 1973). Some individuals in a population are likely capable of long-distance dispersal. Although about one-third of beetles were poor fliers in flight-mill tests, other beetles flew several times between rest periods, with each flight exceeding 30 minutes (Chansler 1960). Based on Chansler's experiments and assuming no wind assist, many spruce beetles could theoretically disperse at least 7.5 km, and likely over 20 km with a correction for flight-mill drag. Flight distance would presumably be longer under wind assist. Beetles likely disperse in the direction of the prevailing wind until attractive odours are encountered (Safranyik and Linton 1993). Anecdotal reports from foresters suggest that spruce beetle may disperse and establish new infestations 24 to 48 km from existing outbreaks (Schmid and Frye 1977). Beetles dispersing above the canopy or potentially carried by convective air currents above the canopy and into the upper atmosphere may presumably disperse even longer distances assisted by wind; however, the conditions needed for such an event may align only occasionally (Chapman 1967; Jackson et al. 2008). In addition to wind direction and speed, factors such as light intensity, temperature, relative humidity, host availability, and population density may also influence dispersal. Beetles may spend several days to a week locating a suitable host (Schmid 1970; Holsten and Hard 2001).

Dispersing beetles respond to both host tree volatiles (primary attraction) and pheromones released by congeners (secondary attraction) to locate suitable hosts (see Chapter 3, Host Finding and Communication). Female beetles are the pioneering sex, being the first to arrive at a new host and to initiate attack.

#### 2.1.3. Attack on host

Once a suitable tree is selected, females bore in under flakes of bark or in crevices and furrows where leverage can be obtained (Figure 2.2). Semiochemical and acoustic cues are used to attract conspecifics, including mates, as well as to regulate attack density and limit the negative effects of overcrowding (see sections 2.5.4, Intraspecific competition, and 3.2, Spruce Beetle Pheromones).



**Figure 2.2.** (a) Pitch tubes coloured orange from boring dust produced by spruce beetles as they successfully initiate galleries in the phloem (inner bark); (b) an adult spruce beetle battling tree resin as it reaches the inner bark and starts constructing an egg gallery; (c) egg and larval galleries etched into the sapwood of a tree mass attacked and killed by spruce beetle; and (d) tree defensive lesions (hypersensitive response) around unsuccessful spruce beetle egg galleries. Photos: J. Robert (a, b, c) and M. Duthie-Holt (d).

Attack density varies greatly, depending on host exposure, resistance, abundance, and distribution, as well as on the height on the tree and the size of the beetle population (e.g., Dyer and Taylor 1971; Schmid and Frye 1977; Werner and Holsten 1985; Safranyik and Linton 1999). Beetles avoid surfaces with direct exposure to solar radiation, such that attack density generally increases with shading. For example, on downed trees such as windfall and logging debris that are not sitting

directly on the ground, attack density is highest on the bottom side, lowest on the top side, and moderate on the lateral sides. Similarly, attack density is highest on trees in dense shade compared to trees in light shade or full sun.

Host resistance can also influence attack density on healthy defended trees (see section 2.4, Tree Defences). A threshold density of attack is needed to overwhelm the defences of living trees for successful attack; however, there is a compensatory density-dependent trade-off due to the negative effects of overcrowding and intraspecific competition. In general, average attack densities range from 58 to 97 attacks per square metre on standing trees during outbreaks, with attack density being highest on the lower bole (e.g., Swaine 1924; Massey and Wygant 1954; Nagel et al. 1957; McCambridge and Knight 1972). On downed trees, attack densities are similar along the bole or they peak mid-bole (Massey and Wygant 1954; Schmid and Frye 1977). Attack density on downed trees is similar to that on standing trees, or slightly higher, during outbreaks. McCambridge and Knight (1972) reported similar attack densities on standing and downed trees of 80 attacks per square metre during a small outbreak. For sub-outbreak populations, average attack densities of 8 to 51 attacks per square metre have been reported for the infested portion of downed trees and stumps (Dyer and Taylor 1971; Safranyik and Linton 1999). Generally, attack density tends to increase with density of beetles and also depends on host availability (Lister et al. 1976). The height to which trees are infested is a function of beetle population size and tree diameter. Standing trees at least 25 cm in diameter at 1.4 m above ground are usually attacked to heights of 3 to 15 m (Swaine 1924; Massey and Wygant 1954; Schmid and Frye 1977). Spruce beetle infests a greater proportion of the bole of downed trees, often attacking well into the crown until a diameter of about 10 cm.

# 2.1.4. Gallery construction

Each female constructs her own egg gallery in the inner bark (phloem), engraving the surface of the sapwood in the process (Figure 2.2). The entrance hole is kept clear of boring dust and resin until a male enters and mating occurs. After mating, the entrance hole and the ensuing egg gallery are packed with frass. The male beetle usually stays with the female to assist with egg gallery construction, but some male beetles may leave to join unmated females.

Egg galleries generally run with the grain of the wood, although an initial section of gallery about 2.5 cm long that is devoid of eggs is sometimes angled across the grain (Massey and Wygant 1954). Crusty resin is usually visible along the edges of the initial section. Although egg-gallery length varies, most are in the range of 13 to 15 cm, regardless of whether they are in naturally mass-attacked trees, stumps, or windfall (Swaine 1924; Massey and Wygant 1954; Safranyik and Linton 1999). Under putatively ideal laboratory conditions with respect to temperature and available phloem, total gallery lengths reach 19 to 22 cm (Sahota and Thomson 1979; Safranyik and Linton 1985). Beetles periodically construct ventilation holes along the galleries, as well as small nooks to facilitate turning and egg laying. The egg gallery often splits into a 'Y' just before the terminus, where each parent takes an arm. No eggs are laid in this section (Swaine 1924; Massey and Wygant 1954; Sahota and Thomson 1979).

## 2.1.5. Oviposition

After the female enters the tree, her flight muscles start to degenerate, and resources are redirected toward ovarian development (Sahota et al. 1970; Gray and Dyer 1972; Sahota and Farris 1980). The lower temperature threshold for oviposition is estimated at 11 °C, and the first egg is usually laid within 2 to 5 days of attacking a new host tree (Massey and Wygant 1954; Sahota and Thomson 1979, Thomson and Sahota 1981). One to four sets or groups of eggs are deposited in each egg gallery (Swaine 1924; Massey and Wygant 1954). Each set of eggs is deposited in a groove about 3.5 cm long; the grooves are arranged on alternating sides of the egg gallery (Patterson 1950; Massey and Wygant 1954; Schmid and Beckwith 1975).

About 80 to 85 eggs per gallery are laid in most host types, including mass-attacked standing trees, fresh windthrow, and stumps (Swaine 1924; Watson 1928; Massey and Wygant 1954; Knight 1961; McCambridge and Knight 1972; Safranyik and Linton 1999). McCambridge and Knight (1972) report fewer eggs in downed trees than in standing trees; however, the comparison is potentially confounded by site and year effects. Some females have deposited around 150 eggs in a gallery (Watson 1928; Massey and Wygant 1954). These field reports are similar to the range reported from laboratory experiments, in which 100 to 150 eggs per gallery have been laid under favourable conditions over a three- to four-week period regardless of voltinism (Sahota and Thomson 1979; Hansen and Bentz 2003).

The reproductive output of spruce beetle is affected by a number of abiotic and biotic factors. The total number of eggs laid increases with gallery length, which is positively correlated with temperature (Massey ad Wygant 1954; McCambridge and Knight 1972; Sahota and Thomson 1979). A higher rate of egg deposition at warmer temperatures may be due to increased activity of the *corpora allata*, the endocrine glands that secrete juvenile hormone; these glands are also affected by nutrition (Sahota and Thomson 1979). However, the glands may be active for a shorter period of time at warmer temperatures, which could limit the potential maximum duration of the ovipositional period (Sahota and Thomson 1979). Female productivity decreases as the length and density of egg galleries increases due to intraspecific competition (Thomson and Sahota 1981; Safranyik and Linton 1985). The behaviour of the male beetle also influences reproductive output: egg gallery length and egg production are about 20% higher when males remain with females and assist with gallery construction (McCambridge and Knight 1972). The reproductive output of female beetles declines as population levels decline (Massey 1956; McCambridge and Knight 1972). The decline may be due in part to internal nematodes; however, fecundity is also lower in beetles that were apparently nematode-free, indicating other unknown contributing factors.

## 2.1.6. Brood development

#### Eggs and larvae

Eggs hatch in two to four weeks, depending on temperature. Hansen et al. (2001a) report that egg hatch takes 10 days at 21 °C and 46 days at 9 °C and that eggs will only hatch at 5.5 °C if they have developed to the fourth stage (i.e., larval head capsule visible) at a warmer temperature. Eggs are sometimes found in September and October but are unlikely to survive the winter (Humphreys and Safranyik 1993). Safranyik (2011) reports substantive mortality—more than 50%—from eggs to first instar for brood developing in stumps and windthrow.

After eggs hatch, first-instar larvae mine at right angles to the egg gallery, creating larval galleries. The larval galleries soon coalesce, and the larvae feed gregariously until they are about one-third grown (Swaine 1924; Massey and Wygant 1954). After the communal feeding period, the larvae feed individually for the remainder of their development. Spruce beetle is unique within the genus *Dendroctonus* for displaying both feeding styles during the larval stage: larvae of other *Dendroctonus* species feed either individually or communally. The temperature threshold for larval development is estimated to be 6.1 °C (Dyer 1968, 1970). Temperature determines the length of the life cycle and whether larvae enter a facultative diapause and overwinter (see section 2.3, Regulation of Voltinism). Late-instar larvae construct individual pupal cells either in the phloem or within the inner bark.

Larval density is highly variable over space and time, being affected by a number of density-independent and density-dependent processes (see section 2.5, Population Dynamics). Massey and Wygant (1954) reported densities ranging from 710 to 5800 larvae (mean 3400) per square metre of bark surface, depending on tree diameter, height of attack, and study year during the 1940s outbreak in Colorado. Larval density will undoubtedly change over time as mortality accrues. First-instar larvae are susceptible to the host tree's pitch defences, and approximately 5% die in standing and downed trees when they inadvertently chew into a small pitch pocket in the phloem (McCambridge and Knight 1972). Mortality of late-instar larvae is substantive (> 90%), due to cold winter temperatures, natural enemies, and competition. Interestingly, larval density is generally highest on the lower bole of the tree where attack density is highest, but the number of larvae per gallery is higher on the upper bole where intraspecific competition is lower (Massey and Wygant 1954).

#### **Pupae**

Pupation typically requires 10 to 15 days (Massey and Wygant 1954). In laboratory experiments, pupation took eight days at 21 °C, 38 days at 9 °C, and 80 days at 5.5 °C (Hansen et al. 2001a). The 5.5 °C treatment was the lowest temperature tested. Massey and Wygant (1954) stated that pupae may slowly transform into the adult stage during the winter, but no data or specific temperatures during which development occurred are provided. The cold tolerance of spruce beetle pupae has not been investigated, but pupae of other bark beetles such as mountain pine beetle are very chill-susceptible despite being able to survive brief exposure to relatively cold temperatures (Bleiker and Smith 2019). Survival and development of spruce beetle pupae at temperatures that are below 0 °C for a substantial period of time seems unlikely; however, given that pupation can progress at 5.5 °C, individuals could potentially eclose to the more cold-hardy adult stage very late in the autumn.

#### Young adults

Pupae eclose to adults that have exoskeletons that sclerotize, turning to black or a dark reddish brown over a period of approximately two weeks. Initial field observations have suggested that new adults may disperse and reproduce without overwintering (Swaine 1924; Watson 1928). However, the beetles that were observed emerging may have been relocating before winter, a behaviour that was not recognized at the time. Subsequent research indicates that adults overwinter once, before dispersing to new host trees. Adults that have not overwintered once are incapable of flight (Gray and Dyer 1972). Reproduction can occur before overwintering, but it is greatly reduced (e.g., Massey and Wygant 1954; Knight 1961). Additionally, the emergence period is delayed and extremely protracted in the absence of a substantive cold period (Bleiker and Meyers 2017; Bleiker and Willsey 2020). Schebeck et al. (2017) hypothesize that the adult diapause may be facultative in some beetle populations, based on observations in the southern United States of beetles reproducing in logs without overwintering. However, a cold-associated rest appears to be at least functionally obligate for spruce beetle populations in western Canada (Bleiker and Willsey 2020). Reduced emergence, as well as a delayed and prolonged emergence period, would be maladaptive for survival and coordinating mass attack of healthy trees. Most adults from populations sampled in western Canada appear to complete diapause within 75 days, whereas only 50% to 60% of beetles complete diapause in 50 days (Bleiker and Meyers 2017; Bleiker and Willsey 2020). Some beetles emerge over an extremely extended period of time without a cold period, but they may still be experiencing diapause (Bleiker and Willsey 2020). An obligate cold-associated adult diapause would serve to synchronize emergence and potentially to maximize flight capacity upon emergence.



**Figure 2.3.** New adult spruce beetles overwintering under the bark at the base of a standing infested tree. A proportion of new adult beetles relocate from higher on the bole where they developed to the base of the tree prior to winter at some sites (see text). Photo: L. Maclauchlan.

New adults usually overwinter in the natal host tree. In standing trees, adults either overwinter at the location on the tree where they developed or a proportion may relocate to the tree's base to overwinter in large aggregations in feeding galleries (Massey and Wygant 1954; Knight 1961; Gray and Dyer 1972). Beetles that relocate emerge and then drop or crawl to the base of the tree, where they bore in under the bark around the root collar and in exposed roots above the mineral soil (Figure 2.3). A single entrance hole may be used by about 14 beetles, and an average of 200 beetles can congregate under a 900 cm<sup>2</sup> area of bark at the base of a mass-attacked tree (Massey and Wygant 1954). This behaviour of emergence and re-entry at the tree's base in order to overwinter was initially thought to be an idiosyncrasy of spruce beetle within the genus Dendroctonus (Schmid and Frye 1977); however, Langor and Raske (1987) have since reported the same behaviour in D. simplex from Newfoundland. The proportion of adults that relocate to overwinter is highly variable. Knight (1961) estimated that the percentage of adults relocating ranged from 3% to 88% annually, and studies have reported that from 4% to 10%, up to 34%, 50%, and from 48% to 62% of beetles relocate to overwinter (Massey and Wygant 1954; McCambridge and Knight 1972; Hodgkinson et al. 2015). The factors driving the variation in the proportion of adults that relocate before winter are unknown, but temperature, positive geotrophism, and negative phototaxis might play a role (Hansen et al. 2001a; Hodgkinson et al. 2015). The snowpack likely affords beetles that overwinter at the base of trees some protection from extreme temperatures and woodpeckers.

#### Parent beetles

Once adult beetles establish one brood, they are parents. Almost all parent beetles re-emerge at some sites later in the same season; re-emergence of parent beetles is more likely at warmer sites than at colder sites. The re-emergence of parents is common and widespread and starts about three or more weeks after the main flight (e.g., Swaine 1924; Watson 1928; Massey and Wygant 1954; Knight 1961; Lawko and Dyer 1974; Safranyik et al. 1983). About 59% of re-emerging parent beetles are female (Massey and Wygant 1954). Thus, both sexes are equally likely to re-emerge because populations are 56% female-biased (Watson 1928; Dyer 1973; Safranyik and Linton 1985). Schmid and Frye (1977) posit that females probably attack only once. Interestingly, re-emerged beetles retain their reproductive ability (Hansen and Bentz 2003), although only 18% would be capable of flight upon emergence (Lawko and Dyer 1974). Most parent beetles that re-emerge move directly to the base of trees to overwinter, without dispersing or establishing a second brood (Watson 1928; Massey and Wygant 1954). A few re-emerging beetles may establish a second brood in the same season, but usually they fill in available phloem above or below the main attack zone or between galleries on trees that are already colonized (Swaine 1924; Watson 1928; Massey and Wygant 1954). Spruce beetle can apparently reproduce in more than one summer, and it has been suggested that these re-emerging, twice-reproducing beetles may significantly affect spruce beetle population levels (Swaine 1924; Hansen and Bentz 2003; but see Schmid and Frye 1977). Swaine (1924) reported that an adult female can establish up to three broods: two during her first reproductive year and a third during the following season before dying.

## 2.2. Thermal Limits for Survival

## 2.2.1. Hot temperatures

Temperature extremes directly affect survival of spruce beetle. Temperatures above approximately 43 °C kill varying percentages of the brood, depending on the length of the exposure (Mitchell and Schmid 1973). In the laboratory, inner-bark temperatures of 49 °C killed 92% of insects. In the field, solar radiation treatment killed 90% or more of the insects on the top side of cull logs in clearcuts, but insects developing on the sides and bottoms of the logs survived. Solar radiation has potential for use as a method of control for infested logs at some sites; however, the logistics involved to ensure full exposure and to turn the logs limit the method's practical application.

## 2.2.2.Cold temperatures

Spruce beetle acquires cold tolerance during the autumn by accumulating cryoprotectants, thermal hysteresis proteins, and other measures such as voiding the gut to reduce ice-nucleating agents. Cold tolerance is lost in the spring as temperatures warm. Spruce beetle is most cold hardy late in the autumn or in January (Massey and Wygant 1954; Miller and Werner 1987; Rousseau et al. 2012). Anecdotal reports indicate that extreme, rare cold events, especially in autumn before insects have acquired maximum cold tolerance, can be sufficient to end outbreaks (Massey and Wygant 1954).

Estimates of cold tolerance and cold-associated mortality vary by study and region. The mean supercooling point of both larvae and adults near Fairbanks, Alaska, dropped from a mean of –12 °C in late summer to –31 °C in late autumn and winter, before rising slowly in the spring (Miller and Werner 1987). The lowest supercooling points recorded in the study were –41 °C and –37 °C for larvae and adults, respectively. Adult beetles in Nova Scotia were putatively more cold tolerant, with a mean supercooling point of –38 °C in January, and some adults supercooled to –44 °C (Rousseau et al. 2012). Adult beetles from Colorado suffered 98% mortality when exposed to –29 °C in Petri dishes; in contrast, mortality of larvae in slabs of wood was only 14% after the temperature dropped to –29 °C under the bark (Massey and Wygant 1954). Larval mortality increased to just above 50% at –32 °C and was 100% at only –34.5 °C. Minimum ambient air temperatures dipping to –49 °C in Colorado, –57 °C in Idaho and Montana, and –40 °C in Arizona were associated with 42%, 75%, and 88% mortality, respectively (Massey and Wygant 1954; Terrell 1954; Frye et al. 1974).

It is not known if cold tolerance of spruce beetle populations varies geographically or if the variation in the aforementioned studies is due to differences in methods or equipment. Regardless, minimum air temperatures in some regions will likely periodically exceed the cold tolerance of both larvae and adults. Temperatures under the bark lag ambient air temperatures due to the large thermal mass of trees and the insulating properties of the bark. In most years, at least some of the cold-hardiest larvae and adults likely will survive on the bole; however, in the coldest years, when temperatures under the bark fall below the lethal threshold in some regions, only larvae and adults protected by the snowpack survive (e.g., Knight 1958; Miller and Werner 1987). Thus, cold survival may vary with voltinism, the proportion of adults that relocate to the base of the tree to overwinter, and host type (i.e., standing *versus* downed trees).

# 2.3. Regulation of Voltinism

Temperature determines voltinism in spruce beetle through a developmental delay in larvae during what is considered to be a facultative diapause (e.g., Massey and Wygant 1954; Dyer 1969, 1970; Dyer and Hall 1977; Werner and Holsten 1985). Under certain environmental conditions, the facultative diapause occurs at the end of the fourth—the last—larval instar, also referred to as prepupae (Dyer 1970; Dyer and Hall 1977; Hansen et al. 2001a). In the two-year life cycle, prepupae or fourth-instar larvae overwinter in diapause the first winter after eggs are laid, although a small proportion of insects may enter winter as third-instar larvae (Werner and Holsten 1985). Pupation occurs the following summer, and new adults enter an apparent obligate diapause to overwinter the second year before dispersing the following spring. In the one-year life cycle, eggs develop through to adults in the same growing season and overwinter as described above before dispersing in the spring one year after the tree was attacked. In the three-year life cycle, the first winter is spent as an early-instar larva in an apparent quiescence before it aligns with the twoyear life cycle. A three-year life cycle has been reported at high-elevation sites with very cool summer temperatures in the southern Rocky Mountains (Massey and Wygant 1954; Knight 1961; McCambridge and Knight 1972). The three-year life cycle has been documented on shaded hosts in cool environments in Canada, but it is rare (Safranyik et al. 1983; Safranyik 2011). The discussion here focuses on the facultative developmental delay in older larvae (prepupae) that ultimately determines whether the life cycle is completed in one or two years.

A number of studies have started to elucidate the environmental conditions that determine spruce beetle voltinism, but results vary on the default developmental pathway. Initial work by Dyer (1969) in British Columbia found that spruce beetle sites with semivoltine populations had earlier frost dates and slightly fewer degree-hours above 6.1 °C but similar daily maximum temperatures than univoltine sites did. Controlled laboratory studies in which larvae were reared under decreasing thermoperiods over time showed a developmental delay suggestive of diapause occurring in fourthinstar larvae compared to insects reared at a constant 21 °C (Dyer 1970). (No larval diapause occurs at a constant 21 °C, and studies typically use this temperature as a reference temperature against which any potential delays are compared.) At least one exposure below 0 °C, which was applied when most larvae were third or fourth instars, increased the intensity of the apparent diapause. However, a subcortical temperature of -0.5 °C for one hour during the third or fourth instar had no effect on development (unpublished experiments referenced in Dyer and Hall 1977). Further laboratory experiments identified 16 °C as a key threshold temperature that induced developmental delays characteristic of diapause in 46% of individuals (Dyer and Hall 1977). Diapause induction was also inversely related to degree-days above 6.1 °C: diapause was averted in young larvae receiving a daily heat accumulation of 10 or more degree-days above 6.1 °C. Dyer and Hall (1977) concluded that the prepupal diapause was induced by cool temperatures in the spring or early summer during instar three or earlier, because fourth-instar larvae that were moved to putatively diapause-inducing temperatures continued developing. Werner and Holsten (1985) also found that univoltinism was prevalent when average phloem temperatures were 16.5 °C or higher. Based on the data presented in Werner and Holsten (1985, figures 3 and 6), most insects were early-instar larvae when phloem temperatures exceeded 16.5 °C.

Subsequent research by Hansen et al. (2001a) found no evidence of a substantive developmental delay when second- to fourth-instar larvae from Utah were exposed to 12 °C but were otherwise reared at 21 °C. The sine-wave and square-wave thermoperiods simulated, based on average daily or weekly temperatures from a field site that had no univoltine insects, yielded only minimal developmental delays of one to seven days. There was no evidence that development was regulated by a true diapause and not a life stage-specific lower developmental-temperature threshold. However, when insects were maintained at a constant temperature throughout their development, significant developmental delays indicative of diapause occurred below a threshold temperature of 15 °C or slightly lower, depending on the experiment. Hansen et al. (2001a) concluded that voltinism was not determined by low-temperature induction of diapause during the third instar or earlier as suggested by Dyer's studies but was instead under direct temperature control, such that the default developmental pathway is a prepupal diapause for insects not reaching the adult stage by autumn.

The difference between the studies led by Dyer and by Hansen is whether univoltinism or semivoltinism is the default developmental pathway; that is, whether larval diapause is induced when young larvae experience cool temperatures or whether it is averted when mature larvae experience warm temperatures. Regardless of the default developmental pathway, the studies highlight that a critical temperature threshold exists around 15 to 17 °C that influences voltinism. A voltinism model developed by Hansen et al. (2001b) examined numerous variables used to characterize air temperatures at various sites that were associated with univoltine and semivoltine populations. Out of many variables examined, the best predictive model required only cumulative hours above 17 °C between 40 and 90 days after peak adult funnel-trap capture.

Spruce beetle voltinism may vary regionally with climate, locally with topography and exposure, and temporally with annual weather patterns (e.g., Watson 1928; Massey and Wygant 1954; Knight 1961; Dyer 1969; Werner and Holsten 1985; Safranyik 2011). For example, temperature inversions in mountainous terrain can promote univoltinism on mountain slopes even as semivoltinism predominates in nearby valley bottoms (Dyer 1969). Stand aspect and exposure affect voltinism due to differences in solar radiation at different spatial scales, including site, tree, and within-tree scales (e.g., Werner and Holsten 1985; Safranyik 2011). In central British Columbia, the percentage of univoltine insects ranged from 43% to 95% at one site over a five-year study (Safranyik 2011). Insects also developed more quickly in exposed stumps in clearcuts than in shaded downed trees in stands. At sites with mixed voltinism, semivoltinism is most common on the north and west aspects of standing trees and along the bottom sides of felled trees, whereas univoltinism is most common on the south aspect of standing trees and along the top sides of felled trees.

## 2.4. Tree Defences

Spruce trees, similar to other conifers, have evolved defences to fend off a suite of herbivores and pathogens, including bark beetles and their microbial associates. Tree defences are likely one of the key factors regulating spruce beetle populations (see section 2.5, Population Dynamics). Only a tiny fraction of bark beetle species, one of which is spruce beetle, are capable of killing trees, and only when population densities are high. Even when population densities are high, spruce beetle preferentially attacks freshly downed or stressed trees when these are available. Spruce beetle and its symbionts (see below, and Chapter 4, Ecological Interactions) must overcome tree defences to successfully reproduce in living trees. Insects can complete development only if the tree's defence response is immobilized, which means killing the cambium and other cells that are capable of mounting a response. This usually results in tree death or at least the death of tissues surrounding a developing brood.

Attacks are considered either successful or unsuccessful from the perspective of the beetle. Success is measured as the establishment of a brood, which requires the death of tree tissues. Successful mass attack of trees occurs when the colonization density around the bole is sufficient to overwhelm the tree's defences, eventually resulting in the tree's death. Less common are successful strip attacks, in which only a portion of the tree dies. In strip attacks, usually one side or less than one-half of the tree's circumference is successfully attacked and dies. Beetles successfully reproduce within the strip, but the tree survives. Brood production can vary greatly in strips, and strip-attacked trees are often re-attacked by multiple generations of beetles and killed in subsequent years. Unsuccessful attacks occur when the tree's defences repel or kill attacking beetles and eliminate any chance of the beetle establishing a brood. Like strip attacks, trees that are unsuccessfully attacked may be re-attacked and killed in subsequent years. Unsuccessful attacks tend to occur when populations are transitioning into healthy (well-defended) standing trees after depleting downed or weakened hosts. Mass attacks tend to occur when spruce beetle population densities are high. Strip attacks are more common when beetle populations are declining, as well as among trees along the periphery of infestations.

Conifers have two types of defences. These are mechanical defences, which include structural elements such as tough, lignified tissues and stone cells; and chemical defences, such as toxic terpenes in oleoresin and polyphenolic parenchyma cells (Franceschi et al. 2005; Krokene 2015). The general defence strategy of conifers against herbivores moves through gradations from repel to defend to kill and compartmentalize, with two overlapping and coordinated defence systems (Franceschi et al. 2005). Preformed defences, also known as constitutive defences, repel or inhibit attackers and can also kill. Inducible defences are up-regulated in response to attack and aim to kill and wall-off invaders. There can be both interspecific and intraspecific variation in the defences of spruce trees. Engelmann spruce has two distinct co-occurring phloem monoterpene chemotypes that may vary in their toxicity to spruce beetle and its microbial associates (Davis 2020). Spruce beetle's preference for Engelmann spruce over blue spruce may be due to bark characteristics, including the defence capabilities of blue spruce. Compared to Engelmann, blue spruce has thicker outer bark, thinner phloem, higher resin flow, and higher concentrations of constitutive terpenes in the phloem (Ott et al. 2021).

Preformed resin ducts may inadvertently be severed by spruce beetles as they use their strong, heavily sclerotized mandibles to tunnel through the tough bark. The constitutive oleoresin is stored under pressure, and the viscous flow that results when a beetle pierces a duct may entomb beetles or physically expel them from the tree (Safranyik et al. 1983). The oleoresin is also highly toxic (Werner 1995). To overwhelm and deplete a tree's preformed resin reserves, bark beetles employ a rapid mass attack strategy, in which large numbers of beetles attack an individual tree within a short period of time (i.e., within two to three days; Raffa and Berryman 1983). Induced defences challenge bark beetles by initiating changes in cell metabolism, such as cell wall lignification, induction of the hypersensitive response, production of resin in existing resin ducts, and changes in cell division and differentiation, that result in the formation of traumatic resin ducts and wound periderm (Figure 2.2; Franceschi et al. 2005; Krokene 2015). The formation of traumatic resin ducts may be especially important. DeRose et al. (2017) found that the ability of spruce to survive a spruce beetle outbreak was correlated with traumatic resin duct formation. Inducible defences of conifers may be primed by mechanical injury or prior unsuccessful attack, indicating the potential for acquired resistance (Krokene 2015).

The attack density required to overwhelm tree defences during a rapid mass attack depends on the vigour of each individual tree (Berryman 1972; Raffa and Berryman 1983). Impaired vigour caused by moisture stress, competition, advanced age, phenology, management treatments, and other factors can affect both the susceptibility and defence response of spruce trees to attack (e.g., Watson 1928; Safranyik et al. 1983; Hard 1985, 1987; Hard and Holsten 1985; Hart et al. 2014). For example, the impact of drought stress on the water balance of trees reduces pressure in resin ducts and lowers the flow rate of preformed oleoresin. Impaired host tree vigour helps beetle populations transition from attacking downed trees to standing trees; however, few large trees may be able to resist attack during severe outbreaks regardless of vigour (Schmid and Frye 1977). Attack densities between 58 and 97 attacks per square metre on the lower bole are sufficient to kill a healthy, standing tree during outbreaks when trees are attacked rapidly (e.g., Swaine 1924; Massey and Wygant 1954; Nagel et al. 1957; McCambridge and Knight 1972). In addition to the host's defence response, beetle pressure (population density), and host availability may also affect attack density.

Spruce beetle, like many other species of bark beetles, carries a number of microbial associates, including filamentous fungi, yeasts, and bacteria that may interact with tree defences (see Chapter 4, Ecological Interactions). For example, spruce beetle is associated with a number of species of ophiostomatoid fungi, or blue-stain fungi, which are known for eliciting conifer defences and ameliorating the subcortical environment in the beetles' favour (Safranyik et al. 1983; Solheim and Safranyik 1997; Six and Bentz 2003; Davis et al. 2018; Davis 2020; Stewart et al. 2020). The pathogencity of fungi varies among species and among isolates within a species (see section 4.1.1, Filamentous fungi and yeasts). In addition to their potential role in reducing tree defences, microbial associates may also alter the chemical defence response of trees and condition host tree tissues for brood development. Davis et al. (2019) reported that the ophiostomatoid fungus *Grosmannia abietina* (= *Leptographium abietinum*) reduced a defensive compound toxic to spruce beetle in the laboratory. Some isolates of *Endoconidiophora rufipennis* (= *Ceratocystis rufipenni*) proved highly virulent when inoculated into spruce (Solheim and Safranyik 1997). A full understanding of the role tree defences play in regulating spruce beetle populations requires elucidating the complex ecological interactions that occur among beetles, microbes, and host trees.

# 2.5. Population Dynamics

The potential for rapid exponential growth of spruce beetle populations has long been recognized: Swaine (1924) observed that one infested tree could produce enough beetles to kill another 5 to 20 trees. Yet, most of the time, spruce beetle populations are stable, residing in ephemeral downed or stressed material that is part of mature spruce forests. Low-density populations may be regulated, at least in part, by the availability of suitable, poorly defended host trees. At low densities, beetles are unable to coordinate the rapid mass attack necessary to overcome the defences of healthy trees. Attacks on defended trees are rare when populations are low and usually are the result of spillover attack due to the healthy trees' proximity to downed material that is heavily attacked (Safranyik et al. 1983).

Spruce beetle populations can rapidly increase under certain conditions. Safranyik et al. (1990) found that host and climatic factors had the greatest effect on population growth. Furthermore, positive density-dependent feedback can occur at high densities when beetles are better able to coordinate the mass attack needed to overwhelm the defences of healthier trees. However, regardless of population density, spruce beetle transitions to attacking healthy standing trees only when suitable downed and stressed hosts have been exhausted. Safranyik (2011) hypothesized that the development of expansive outbreaks may require a large-scale change in host susceptibility. Within individual stands, outbreaks in standing trees often persist for two to five years; at a regional scale, outbreaks tend to last five to ten years (see section 1.3, Outbreak History). Negative density-dependent feedback due to the effects of intraspecific competition can be severe in spruce beetle and may contribute to the decline of outbreaks. Other factors, including depletion of susceptible hosts, large-scale changes in host susceptibility, extreme temperatures, and natural enemies, may reduce populations. Our understanding of outbreak collapse is incomplete. Some outbreaks subside for unknown reasons; a complex of interacting factors is likely involved.

In the following sections, factors that are known to or are likely to have a significant effect on the abundance of spruce beetle are discussed, including spruce beetle's reproductive capacity and the insect's ability to respond to conditions favourable for population growth, host tree and stand characteristics, weather, competition, and natural enemies. Management activities, such as the direct control of beetle populations, may also have an impact on population levels and are covered in Chapter 5, Management.

# 2.5.1. Reproductive potential of spruce beetle

Spruce beetle has relatively high fecundity, with each female capable of laying 80 eggs, on average (see section 2.1.5, Oviposition). This means that spruce beetle populations can persist and even grow despite surprisingly high mortality rates. It also means that small changes in survival can lead to big changes in population growth rates. The sex ratio is slightly biased to females (56%; e.g., Watson 1928; Dyer 1973; Safranyik and Linton 1985); however, males can mate with more than one female, which makes unmated females rare. Thus, populations will remain static if females are replaced or if about 1 in 45 eggs survives to reproduce successfully. This translates into a stable population at only a 2.2% survival rate and a doubling of the population with each generation if survival increases to 4.4% or, conversely, 97.8% and 95.6% mortality, respectively.

Applying the logic above to data extracted from several studies indicates that population growth rates are highly variable. For an endemic, non-outbreak population of mixed voltinism developing in windfalls, Safranyik and Linton (1999) reported an average of 4.2 brood adults emerging per female gallery over five generations. This translates into a growth rate of 2.4 at the time of emergence, with additional mortality occurring during dispersal and host colonization. Safranyik (2011) found that the size of an endemic spruce beetle population developing primarily in stumps and windfall increased 60-fold over a five-year period. Interestingly, the growing population was still largely contained in downed trees and adjacent weakened standing trees. Watson (1928) reported an average of 6.8 beetles emerging per gallery from a windfall at a site where populations were also attacking standing trees. This would be a 3.8 potential growth rate at the time of emergence: even if 25% of the emerging females failed to reproduce, the population would nearly triple every generation. Watson (1928) noted that fewer beetles emerged from standing trees than from downed trees because of woodpeckers preferentially feeding on standing trees.

For a small outbreak of semivoltine insects, McCambridge and Knight (1972) reported average mortalities of 95.5 and 98.5% for two generations in standing trees and 99.5% for a generation developing in trap trees that were deployed to control the outbreak. These figures also exclude potential losses during dispersal and host colonization but highlight how seemingly small changes in spruce beetle mortality between years or host types can mean the difference between expanding or contracting populations. The high level of natural mortality, along with active control measures (trap trees), likely led to the rapid collapse of the infestation being studied, despite the presence of susceptible host trees (McCambridge and Knight 1972). Swaine (1924) estimated about 15 brood beetles emerged per gallery from standing trees attacked during outbreaks (30 mature brood were counted per galley, but it was estimated that subsequent intraspecific competition would kill 50% of them). This equates to a potential growth rate of 8.4 at the time of emergence. Losses due to dispersal and colonization may be reduced during outbreaks due to the higher probability of locating and joining a successful mass attack. Even if 25% of all emerging females failed to reproduce, the population would still increase over six-fold every generation. The high reproductive capacity of spruce beetle contributes to its eruptive potential when favourable conditions are present.

#### 2.5.2. Host and stand conditions

The most intense and extensive spruce beetle outbreaks are usually preceded by a widely distributed pulse of ideal breeding habitat that occurs in an area with stands with high susceptibility to spruce beetle. Trees felled by wind storms in late autumn, winter, or spring just before the dispersal period are ideal habitat because the phloem in the newly fallen trees has not yet been degraded by competing insects or excessive drying. Other sources of ideal breeding habitat include breakage from snow storms, large-diameter logging residue (cull logs, stumps, tops), and trees felled for construction and highway projects (e.g., Swaine 1924; Morris 1958; Dyer and Taylor 1971; Dyer and Safranyik 1977; Safranyik et al. 1983; Halleran 1992; Safranyik and Linton 1999; Cozens 2004; Berg et al. 2006; Garbutt et al. 2007; Safranyik 2011; see section 1.3, Outbreak History). Windthrow is three to five times greater along stand edges than in stand interiors (Safranyik et al. 1983), such that clearcutting can facilitate or exacerbate outbreaks (Safranyik 2011). Some evidence exists showing that populations may occasionally build up in standing trees that are stressed due to senescence, competition, defoliation, disease,

dry and cold soils, or other injury (e.g., Watson 1928; Balch 1942; Morris 1958; Sterner and Davidson 1981; Hard et al. 1983; Safranyik et al. 1983; Holsten 1984; Hard 1985, 1987). Spruce trees that are killed by root damage from surface fires but have minimal charring of the bole may also provide ideal breeding habitat (Swaine 1924). Climate-induced stress on trees, such as that resulting from prolonged droughts, could also weaken tree defences and facilitate outbreaks, especially in the future under climate change (e.g., Berg et al. 2006; Fettig et al. 2007; Hebertson and Jenkins 2008; DeRose and Long 2012; Hart et al. 2014, 2017).

Under favourable environmental conditions (see section 2.5.3, Weather and climate), beetle populations rapidly increase in downed or stressed material. Tree defences are negated or reduced, and snowpack likely helps to protect spruce beetle developing in downed material from woodpeckers and cold temperatures (Knight 1958; Fayt et al. 2005). Spruce beetle's behaviour may change with population density. Compared to individuals from low-density populations, individuals from high-density populations are more likely to enter healthy, defended trees (Wallin and Raffa 2004). However, regardless of population density, beetles always seem to prefer fresh downed material and weakened trees to healthy trees.

Population buildup in downed or stressed material, such as windthrow or stumps, is not sufficient in itself to trigger an outbreak: the stand must also be susceptible to spruce beetle and other factors, specifically weather, that are conducive for beetle population growth (see section 2.5.3, Weather and climate; Safranyik et al. 1983, 1990). The most susceptible stands are those growing on good sites at lower elevations with a high proportion of large-diameter, mature, stressed, or senescing spruce (Watson 1928; Knight et al. 1956; Schmid and Hinds 1974; Safranyik et al. 1983; Holsten 1984). Most spruce trees in susceptible stands are larger than 25 cm in diameter at 1.4 m above ground level, and during outbreaks, tree mortality is usually proportionately higher in the largerdiameter classes, with only a fraction of trees less than 25 cm in diameter at that height being killed (Balch 1942; Mielke 1950; Morris 1958; Werner and Holsten 1983; Safranyik 1985). Mean recent radial growth and basal area growth are inversely related to the probability of attack by spruce beetle (Hard 1985, 1987). Stand susceptibility indices (SSIs) developed for spruce beetle are based on measures that reflect the abundance and vigour of large spruce, such as tree diameter, recent growth rate, stand density, age, species composition, and site quality (see Chapter 6, Decision Support Systems). Any factors that cause a depression of radial growth, such as competition due to high stand density, moisture stress, advanced age, defoliation, or disease, may potentially increase stand susceptibility to spruce beetle. Beetles initially cull from stands the largest stressed or senescing standing trees that have reduced growth, then attack more vigorous trees in sequentially smaller-diameter classes as the outbreak progresses (Watson 1928; Hard et al. 1983; Holsten 1984; Hard 1985; 1987; Safranyik 1985).

The size, intensity, and duration of outbreaks are related to the events or conditions that facilitated rapid population growth and stand susceptibility. Localized outbreaks that usually subside within a couple of years are generally associated with small pulses of ideal breeding habitat. Expansive, severe, and longer outbreaks usually develop from significant increases in ideal breeding material in areas with many highly susceptible stands. In addition to the availability of predisposed hosts and the susceptibility of stands, other factors, including favourable weather, play a role in facilitating and maintaining outbreaks (see below).

#### 2.5.3. Weather and climate

Weather and climate affect spruce beetle populations in two ways—directly, through the behaviour and physiology of individual beetles, and indirectly, through the host tree. Of the climatic factors, temperature and wind are the most important. Numerous studies have linked outbreaks to periods, sometimes decades long, of warmer temperatures (e.g., Massey and Wygant 1954; Dyer and Hall 1977; Barber et al. 2000; Berg et al. 2006; Sherriff et al. 2011). Warm growing season temperatures increase the proportion of the beetle population completing the life cycle in one *versus* two years, which promotes population increases and outbreaks (Hansen and Bentz 2003; Berg et al. 2006). Relative to the initial population, most brood mortality occurs in the first year of development, regardless of voltinism; however, mortality due to cold, natural enemies, and other factors will still accrue in subsequent years, such that survival will be higher for univoltine insects (e.g., Watson 1928; McCambridge and Knight 1972; Safranyik and Linton 1999).

Mild winters promote survival. Overwinter mortality can be substantial in colder years or when cold snaps occur at a time when insects are not fully cold hardy (e.g., Massey and Wygant 1954; Knight 1958; Miller and Werner 1987). Univoltine insects have to survive only one winter, which they pass as adults, whereas semivoltine insects have to survive one winter as larvae and one winter as adults. Larvae overwinter under the bark along the tree's bole at the locations where they developed, where they are exposed to cold temperatures on standing trees. However, adults can relocate to the base of the tree to overwinter, where the snowpack may provide some protection from cold temperatures and predation. The habit of adult relocation may be a winter survival strategy; however, it remains to be determined why the proportion of adults that relocate is so variable over time and space and if a cost is associated with overwintering at the base. Cold temperatures may indirectly affect spruce beetle population dynamics by amplifying the impact of some parasites and predators that are more cold hardy than spruce beetle (Terrell 1954; Frye et al. 1974).

Summer temperatures affect beetle survival and behaviour, as well as potential host trees. Spruce beetle mortality can be significant along the top sides of logs that are directly exposed to solar radiation (Mitchell and Schmid 1973). Beetles tend to avoid attacking such exposed surfaces, such that a main effect of solar radiation may be to reduce the amount of habitat available for reproduction. Spruce beetle may also avoid the top sides of logs because of competition from other bark beetles that attack the top sides (see section 4.2.4, Competing species of bark beetles). Drought stress caused by warm temperatures and lack of precipitation can affect spruce trees, reducing their defence capacity and increasing their susceptibility to attack (e.g., Hebertson and Jenkins 2008; DeRose and Long 2012; Hart et al. 2014, 2017; but see Pettit et al. 2020). Trees in colder boreal climates and growing along creeks in cool draws may experience drought stress in the spring when beetles are dispersing. Tree trunks or soils may still be frozen, limiting water movement at a time when air temperatures are conducive for transpiration, leading to moisture stress (Hard 1987; Bowling et al. 2018).

Like temperature, wind affects spruce beetle populations both directly through its influence on the host colonization process and beetle dispersal and indirectly by producing ideal breeding habitat. Wind affects the shape and dispersal of pheromone plumes. Pheromone plumes influence the density and rate of attack, which in turn affect the probability of beetles mounting a successful mass attack on defended trees. Wind may also affect the direction and distance of beetle movement

within a stand and across a landscape. Bark beetles avoid initiating flight in strong winds. Dispersing beetles initially fly in the direction of the wind until they encounter an attractive odour, then alter their course in response (Rudinsky 1962; Meyer and Norris 1973; Safranyik and Linton 1993). Long-distance movement of bark beetles may be aided by convective updrafts and winds in the upper atmosphere (Chapman 1967; Furniss and Furniss 1972; Jackson et al. 2008).

Wind can have a strong indirect effect on spruce beetle population dynamics by creating ideal breeding habitat (Figure 2.4). With a period of favourable weather, populations can increase rapidly in trees that are felled or damaged during storms in the autumn, winter, or spring before beetle dispersal. Spruce is a relatively shallow-rooted species and is prone to windfall on certain sites, especially in regions that experience a high frequency of storm-force winds (Stathers et al. 1994). Windthrow is often categorized as catastrophic—being caused by extreme wind events leading to extensive damage across a relatively large area—or endemic—typically spreading from an unstable





**Figure 2.4.** Examples of fresh windthrow and broken spruce trees, which are the preferred hosts of spruce beetle and provide ideal breeding habitat. Photos: R. Hodgkinson (top); J. Robert (bottom).

boundary, such as the edge of a clearcut, and progressing into a stand due to numerous, less extreme and more common wind events. Logging, thinning operations, root and basal decay, and mechanical root and soil disturbance can aggravate the problem by opening stands, which promotes increased within-stand wind speed and turbulence. In British Columbia, some background level of windthrow occurs annually in uncut stands and along cutblock boundaries and road allowances, whereas extreme wind events that occur every 10 to 20 years increase the amount of windthrow by an order of magnitude (Stathers et al. 1994). Small groups of large-diameter, shaded windthrow scattered throughout a region of susceptible stands are especially conducive for the development of extensive and severe outbreaks.

## 2.5.4. Intraspecific competition

The negative density-dependent effects of intraspecific competition can be so severe for spruce beetle that they may contribute to the decline of outbreaks. Swaine (1924, p. 14) describes how "... the mortality of larvae through lack of sufficient food material is very great, and [that] the tendency for a swarm of beetles to overcrowd the brood trees is evidently a factor reducing the intensity of an outbreak". In living, defended trees, compensatory density dependence results in a trade-off between the cooperative group attack required by beetles to successfully overcome tree defences and the negative effects of intraspecific competition. Brood production initially increases with attack density in defended trees, reaches a maximum, and then declines (Swaine 1924; Watson 1928; Knight 1958). Based on field studies, Watson (1928) estimated that in the absence of predators, particularly the exclusion of woodpeckers, 87% of larvae died due to starvation in a downed tree with a moderate attack density (~54 attacks/m² of bark surface). Heavy predation may negate potential future losses to intraspecific competition. McCambridge and Knight (1972) reported that spruce beetle suffered 75% brood mortality due to the combined effects of intraspecific competition and woodpecker predation. In laboratory studies, increased attack density or increased brood density has been associated with shorter egg galleries, a lower total number of eggs laid per female, a lower number of surviving adult offspring per female, and a reduced pronotal width of brood adults (Thomson and Sahota 1981; Safranyik and Linton 1985; Sahota et al. 1987). Female size is likely correlated with fecundity (McGhehey 1971); therefore, the effects of overcrowding may affect brood production in the next generation.

# 2.5.5. Natural enemies and spruce beetle quality

Other factors that may play a role in spruce beetle population dynamics include the impact of natural enemies and the quality or health of insects. Natural enemies are covered in detail in Chapter 4, Ecological Interactions. Here, the focus is on the potential overall combined effect of natural enemies on spruce beetle population dynamics. Some natural enemies cause impressive levels of mortality, killing 50% to 75% of developing brood (Swaine 1924; Hutchison 1951; Massey and Wygant 1954; Knight 1958). However, their overall effects are highly variable in time and space, and their potential impacts on population dynamics are poorly understood. Some of the mortality caused by natural enemies may simply pre-empt future losses that would have occurred due to other mortality factors such as intraspecific competition or cold temperatures. Furthermore, spruce beetle's high reproductive potential ensures populations can sustain relatively high mortality levels without crashing. Nonetheless, in the case of endemic or incipient populations or small localized outbreaks, natural enemies may serve to regulate populations and may even limit the size or duration of spruce beetle infestations.

#### Chapter 2. Biology and Population Dynamics

Research and observations on natural enemies have largely focused on woodpeckers, invertebrate predators and parasitoids, and entomopathogenic fungi. Little is known about the potential pathogenic effects of viruses, bacteria, algae, yeasts, microsporidia, and protists on bark beetle population dynamics (Wegensteiner et al. 2015). Interestingly, changes in insect quality have been correlated with spruce beetle outbreak status. Knight (1969) reported that females in endemic, epidemic, and declining epidemic populations produced 3.6, 7.2, and 4.8 eggs/cm of gallery, respectively, and McCambridge and Knight (1972) suggested that a change in fecundity was the first sign of population decline. Although nematodes that reduce fecundity were present, nematode-free females also had similarly reduced fecundity. Unknown agents were thought to be contributing to the decline. A variety of poorly described pathogens (e.g., Wegensteiner et al. 2015) or even overcrowding could potentially lead to changes in the quality or health of a spruce beetle population.

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## **CHAPTER 3**

# Host Finding and Communication

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Semiochemicals produced by trees, conspecifics, allospecifics, and even associated organisms affect the behaviour of spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae). Dispersing beetles use both nonhost and host tree volatiles to locate the appropriate tree species and even to assess the physiological condition of a potential host. Attacking beetles produce aggregation and anti-aggregation pheromones that mediate the colonization process, which includes mate finding and regulation of attack density. Some tree volatiles are synergistic with certain pheromones. Organisms associated with spruce beetle, such as microbial symbionts and secondary bark beetle species that attack only dead or moribund hosts, also produce semiochemicals that may affect spruce beetle behaviour. In addition, predators, parasitoids, and competitors may exploit the complex semiochemical communication system of spruce beetle (see Chapter 4, Ecological Interactions).

Senses other than olfaction may also be involved in spruce beetle host finding and communication. Dispersing beetles may use visual cues, such as the silhouette of a standing or downed tree, to locate hosts, although spruce beetle is capable of orienting towards host odours in the absence of visual cues (Moeck 1978). Gustatory cues could influence the beetle's host acceptance behaviour, especially among the first pioneering beetles that arrive at a potential host and decide to initiate boring in the absence of beetle-produced pheromones. Unfortunately, our understanding of the role of these cues in host finding is limited. Spruce beetle may also use acoustic cues for both intra- and interspecific communication.

This chapter focuses primarily on the semiochemistry involved in spruce beetle host finding and conspecific communication, including the biosynthesis and regulation of pheromones. We also consider how associated organisms may affect spruce beetle's semiochemical communication and offer a brief synopsis of the potential roles of acoustic communication that is based on research from other *Dendroctonus* species. The application of semiochemicals for spruce beetle control and forest management is discussed in detail in Chapter 5, Management.

# 3.1. Tree Volatiles and Host Finding

Spruce beetle uses olfactory cues provided by tree volatiles to locate suitable and vulnerable host trees. Spruce beetle responds to spruce trees while actively avoiding nonhost species; thus, host

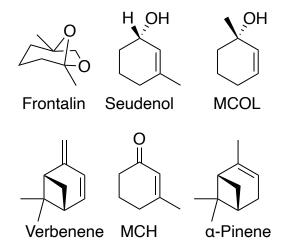
and nonhost volatiles serve as kairomones and synomones, respectively, for dispersing beetles (e.g., Huber et al. 2000; Pureswaran and Borden 2003; Pureswaran et al. 2004a, 2004b; Pureswaran and Borden 2005). Some volatiles found in angiosperms but not in spruce may serve as cues to avoid nonhost trees (Huber et al. 2000; Hansen et al. 2019). For tree species that have the same monoterpenes, evidence indicates that beetles may recognize the chemotype (i.e., the relative amounts of various compounds), which varies among and within tree species (Robert et al. 2010; Davis et al. 2018). The "chemotype discrimination" hypothesis is based on the ability of four species of bark beetles to differentiate among their respective coniferous hosts, which are often sympatric and do not vary qualitatively in the terpenes present: spruce beetle (spruce); mountain pine beetle (*D. ponderosae*; pine), Douglas-fir beetle (*D. pseudotsugae*; Douglas-fir), and western balsam bark beetle (*Dryocoetes confusus*; subalpine fir) (Pureswaran et al. 2004a, 2004b; Pureswaran and Borden 2005). Attacks on the wrong tree species by these beetles under natural conditions are relatively rare, suggesting that host recognition may be based on chemotype.

Primary attraction of spruce beetle to its host was first demonstrated by Moeck (1978). Spruce beetle is able to discriminate between spruce and nonhost conifers even in the presence of secondary attraction. Spruce beetles did not attack nonhost conifers that are sympatric with spruce when the trees were baited with aggregation pheromone (Pureswaran and Borden 2003). The attraction of spruce beetle to ethanol, which is a host tree derivative produced in response to stress, explains how the beetle locates stressed and freshly downed spruce, its preferred hosts (Moeck 1981). Spruce beetle, like some other bark beetles, has a high tolerance to monoterpenes compared to other insects, but these compounds are still toxic at high levels (e.g., Werner 1995; Keeling 2016; Chiu et al. 2017). Spruce beetle's strong primary attraction to downed and stressed hosts with compromised defences is usually maintained regardless of population density: standing, healthy trees are usually attacked once preferred hosts are depleted or if they are near downed hosts that are being attacked. Beetles from high-density, eruptive populations maintain their preference for stressed trees but may display a broader range of host acceptance behaviour than beetles from low-density, endemic populations do (Wallin and Raffa 2004; see section 2.5, Population Dynamics). In addition to their role in primary attraction, host tree volatiles also affect secondary attraction, including the production and effect of beetle-produced pheromones.

# 3.2. Spruce Beetle Pheromones

# 3.2.1. Pheromone components

Identifying the suite of pheromones and their behavioural activities for a beetle species is not trivial. Compounds must be identified from extracts or volatiles of the beetles, and the identified compounds must be subsequently tested for behavioural activity in the field at different doses. Often, additional synergistic components, either from the beetle or the host, are needed for robust activity. These experiments can be further complicated if one or more of the compounds is chiral, such that there is a handedness to the chemical structure, or if pheromone production or perception vary across the beetle's range. All of these challenges appear to be in play with the spruce beetle, and research continues to increase our understanding of pheromone communication in spruce beetle.



**Figure 3.1.** Chemical structures of the main identified pheromone components in spruce beetle and the host volatile  $\alpha$ -pinene.

A number of spruce beetle pheromones have been identified, many of which are also produced by other *Dendroctonus* species. Known aggregation pheromone components include frontalin (1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane), seudenol (3-methyl-2-cyclohexen-1-ol), verbenene (4-methylene-6,6-dimethylbicyclo[3.1.1]hept-2-ene), and MCOL (1-methyl-2-cyclohexen-1-ol), whereas MCH (3-methyl-2-cyclohexen-1-one, also known as seudenone) is an anti-aggregation pheromone component (Figure 3.1; Isitt et al. 2018). Frontalin and seudenol synergize with the host monoterpene α-pinene (Furniss et al. 1976; Ryall et al. 2013).

Early semiochemical work on spruce beetle was aided by the observation of cross-attraction with the Douglas-fir beetle (Chapman and Dyer 1969), which allowed the identification of frontalin as a pheromone component (Dyer and Chapman 1971; Dyer 1973). However, the presence of frontalin in spruce beetles (females) was not reported until much later (Gries et al. 1988). Frontalin production may vary geographically and between sexes. Male beetles from Nova Scotia produce frontalin, whereas it is only occasionally observed in females; in western Canada, frontalin is found in spruce beetles of both sexes (Isitt et al. 2020). Frontalin generally attracts more female beetles than male beetles and is described as being only moderately attractive on its own (Dyer 1973; Setter and Borden 1999). Spruce monoterpenes  $\alpha$ -pinene,  $\beta$ -pinene, camphene, and 3-carene interacted synergistically with frontalin (Werner 1995).

Frontalin is chiral, but little research has been done to determine the enantiomeric ratio produced by spruce beetle. Although only (+)-frontalin is produced by feeding females (Gries 1992), beetles of both sexes produce frontalin with an enantiomeric ratio of approximately 37 (+): 63 (-) when exposed to the presumptive precursor 6-methyl-6-hepten-2-one (Perez et al. 1996). Very recently, Isitt et al. (2020) showed that the enantiomeric ratio of frontalin in beetle hindguts varies across the range of spruce beetle, and in all cases (-)-frontalin was the most abundant enantiomer. Even less research has been done into the optimal enantiomeric ratio for aggregation. No difference was found in the attractiveness among funnel traps baited with (+)-frontalin, (-)-frontalin, and (±)-frontalin [racemic, 50 (+):50 (-)] in the absence of any additional host or pheromone components; however, the numbers of beetles caught were very low, and variation was high (Lindgren 1992). Subsequently, most trapping studies used racemic frontalin. With the current understanding of the pheromone components and host synergists, it would be beneficial to

re-examine whether this enantiomeric ratio is the most appropriate when combined with the other pheromone and host compounds across the beetle's range.

Seudenol was first detected in spruce beetles by Vité et al. (1972). Traps baited with seudenol attract more beetles than unbaited control traps do, but seudenol was not effective in field tests involving host trees (Dyer and Hall 1980). Male beetles are more attracted to seudenol than female beetles are (Furniss et al. 1976). Seudenol is normally found in females (Ryall et al. 2013), but lesser amounts are occasionally observed in males (Isitt et al. 2018). Gries (1992) mentioned the enantiomeric ratio of seudenol found in female spruce beetles is 66 (+):34 (-), although the beetles' origin is unknown. Although seudenol was more dominant in populations in eastern Canada than in western Canada, the enantiomeric ratio was similar across sites at 80 (+):20 (-) (Isitt et al. 2020).

The MCOL component is a regioisomer of seudenol and was identified by Borden et al. (1996) in a steam distillate of female (not male) frass volatiles in a 1:1 ratio with seudenol. Setter and Borden (1999) found that MCOL had a synergistic effect when it was added to racemic frontalin in British Columbia, increasing the attraction of female spruce beetles more than three-fold and of males more than four-fold. In combination with frontalin and  $\alpha$ -pinene, MCOL increased the number of beetles caught in southern Utah (Ross et al. 2005). Ryall et al. (2013) did not detect MCOL in beetles from Newfoundland, nor did MCOL increase trap catches when it was added to frontalin and α-pinene; however, Isitt et al. (2018) found MCOL in beetles from Nova Scotia. A recent study by Isitt et al. (2020) confirmed that the quantity of MCOL varies widely across the geographic range of spruce beetle. The enantiomeric specificity of MCOL also varies regionally, including certain enantiomers having inhibitory effects in some areas (Borden et al. 1996; Setter and Borden 1999). When combined with frontalin and  $\alpha$ -pinene, (+)-MCOL was significantly more attractive to spruce beetles in the interior of Alaska than (-)-MCOL or (±)-MCOL was (Werner 1994). Gries (1992) mentioned the enantiomeric ratio of MCOL as 58 (+):42 (-), presumably from western Canadian beetles, but this ratio has not been examined widely until recently. Isitt et al. (2020) found that the enantiomeric ratio 69 (+):31 (-) was similar among six sites across Canada. It is important to note that in the presence of traces of acid, MCOL will isomerize to seudenol (Setter and Borden 1999).

Gries et al. (1992) identified verbenene, either alone or in combination with frontalin and  $\alpha$ -pinene, as an aggregation pheromone in the female spruce beetle when tested in southwestern British Columbia. They also showed dose-dependent electroantennographic responses by both sexes. However, Borden et al. (1996) found that verbenene was attractive in Alaska only when it was tested in combination with frontalin,  $\alpha$ -pinene, and MCOL, whereas Hansen et al. (2019) did not find verbenene to increase trap catches in Utah when it was added to those same three compounds. In recent analyses, Isitt et al. (2018, 2020) detected verbenene in spruce beetles of both sexes from only one site in Alberta; the detected verbenene had an enantiomeric ratio of 89 (+):11 (-).

Early work showing the cross-activity of spruce beetle to Douglas-fir beetle pheromones identified MCH as an anti-aggregation pheromone (Kline et al. 1974; Rudinsky et al. 1974). Regulation of attack and egg gallery density may be mediated through MCH because it is effective in reducing attack densities by spruce beetle (Furniss et al. 1976; Dyer and Hall 1977; Lindgren and McGregor 1989). Ross et al. (2004) found that MCH was not a repellent in southern Utah, but Hansen et al. (2019) found that it was repellent elsewhere in Utah. Female spruce beetles on their own do not release detectable amounts of MCH, but once a male has entered the gallery, significant amounts

of MCH is released, thereby reducing female attractiveness to other males. However, extracts from the hindguts of females feeding alone contain more MCH than do those of females that are feeding with a male (Isitt et al. 2018). This suggests that the presence of the opposite sex may trigger the release of stored MCH (Rudinsky et al. 1974). Both sexes of emerging adults contain MCH (Rudinsky et al. 1974), and it has also been detected in female beetle frass (Borden et al. 1996).

In addition to the known spruce beetle pheromone components described above, the antennae of spruce beetles respond to 1-octen-3-ol, *trans*-verbenol, verbenone, nonanal, *exo*-brevicomin, *endo*-brevicomin, and acetophenone, which are present in spruce beetle and other bark beetle species (Pureswaran et al. 2004b). However only 1-octen-3-ol, which is found in spruce beetle females and in several other insect species (El-Sayed 2019), reduced trap catches when combined with frontalin,  $\alpha$ -pinene, and MCOL (Pureswaran and Borden 2004). Thus, 1-octen-3-ol would also be considered an anti-aggregation pheromone. The stereochemistry of 1-octen-3-ol has not been determined in spruce beetles, but has been suggested to be (-) (Pureswaran and Borden 2004).

## 3.2.2. Biosynthesis and regulation of pheromones

The pathways of pheromone biosynthesis and their regulation have been studied in several *Dendroctonus* and *Ips* species (Keeling et al. 2020b). The insect hormone juvenile hormone III (JH III) plays a major role in regulating the biosynthesis of many bark beetle pheromones. In spruce beetle, Isitt et al. (2018) showed that pheromone production is affected by feeding but not by mate presence. Juvenile hormone III titre typically increases when adults begin feeding on the host (Tillman et al. 2004). Frontalin is biosynthesized *de novo* (Figure 3.2) in the beetle through the mevalonate pathway (Barkawi et al. 2003; Keeling et al. 2013) and is induced in both sexes by JH III (Barkawi 2002), but males produce much more of it than females do. Males release frontalin when feeding on phloem (Isitt et al. 2018).

The pathways of biosynthesis for seudenol, MCOL, and MCH have not been studied and remain unknown. However, Francke et al. (1995) postulated that these pheromones are of monoterpenoid origin through carbon–carbon bond cleavage in a manner similar to the proposed production of 1-methyl-5-(1-hydroxy-1-methylethyl)-cyclohexa-1,3-diene from 3-carene in the six-toothed bark beetle (*Ips sexdentatus*). Isitt et al. (2018) showed that male spruce beetles produce detectable quantities of seudenol in the 24 hours after phloem feeding commences and that females produce approximately 10 times more during the same period. The researchers also showed that the amounts of both MCOL and MCH increased in feeding females and that the presence of males did not significantly affect those amounts.

Verbenene biosynthesis has not been studied in spruce beetle, but it likely originates from host-derived  $\alpha$ -pinene. The presence of verbenene has been associated with thermal decomposition of verbenyl esters during gas chromatographic analyses of beetle extracts (Chiu et al. 2018). The verbenyl esters in *D. ponderosae* originate from earlier life stages by the apparent hydroxylation of host-derived  $\alpha$ -pinene and esterification of verbenols with fatty acids. These esters appear to be hydrolyzed in female *D. ponderosae* adults to release *trans*-verbenol pheromone when entering a new host (Chiu et al. 2018). Spruce beetles may also sequester  $\alpha$ -pinene as verbenyl esters at earlier life stages. The resulting verbenyl esters could then be retained until cleaved by adults to release

**Figure 3.2.** Hypothesized pathway of *de novo* frontalin biosynthesis. The mevalonate pathway provides the five-carbon precursors from acetate to make geranylgeranyl diphosphate. This is subsequently cleaved, and the eight-carbon portion is isomerized and epoxidized. This epoxide then cyclizes to frontalin.

verbenene through an intramolecular elimination of the fatty acid. This hypothesis, illustrated in Figure 3.3, remains to be tested.

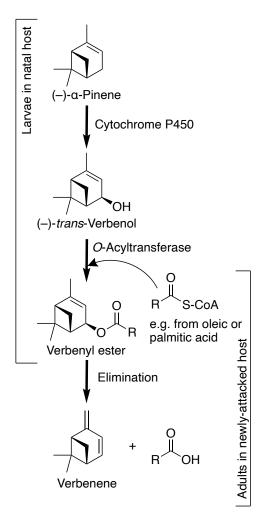
The biosynthesis of 1-octen-3-ol has not been studied in bark beetles (Figure 3.4), but this compound, also known as mushroom alcohol, results from lipoxygenases and hydroperoxide lyases cleaving linoleic acid (Noordermeer et al. 2001; Fauconnier et al. 2002).

The local and geographic variation in the pheromone blend of spruce beetle (Isitt et al. 2020) and field testing results suggest that the genes that regulate, produce, and detect the pheromone components in spruce beetle vary significantly across the species' range. Functional genomics and population genetic studies with the aid of the spruce beetle genome assembly (Keeling et al. 2020a) may provide a greater understanding of these differences.

# 3.2.3. Semiochemical interactions with associated organisms

#### Other bark beetles

Some secondary bark beetles that may compete with spruce beetle for habitat resources also produce semiochemicals. Several studies have investigated the effects of semiochemicals produced by *Dryocoetes* 



**Figure 3.3.** Hypothesized pathway of verbenene biosynthesis from host-derived  $\alpha$ -pinene. It is hypothesized that larvae in their natal tree hydroxylate and esterify host  $\alpha$ -pinene, similar to the way *trans*-verbenol is formulated in *D. ponderosae*. The resulting verbenyl esters are retained until cleaved by adults to release verbenene through an intramolecular elimination of the fatty acid.

**Figure 3.4.** Hypothesized biosynthesis of 1-octen-3-ol in spruce beetle, based upon biosynthesis in other organisms.

affaber [(±)-exo-, (±)-endo-brevicomin], northern spruce engraver [I. perturbatus; (±)-ipsdienol], four-eyed spruce bark beetle (Polygraphus rufipennis; 2-methyl-3-buten-2-ol), and I. tridens [(±)-ipsdienol, (-)-cis-verbenol] on spruce beetle with the aim of developing a new management tactic (Poland and Borden 1998a, 1998b, 1998c; Werner and Holsten 2002). Many of the semiochemicals produced by the secondary bark beetles were found to have a repellent effect on spruce beetle in trapping experiments, suggestive of interference competition (Poland and Borden 1998b; Werner and Holsten 2002). Many of these semiochemicals have proven to be effective in reducing spruce beetle attack and production on downed trees by inducing attack by secondary species; however, to maximize the negative effects of exploitative competition on spruce beetle, attack by secondary bark beetles needs to be induced before spruce beetle attack (Poland and Borden 1998a, 1998b; Werner and Holsten 2002).

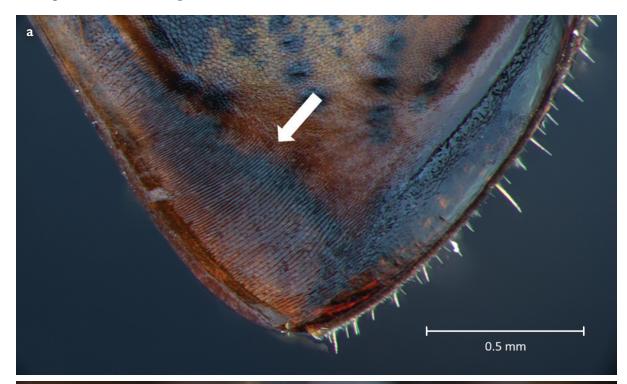
#### Microbial volatile organic compounds

A variety of microorganisms, including yeasts, filamentous fungi and bacteria, are present on the exterior or in the guts of bark beetles, as well as in their galleries. These endo- and ecto-microbial symbionts have multiple ecological roles, from nutrition and habitat amelioration (see Chapter 4, Ecological Interactions) to affecting communication and behaviour of bark beetles through the emission of microbial volatile organic compounds (e.g., Davis et al. 2013, 2019). Microbial associates may indirectly affect bark beetle communication by providing precursory compounds for pheromone production, such as ergosterol (Bentz and Six 2006). A growing number of studies have indicated that microbial volatile organic compounds produced by gut bacteria and fungal associates carried on the exoskeleton or within mycangia are common components of bark beetle aggregation and anti-aggregation pheromones that have potential to affect beetle behaviour (e.g., Brand et al. 1975, 1976; Hunt and Borden 1990; Davis et al. 2013; Xu et al. 2015; Kandasamy et al. 2016; Zhao et al. 2019; but see Blomquist et al. 2010). Microbial volatile organic compounds may also be used by natural enemies of bark beetles to locate their hosts (Boone et al. 2008). Although spruce beetle is associated with a variety of microbes (see Chapter 4, Ecological Interactions), their potential effect on spruce beetle communication and behaviour has yet to be examined.

#### 3.3. Acoustic Communication

Limited work has been done on spruce beetle's use of acoustic communication. However, stridulation or acoustic signalling is prevalent in many bark beetles, including *Dendroctonus* species, for recognizing species, mating, reducing competition, defending territory, and deterring predators (Barr 1969; Rudinsky and Michael 1973; Wood 1982; Lindeman 2015; Hofstetter et al. 2018). Different sounds have been associated with stress or disturbance, male—male rivalries, and male—female interactions during host colonization (e.g., Rudinsky and Michael 1973, 1974; Fleming et al. 2013). Playback of sound has been shown to affect beetle behaviour, reproduction, and survival (Aflitto and Hofstetter 2014). In *Dendroctonus*, the stridulation motif is a file (pars stridens), which is stimulated by a scraper (plectrum) to create sounds, described as chirps, that are broadband and vary in complexity (Figure 3.5; e.g., Barr 1969; Oester 1977; Lyal and King 1996; Fleming et al. 2013; Lindeman 2015). Acoustic communication apparently functions at close range through both airborne sonic and ultrasonic signals, as well as through substrate-borne vibrations; however, an auditory receptor has yet to be described in *Dendroctonus* (Fleming et al. 2013). In addition to acoustic effects

on social interactions, it has been hypothesized that acoustics play a role in helping beetles locate suitable habitat because drought-stressed trees produce an ultrasonic emission caused by cavitations in the xylem (Mattson and Haack 1987; Haack et al. 1988). Further research is warranted on acoustic communication in various species, including spruce beetle, because of its potential for use in the development of novel management tools (Hofstetter et al. 2018).





**Figure 3.5.** The stridulation motif on a male spruce beetle, which consists of (a) a file (pars stridens) on the underside of the left elytron (white arrow); and (b) a scraper (plectrum), which is located on the seventh tergite on males (white arrows). Photos: G. Smith.

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# **CHAPTER 4**

# **Ecological Interactions**

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Spruce Beetle, Dendroctonus Rufipennis (Kirby) (Coleoptera: Curculionidae), interacts with many species in its habitat. Interactions between species can be classified as: mutualistic, where both partners benefit; commensal, where one species benefits and the other is not affected; antagonistic or competitive, where both species are negatively affected; or parasitic or predatory, where the predator or parasite benefits at the expense of the other species. Interactions may occur directly between species or indirectly via a chain of effects involving multiple species. The strength and nature of interactions may change over time, depending on environmental conditions and ecological factors such as the presence of other species. The result is a potentially dynamic, complex web of direct and indirect interspecific interactions affecting spruce beetle. Here, we focus on spruce beetle's interactions with other species that are considered as being either generally beneficial or detrimental to the beetle, and where there is evidence, we note the potential for alternative outcomes.

# 4.1. Beneficial Associations

# 4.1.1. Filamentous fungi and yeasts

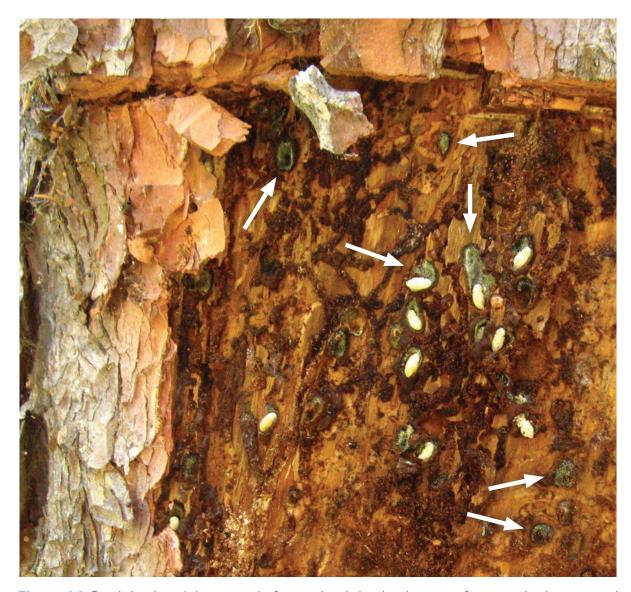
Research on the mycobiome of spruce beetle has focused largely on filamentous fungi in the families Ophiostomataceae and Ceratocystidaceae, specifically the genera *Grosmannia*, *Leptographium*, *Endoconidiophora*, *Ceratocystis*, *Graphilbum*, and *Ceratocystiopsis*. These fungi are commonly referred to as ophiostomatoid fungi despite their different taxonomic positions. The fungi have undergone a number of taxonomic revisions and have a messy nomenclature. Here, all fungi (filamentous fungi and yeasts) are referred to by the current name listed on www. indexfungorum.org as of March 2021, and relevant taxonomic synonyms used in cited publications are noted in parentheses. Some ophiostomatoid fungi are known as blue- or black-staining fungi because of the colour they impart to sapwood, caused by melanin production in the hyphal cell wall. Many ophiostomatoid fungi are mutualists of bark beetles, conferring nutritional benefits, facilitating digestion of tree tissues, detoxifying chemical defences of trees, deterring antagonistic or entomopathogenic microbes, and mediating intraspecific communication; however, some species are detrimental to certain developmental stages of bark beetles.

The most common ophiostomatoid fungi associated with spruce beetle are Grosmannia abietina (= Leptographium abietinum; = L. engelmannii) and Endoconidiophora rufipennis (= Ceratocystis rufipenni; = C. coerulescens). Grosmannia abietina has been isolated at high frequencies from beetle populations in Alaska, British Columbia, Colorado, Utah, and Minnesota, although it is poorly represented or absent in some populations and at some points in time (Rumbold 1936; Davidson 1955; Hinds and Buffam 1971; Safranyik et al. 1983, 2010; Reynolds 1992; Solheim 1995; Ohsawa et al. 2000; Six and Bentz 2003; Aukema et al. 2005). To date, E. rufipennis has been associated with spruce beetle infestations in Alberta, British Columbia, and Colorado, but it has been isolated only from tree tissues around galleries and has not been isolated from spruce beetles (Davidson 1955; Hinds and Buffam 1971; Solheim 1995; Ohsawa et al. 2000). Grosmannia abietina is associated with a number of bark beetles that colonize Picea and non-Picea hosts, but E. rufipennis appears to be specific to trees infested with spruce beetle (e.g., Jacobs and Wingfield 2001; Haberkern et al. 2002). Other fungi isolated from spruce beetle or infested tree tissues include Grosmannia piceaperda (= Ceratostomella piceaperda), Ophiostoma piceae, L. olivaceum (= O. olivaceum), O. piliferum, O. bicolor, O. penicillatum, O. ips, and Grosmannia truncicola (= O. truncicola). However, most of these species were isolated at low frequencies and are likely incidental associates (Rumbold 1936; Davidson 1955; Safranyik et al. 1983, 2010; Ohsawa et al. 2000; Six and Bentz 2003; Aukema et al. 2005).

Both *G. abietina* and *E. rufipennis* may play a role in nullifying or detoxifying host defences as they elicit a defence response when inoculated into trees (e.g., Harrington and Cobb 1983; Werner and Illman 1994; Ross and Solheim 1997; Solheim and Safranyik 1997; Solheim and Krokene 1998; Ohsawa et al. 2000; Davis et al. 2018; Stewart et al. 2020). *Endoconidiophora rufipennis* is posited to play a role in tree death because it tolerates low-oxygen conditions, promotes sapwood occlusion, and is highly pathogenic to spruce trees (Solheim and Safranyik 1997; Solheim and Krokene 1998). In contrast, *Grosmannia abietina* is described as only weakly pathogenic, but it can tolerate and metabolize some monoterpenes that are toxic to spruce beetle such that it may play a role in ameliorating tree tissues for insect development or excluding opportunistic and entomopathogenic fungi (Davis et al. 2019).

The induced tree defence response elicited by fungi may temporarily be detrimental to spruce beetle (Werner and Illman 1994). Larvae may gain nutritional benefits from feeding on phloem colonized by fungi. Mycelia of *G. abietina* contain significant amounts of nitrogen, phosphorus, protein, and sterols, which are important for insect development and reproduction (Bentz and Six 2006; Davis et al. 2019). Young adults may gain nutritional benefits from maturation feeding on spores lining the pupal chambers (Figure 4.1; Bleiker and Six 2007). One study found spruce beetle gallery construction was reduced with *G. abietina*, but no effect on oviposition or survival occurred, and results varied from another study using a different rearing method (Cardoza et al. 2006b, 2008). Other potential negative effects of fungi include natural enemies using microbial volatile organic compounds to locate their bark beetle prey (see section 3.2.3, Semiochemical interactions with associated organisms).

Yeasts, especially those in the Saccharomycetaceae family, are ubiquitous associates of bark beetles (e.g., Grosmann 1930; Callaham and Shifrine 1960); however, little is known about their role in the bark beetle holobiont (Davis 2014). Almost every individual adult spruce beetle carries one or more species of yeast (Safranyik et al. 1983, 2010; Ohsawa et al. 2000; Six and Bentz 2003). Rivera et al.



**Figure 4.1.** Pupal chambers (white arrows) of spruce beetle lined with spores of associated ophiostomatoid fungi. The conidiophores are black, and the conidia (spores) appear white. Photo: L. Maclauchlan.

(2009) identified yeast strains isolated from nine species of *Dendroctonus*, including 20 individual spruce beetles from Oregon. The most common yeast species was *Kuraishia molischiana*, which was isolated only from spruce beetle. The other species isolated from spruce beetle by Rivera et al. (2009) are also associated with other bark beetle species. These include *Nakazawaea ernobii* (= *Candida ernobii*), *Ogataea glucozyma* (= *Pichia glucozyma*), and *Wickerhamomyces canadensis* (= *P. canadensis*), as well as several unidentified species. Experiments suggest that yeast may be beneficial to developing insects. Safranyik et al. (1983) reported that the addition of 10% brewer's yeast to a ground phloem diet halved the time required for insects to develop from eggs to adults. Yeasts may also play a role in detoxifying host defences and conditioning tree tissues for brood development (Davis 2014; Davis et al. 2019). Rumbold (1936) noted that the growth of a filamentous fungal associate of spruce beetle was greater in the presence of yeast.

Spruce beetles can carry fungal propagules in pits or under hairs on the exoskeleton, as well as in the alimentary canal (e.g., Rumbold 1936; Solheim and Safranyik 1997; Six and Bentz 2003; Vega and Dowd 2005; Rivera et al. 2009; Safranyik et al. 2010; Davis et al. 2019). Fungal propagules are introduced to tree tissues as the beetles bore into the bark. The spread of the fungi may be facilitated by the construction of egg and larval galleries, as well as by other associated organisms such as mites and nematodes (Cardoza et al. 2008). Mycangia, specialized sacs in the integument for transporting fungi, are considered absent in spruce beetle; however, Cardoza et al. (2006b) report on the presence of a melanized crypt-like structure on the hind wings, which appears to contain spores and hyphal masses and may substitute for or be analogous to mycangia. Even outside of these crypts, the wings of spruce beetle were observed to be covered in mucilaginous secretions and fungal spores and mycelia. Fungi were also observed in close association with nematodes on the hindwings of some spruce beetles in cocoons (see section 4.2.2, Invertebrate predators, parasitoids, and parasites – Nematoda, below; Cardoza et al. 2006b). These observations highlight the potential for complex multipartite interactions in this system (Cardoza et al. 2008).

### 4.1.2. Bacteria

Bacteria are commonly isolated from bark beetles and may also be carried by other species, such as mites or nematodes, that are associated with bark beetles (Cardoza et al. 2006b; Vasanthakumar et al. 2006; Delalibera et al. 2007; Hernandez-Garcia et al. 2017). Despite the potential significance of bacteria-insect mutualisms, little is known about the specificity and nature of such associations in bark beetles. Bacterial associates could potentially confer both protective and nutritive benefits to their bark beetle partners. Cardoza et al. (2006a) observed adult spruce beetles producing and spreading oral secretions in galleries using their legs. Nine bacteria were isolated from the secretions, and the authors posited that antibiotic secondary metabolites produced by the bacteria inhibited the growth of opportunistic and antagonistic fungi in beetle galleries and controlled the growth of G. abietina. All major taxa of bacteria were isolated in a survey of spruce beetle mouthparts and oral secretions, but the most common class was Actinobacteria, specifically the genus Streptomyces (Cardoza et al. 2009). A number of the genera isolated from spruce beetle have been found in the guts of other Dendroctonus species (Vasanthakumar et al. 2006; Hernandez-Garcia et al. 2017). In addition to providing protection from unwanted fungi, bacteria may also detoxify tree defence compounds and digest tree and fungal tissues (e.g., Vasanthakumar et al. 2006).

#### 4.1.3. Other bark beetles

Swaine (1924) recognized that secondary bark beetle species may help low-density spruce beetle populations kill trees, especially early in the season. Swaine even suggested that secondary bark beetles may be a factor in the development of spruce beetle outbreaks; however, this has not been investigated to date. The nature of spruce beetle's relationship with some secondary bark beetles may depend on density. Low-density spruce beetle populations may benefit through facilitation, as has been reported for mountain pine beetle (Smith et al. 2011), but high-density spruce beetle populations may suffer from high levels of interspecific competition (see section 4.2.4, Competing species of bark beetles).

# 4.2. Natural Enemies and Competitors

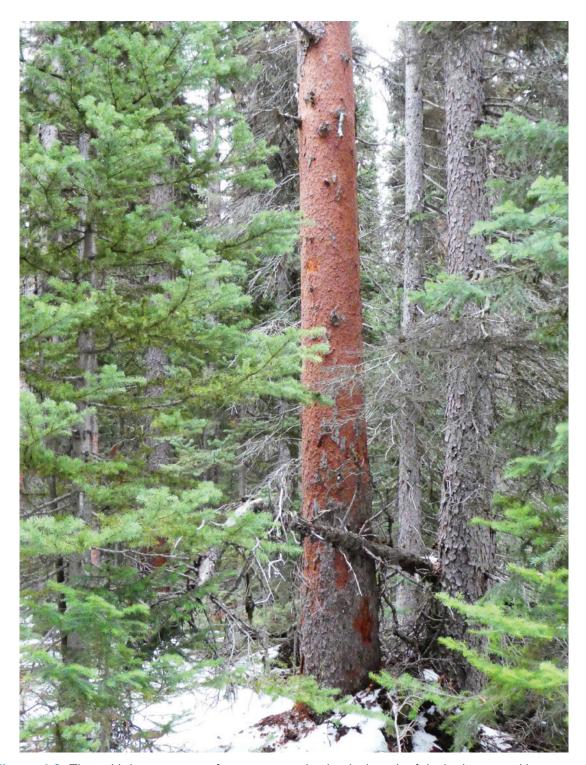
Considerable information exists on the diversity of the natural enemies of spruce beetle, but the overall impact of many species on beetle populations remains largely undetermined. Some natural enemies cause what appear to be impressive levels of mortality, killing between 50% and 75% of developing brood, but their impact is often highly variable over time and space (Swaine 1924; Hutchison 1951; Massey and Wygant 1954; Knight 1958). Some of the mortality caused by natural enemies may in part pre-empt future losses to other density-dependent mortality factors, such as intraspecific competition. Furthermore, the high reproductive potential of spruce beetle means populations may remain stable even with relatively high mortality levels (see section 2.5, Population Dynamics). Nonetheless, in the case of endemic and incipient populations, localized outbreaks, and even larger outbreaks with relatively low growth rates, natural enemies might play a role in regulating populations. Research or observations to date on the natural enemies of spruce beetle have largely focused on woodpeckers, insect predators and parasitoids, and entomopathogenic fungi. Comparatively little is known about the ecology of nematodes associated with bark beetles or the effects of viruses, bacteria, algae, yeasts, microsporidia, and protists (Mills 1983; Wegensteiner et al. 2015).

# 4.2.1. Vertebrate predators

#### **Aves**

Woodpeckers (Picidae) are undoubtedly one of the most important biotic mortality agents of spruce beetle. In addition to direct mortality caused by consumption, woodpeckers remove a lot of bark while foraging, which results in indirect beetle mortality from desiccation or exposure (Figure 4.2). The most notable species feeding on spruce beetle are the American three-toed woodpecker (Picoides dorsalis), the hairy woodpecker (Dryobates villosus), and the downy woodpecker (D. pubescens) (e.g., Massey and Wygant 1954; Yeager 1955; Koplin 1969; Koplin and Baldwin 1970; Kelly et al. 2018). Woodpeckers can exhibit both a functional and a numerical response to spruce beetle outbreaks (e.g., Watson 1928; Hutchison 1951; Yeager 1955; Amman and Baldwin 1960; Baldwin 1968a; Koplin 1969, 1972; Koplin and Baldwin 1970; Fayt et al. 2005; Kelly et al. 2018). As opportunistic feeders, woodpeckers will switch to an abundant prey source and migrate to areas where food is plentiful. Starting in the summer, woodpeckers make small holes in the bark to extract adult beetles that are constructing egg galleries. Feeding on small larvae is limited, but later in the autumn and especially over the winter, substantial amounts of bark are removed as woodpecker foraging for larger larvae and new adults intensifies (Watson 1928; Koplin and Baldwin 1970). During outbreaks, spruce beetle may comprise 65% of a woodpecker's food source in the summer, rising to 99% during the winter (Hutchison 1951; Massey and Wygant 1954). Bark flakes amassed on the snow around the base of standing spruce trees in the winter is a characteristic sign of woodpecker foraging on spruce beetle.

Woodpeckers can destroy roughly 50% of spruce beetle brood during outbreaks in standing trees, and up to 99% mortality has been reported (e.g., Swaine 1924; Hutchison 1951; Massey and Wygant 1954; Knight 1958; McCambridge and Knight 1972). Lower levels of mortality ranging from 2% to 26% have been reported for endemic spruce beetle populations in downed trees; lower mortality rates in downed trees have been attributed to woodpeckers' preference for feeding



**Figure 4.2.** The reddish appearance of a spruce tree that has had much of the bark removed by woodpeckers foraging for spruce beetle larvae. A pile of bark flakes is visible on the snow around the base of the tree. Photo: L. Maclauchlan.

on standing trees and to snow protecting downed trees over winter (Koplin and Baldwin 1970; Schmid and Frye 1977). In contrast, Baldwin (1968b) reported 70% to 79% mortality in a high-density beetle population contained in downed trees, suggesting that beetle density may also be a factor. Low-density spruce beetle populations are restricted to downed (or weakened) trees, with

woodpeckers likely feeding on more abundant food sources at these times. Furthermore, spruce beetle primarily infests the bottom side of downed trees, such that woodpecker access to trees laying on or near the ground may be limited. Interestingly, Watson (1928) reported that when downed trees rested approximately 1.5 m off the ground, woodpeckers consumed 50% to 60% of the spruce beetle brood. In addition to beetle density and host type, forest habitat characteristics may also affect woodpecker activity. Woodpecker activity tends to occur higher above the ground in semi-open forests than in open or dense forests (Shook and Baldwin 1970; Fayt et al. 2005).

A pair of woodpeckers usually confines their efforts to a limited area within a forest stand, focusing on a small group of up to eight infested trees for several weeks (e.g., Massey and Wygant 1954; Knight 1958). Such focused feeding often results in near-complete mortality of insects along the bole of some heavily infested trees but a patchy distribution of predation across an outbreak, depending on its extent. Even on heavily foraged trees, some insects usually survive at the base. Woodpeckers may also consume other invertebrates that are natural enemies of spruce beetle, potentially reducing mortality from other sources. The impact of woodpeckers may be greatest for semivoltine beetle populations that overwinter the first year as large larvae along the bole of the tree where they developed. New adults that move to the base of the tree to overwinter may be protected from predation by the snowpack. In a large spruce beetle outbreak in Colorado, Yeager (1955) reported that woodpecker density peaked at 22 birds per hectare. Woodpeckers likely play a role in regulating spot infestations and small- to moderate-sized outbreaks, and in hastening the demise of large outbreaks that are already declining.

The northern flicker (*Colaptes auratus* sp.) and sapsuckers (*Sphyrapicus* spp.) feed on insects as part of their diets but do not feed substantially, if at all, on spruce beetle (Massey and Wygant 1954). Other insectivorous birds, including perching birds, that may eat bark beetles consume only dispersing adults and likely have little impact on bark beetle populations.

#### Mammalia

North American red squirrels (*Tamiasciurus hudsonicus*), which are primarily granivorous, have been observed peeling the bark off spruce beetle-infested downed trees and the bottom of infested standing trees to feed on developing beetles (Werner and Holsten 1985). Pretzlaw et al. (2006) reported that foraging on spruce beetle by red squirrels increased over the course of an outbreak in the Yukon, reaching a peak in the autumn when larvae comprised 20% of the squirrels' daily energy requirement. However, it was likely the loss of spruce cones, the main food source of the squirrels, rather than a preference for spruce beetle that drove the animals' increased consumption of spruce beetle larvae. Unfortunately for the squirrels, spruce beetle is not cacheable, and overall outbreaks have a negative effect on squirrels by reducing both a winter food source and nesting sites (Zugmeyer and Koprowski 2009; Hankinson 2014). The impact of squirrels on beetle populations is considered negligible (Werner and Holsten 1985).

# 4.2.2. Invertebrate predators, parasitoids, and parasites

## **Diptera**

Dipteran predators comprise the greatest proportion of the invertebrate natural enemy complex of spruce beetle. The most abundant and impactful predators are species of long-legged flies (Dolichopodidae) in the genus *Medetera*, followed by some species of lance flies (Lonchaeidae) in the genus Lonchaea. Medetera aldrichii is perhaps the most well-known and common dipteran predator of bark beetles, including spruce beetle, in North America (Massey and Wygant 1954; Knight 1961; McCambridge and Knight 1972; Gara et al. 1995). The Palaearctic M. signaticornis is also a common predator of spruce beetle in Alaska (Gara et al. 1995). Dipteran predators initially exhibit a positive density-dependent response to spruce beetle and secondary bark beetles until a point at which they become sated (Whitmore 1983; Gara et al. 1995). The larval stages of dipteran predators feed indiscriminately on spruce beetle under the bark and also consume other natural enemies of spruce beetle. Some dipteran predators deposit their eggs in protected locations on the outer bark, with the tiny larvae crawling to the beetle's entrance hole, whereas other species deposit their eggs in beetle galleries (Schmid and Frye 1977). Gara et al. (1995) describe a female Lonchaea sp. hovering around a spruce beetle's entrance hole before landing, backing into the hole, and depositing eggs around the entrance's inner margin. To deter predators, spruce beetle packs egg and larval galleries with frass. Estimates of spruce beetle mortality due to dipteran predators range from 0.2% to 14.0% (McCambridge and Knight 1972; Whitmore 1983).

## Hymenoptera

There are a number of hymenopteran ectoparasitoids commonly associated with spruce beetle, mainly in the families Braconidae and Pteromalidae. Their occurrence and abundance may vary geographically, but the following are the most commonly reported species: Coeloides rufovariegatus (= C. dendroctoni), Roptrocerus xylophagorum (= R. eccoptogastri), Dinotiscus dendroctoni (= D. burkei; = Cecidostiba burkei), and D. eupterus (Massey and Wygant 1954; Knight 1961; McCambridge and Knight 1972; Gara et al. 1995; Wesley et al. 2006). Wesley et al. (2006) also reported Bracon tenuis, and Gara et al. (1995) listed an unidentified Bracon sp. The hymenopteran larvae feed on the body fluids of their bark beetle hosts, with one parasite per host. A strong density-dependent relationship has been observed for hymenopteran parasitoids in other bark beetle systems but not in spruce beetle. This may be due to the abundance of secondary bark beetles associated with all population phases of spruce beetle. Whitmore (1983) and Gara et al. (1995) noted that hymenopteran parasitoids exhibited a preference for secondary bark beetles over spruce beetle in both downed and standing trees. Such a preference may be due to insect phenologies and life cycles and the location of the bark beetles on the trees. Many parasitoid species, such as C. rufovariegatus, use their ovipositor to penetrate the bark and deposit eggs on larvae or pupae developing under the bark (Wegensteiner et al. 2015). Oviposition sites are a function of ovipositor length and bark thickness, and parasitism generally increases with bole height as bark thickness decreases (Massey and Wygant 1954; Whitmore 1983; Gara et al. 1995). Some species, such as R. xylophagorum, enter galleries through the beetle's entrance hole. Parasitoid density may vary, but one parasitic larva kills only one host. Whitmore (1983) found that hymenopteran parasitoids caused less than 2% mortality in spruce beetle, whereas McCambridge and Knight (1972) reported 0.4% to 6.0% mortality.

#### Coleoptera

Coleopteran predators are common in the galleries of bark beetles, although they do not exhibit the same strong density-dependent response as dipterans do. The most abundant coleopteran in the galleries of spruce beetle in studies conducted in Alaska and Colorado were species in the genus *Rhizophagus* (Monotomidae), particularly *R. dimidiatus* (Massey and Wygant 1954; Whitmore 1983; Gara et al. 1995). Some Rhizophagous species are facultative predators, scavengers, fungivores, or phytophages, whereas others are specialized predators of under-bark insects (Moeck and Safranyik 1984). There is substantial European literature on *Rhizophagus* but a paucity of information from North America. Interestingly, 800 individuals of an unidentified *Rhizophagus* sp. from England were released in 1933 and 1934 in Québec against a spruce beetle outbreak, but the beetles failed to establish (Moeck and Safranyik 1984).

Checkered or clerid beetles (Cleridae) are perhaps the most notorious coleopteran predators of bark beetles, probably due to the striking black and white markings on the elytra and the way they rip the heads off their beetle prey. Enoclerus lecontei (= Thanasimus nigriventris), Thanasimus dubius, and T. undatulus are potential predators of spruce beetle (e.g., Watson 1928; Knight 1961; Dyer 1975; Whitmore 1983; Gara et al. 1995). Some other clerids that feed on other bark beetle species, such as Enoclerus nigrifrons, may also prey on spruce beetle (Haberkern and Raffa 2003). Clerids are attracted to the aggregation pheromones of spruce beetle and associated secondary bark beetles that they prey on (e.g., Dyer 1973; Moeck and Safranyik 1984; Werner and Holsten 1984; Poland and Borden 1997; Haberkern and Raffa 2003). Adult clerids capture beetles as they land on and prepare to bore into the bark of new host trees. Clerid beetles lay their eggs under bark scales, and the larvae enter the tree and feed on developing spruce beetles. Dyer (1975) estimated that adult T. undatulus can kill 4% of attacking spruce beetles; however, Gara et al. (1995) found that T. undatulus fed on only secondary bark beetles and would rather starve than eat spruce beetle. Although clerid larvae consume more individuals than clerid adults do, the overall impact of clerids on spruce beetle populations is relatively limited compared to other mortality factors (Schmid and Frye 1977; Moeck and Safranyik 1984).

#### Acari

Mites are the largest group of arthropods associated with bark beetles (Hofstetter et al. 2015). Many species are merely incidental associates, sharing a common habitat. Some mites practise phoresy, where they temporarily attach themselves to other species for the purpose of transport to a new habitat. Many phoretic mites associated with bark beetles are found on a broad range of taxa favouring subcortical habitats and are likely more habitat-specific than host-specific (e.g., Lindquist 1970; Moser and Roton 1971; Moser 1995). However, some phoretic mites are consistently associated with bark beetles and exhibit varying levels of host-specificity (Moeck and Safranyik 1984).

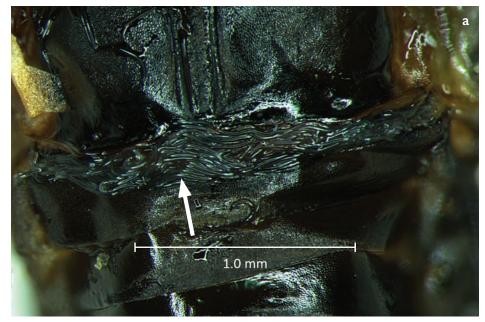
Cardoza et al. (2008) lists eight species of mites on spruce beetles from Alaska: *Tarsonemus ips, T. endophloeus, Histiogaster arborsignis, Dendrolaelaps quadrisetus, Proctolaelaps hytricoides, Trichouropoda alascae, T.* n. sp. nr *dalarenaensis,* and *Urobovella* n. sp. 767. Some of these were likely observed in early studies but not identified to species (Massey and Wygant 1954; Sluss 1955; Boss and Thatcher 1970). The most prevalent species reported in Cardoza et al. (2008) was *H. arborsignis,* a primarily fungivorous mite with a broad distribution in North America.

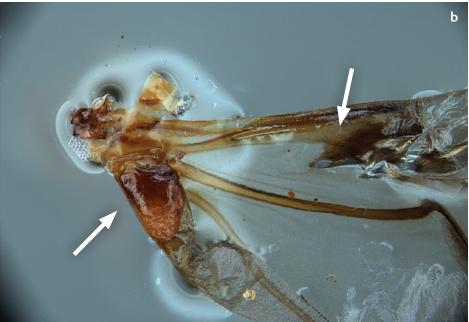
Histiogaster arborsignis is common in subcortical environments as well as in fungal fruiting bodies that grow on wood, and it is commonly associated with insects in its habitat (OConnor 1990). Interestingly, Cardoza et al. (2008) report that *H. arborsignis* preferentially feeds on *G. abietina*, a common ophiostomatoid fungal associate of spruce beetle, and Moser (1975) found that although the mite is primarily mycetophagous, it will feast on southern pine beetle in the laboratory. Some mites are specialized predators of bark beetle eggs, whereas others feed on a variety of taxa that may include nematodes, mites, insects, microbes, and other subcortical dwellers. The impact of mites on spruce beetle and especially the potential for indirect effects mediated by the microbial community are largely unknown.

#### Nematoda

Spruce beetle has both internal and external nematode associates (Figure 4.3). Four species, Sphaerularia dendroctoni, Contortylenchus reversus, Ektaphelenchus obtusus, and Parasitorhabditis obtusa, are known endoparasites and have been collected from body cavities of spruce beetle larvae and adults (Massey 1956, 1974; McCambridge and Knight 1972; Thong 1973; Thong and Webster 1983). Kanzaki et al. (2008) report that Ektaphelenchus obtusus is also ectoparasitic on spruce beetle. In addition, species in a number of genera, including Mikoletzkya, Bursaphelenchus, Aphelenchoides, and Panagrolaimus, have been reported on beetles and in their galleries (Massey 1956; Cardoza et al. 2008). A new species, B. rufipennis, was recently described from spruce beetle by Kanzaki et al. (2008), but most of the nematode associates of spruce beetle are also found with other bark beetle species (e.g., Massey 1956, 1974; Reid 1958, 1960; Martin 1964; Thong 1973; Thong and Webster 1983; Grucmanová and Holuša 2013). The percentage of spruce beetles with internal infections varies greatly. Massey (1974) found internal infection rates of 1% to 39%, whereas McCambridge and Knight (1972) reported rates from 42% to 66%. Sphaerularia dendroctoni and C. reversus negatively affect egg laying, reducing fecundity by more than 50% (Massey 1956; Thong and Webster 1983). The significance of some nematode species on spruce beetle populations remains to be determined; however, McCambridge and Knight (1972) considered a rise in nematode density as one of the first signs that a spruce beetle infestation was declining.

Rühm (1956) reported that females of *Ektaphelenchus* were associated with "leathery cocoons" found under the elytra or on abdominal tergites of a number of bark beetle species. Small cocoons under the elytra of spruce beetle associated with *Ektaphelenchus* were also observed by Massey (1974; Figure 4.3). Cardoza et al. (2006b) proposed the neologism nematangium (plural: nematangia) to describe a nematode-harbouring structure within the jugal folds on the hind wings of spruce beetle in which female *E. obtusus*, ophiostomatoid fungi, and yeasts were found. Interestingly, the researchers noted that the nematodes did not appear to feed while inside the nematangia. The structures appeared only when nematodes were present, and the researchers hypothesized that they were formed through the combined effects of nematodes, fungal associates, and secretions from pores on the wing veins. The structures were rare on pre-flight adults but common on one of the hindwings of overwintering beetles, leaving Cardoza et al. (2006b) to posit that the nematangia were overwintering domatia for female nematodes.





**Figure 4.3.** (a) Nematodes (arrow) on an adult spruce beetle packed between the metathorax and first abdominal tergite; and (b) membranous hindwing of an adult spruce beetle showing a cocoon or nematangium (left arrow) and a crypt (right arrow; see text). Photos: G. Smith.

Nematodes are generally thought to be antagonistic towards their hosts, and Mills (1983) suggests that nematodes hold promise for use in the biocontrol of bark beetles. In contrast, nematodes could potentially benefit bark beetles by detoxifying and degrading tree tissues and through interactions with the microbial community (e.g., Ledón-Rettig et al. 2018).

# 4.2.3. Pathogens

Pathogens of bark beetles include fungi, bacteria, viruses, and protists. Biocontrol studies have largely focused on *Beauveria bassiana*, a naturally occurring soil fungus and ubiquitous pathogen of insects. *Beauveria bassiana* has been isolated from spruce beetle galleries and from oral secretions of spruce beetle in the laboratory (Cardoza et al. 2009). The fungus is extremely effective at killing spruce beetle in laboratory assays, but it has not been effective at reducing populations in field trials (Davis et al. 2018; Mann and Davis 2020). Davis et al. (2018) found that mortality of adult spruce beetles was higher on treated than on nontreated felled trees but there was no effect on brood size or emergence. The environmental conditions under which *B. bassiana* is effective do not align well with the habitat of spruce beetle: the ambient temperatures are too cool for the fungus. Furthermore, secondary metabolites in trees—even in felled trees—may limit the effectiveness of *B. bassiana* and its potential use in biocontrol of spruce beetle (Mann and Davis 2020).

# 4.2.4. Competing species of bark beetles

Many secondary bark beetle species, wood borers, and other Curculionidae colonize spruce trees alongside spruce beetle. Bright (1976) lists 40 species of bark beetles on white spruce alone and 74 species on *Picea* spp. in Canada. Most of the species are found attacking only dead or dying spruce. Dryocoetes affaber is one of the most prevalent and abundant secondary species that are sympatric with spruce beetle attacks on downed and standing trees (McCambridge and Knight 1972; Werner and Holsten 1984; Gara et al. 1995; Haberkern et al. 2002). Dryocoetes affaber was present with spruce beetle in more than two-thirds of the samples taken from downed trees in Alaska (Werner and Holsten 1984). The presence of spruce beetle's aggregation pheromone enhances the response of D. affaber to its own aggregation pheromone (Poland and Borden 1998a). Other bark beetles commonly associated with spruce beetle include Scierus annectens, Polygraphus rufipennis, and Ips spp., particularly I. tridens and I. perturbatus (e.g., Swaine 1924; McCambridge and Knight 1972; Werner and Holsten 1984; Gara et al. 1995; Poland and Borden 1998a; Haberkern et al. 2002). McCambridge and Knight (1972) found that Polygraphus rufipennis attacks were often sympatric with spruce beetle attacks on standing trees, but the authors noted that this secondary beetle species, as well as D. affaber, tend to turn into the outer bark, presumably reducing competition with spruce beetle. Werner and Holsten (1984) found significant numbers of *Ips tridens* and *I*. perturbatus overlapping with spruce beetle attacks on downed trees in Alaska; however, Gara et al. (1995) found that only 17% of samples with spruce beetle contained *I. perturbatus* on downed trees. On standings trees, *Ips* spp. often attack above where spruce beetle attacks. In fact, *I. perturbatus* populations can build up in the tops of trees killed by spruce beetle and then progress to attacking and killing adjacent small-diameter living trees in the absence of sufficient stressed or downed material (Werner 1993; Yukon Energy, Mines and Resources 2010).

Interspecific competition between spruce beetle and secondary bark beetles can be significant, particularly in downed trees. Swaine (1924) observed that "keen competition in the brood trees, between [spruce beetle] larvae, themselves exceedingly overcrowded, and myriads of *Ips*, Polygraphus, Dryocoetes, Pissodes, Monochamus, and other species, must be one of the most important factors in holding outbreaks in check." Gara et al. (1995) attributed a greater proportion of spruce beetle larval mortality to interspecific competition with secondary bark beetles than to invertebrate natural enemies. Haberkern et al. (2002) posited that fierce competition with secondary bark beetles regulates spruce beetle populations in downed trees and limits the development of outbreaks in the Great Lakes region. Poland and Borden (1998a, 1998b, 1998c) examined the potential to exploit the semiochemicals of some secondary bark beetles to manage spruce beetle in downed trees in British Columbia through competitive exclusion, and Werner and Holsten (2002) conducted similar studies in Alaska. The aggregation pheromones of D. affaber show promise, reducing catches of spruce beetle in traps and decreasing attack density and the number of offspring produced in downed trees. The studies suggest that aggregation pheromones of some secondary bark beetles could be used prophylactically on recent spruce windthrow to reduce the potential for spruce beetle populations to build in such ideal hosts.

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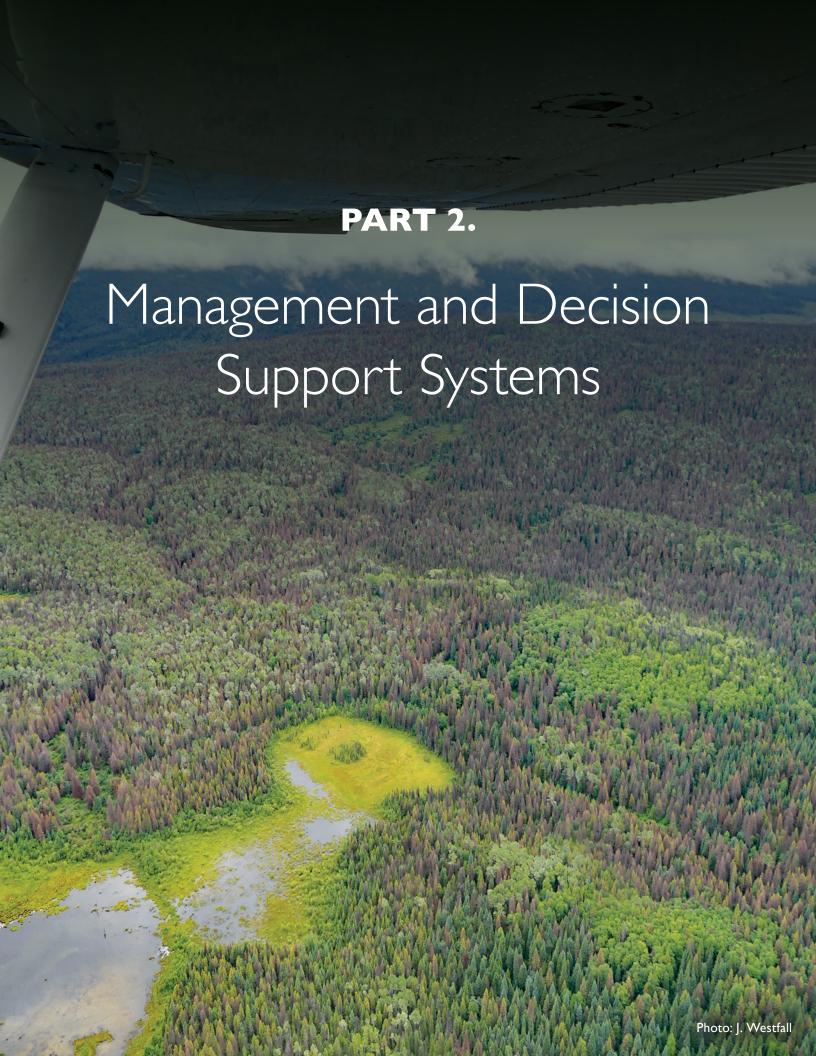
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# **CHAPTER 5**

# Management

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Bark BEETLE OUTBREAKS ARE SIMULTANEOUSLY agents of ecosystem function and renewal and of devastating economic loss. In stands, outbreaks affect forest structure by changing light regimes, releasing understorey vegetation, and altering the amount and type of coarse woody debris. These changes, in turn, affect arthropod and vertebrate habitat and the use of the forests. At the landscape level, bark beetle outbreaks can impact watershed hydrology, landscape connectivity, biodiversity, carbon flux, nutrient cycling, short- and long-term timber supply, and the risk of other disturbances, such as fire, pathogens, and other insect outbreaks. Periodic outbreaks of bark beetles are a normal occurrence in pine, spruce, and fir forests; however, changing climate and weather patterns have promoted outbreaks beyond the range and severity of those observed in recent history. The annual minimum temperature has increased by 2.9 °C to 5.7 °C in central British Columbia (Omineca region) since 1895 (Foord 2016). Milder winters can lead to increased overwintering survival of bark beetles, and warmer and longer growing seasons can shorten the generation time of some species (see Chapter 2, Biology and Population Dynamics). Favourable weather for survival and reproduction, combined with a pulse of susceptible hosts, can result in bark beetle outbreaks that are challenging to control.

The desire to manage and control spruce beetle infestations and mitigate their impacts extends over a century in Canada (e.g., Swaine 1924). The cumulative effects of bark beetle disturbances on forest resources brings increased pressure and scrutiny to management decisions. The recent outbreak of spruce beetle, Dendroctonus rufipennis (Kirby) (Coleoptera: Curculionidae), in British Columbia, which was detected in 2014, comes on the heels of a massive mountain pine beetle epidemic that killed over half of the province's merchantable pine, causing significant socioeconomic and ecological impacts. Increasingly, there is awareness of and a demand that multiple objectives and values and the interests of First Nations be considered and balanced in the decisionmaking process; these complex policy issues are beyond the scope of this chapter. Here, we focus on the applied aspects of spruce beetle management in British Columbia, from the methods used to detect and assess infestations to the various strategies and tactics used to meet management objectives. Challenges unique to spruce beetle detection and control are also discussed. We focus on British Columbia because the most extensive and severe spruce beetle outbreaks in Canada over the last century have occurred in that province (see section 1.3, Outbreak History). As a result, British Columbia has a well-developed process and guidelines for spruce beetle management (BC FLNRO 2016a, 2016b, 2016c; BC FLNRORD 2017a, 2017b; 2018; 2019a, 2019b, 2019c, 2019d; 2020; Government of British Columbia 2018). Some of the provincial documents are in the process of being updated at the time of writing and we use the current terminology where possible (e.g., section 5.2.1, Strategies).

## 5.1. Detection and Assessment

Tactics aimed at reducing beetle populations are most efficacious when applied early to small and localized infestations, so rapid detection of new infestations is key to effective management. Several types of surveys are used to detect, delimit, assess, and monitor infestations. The aerial overview survey (AOS) is conducted annually in British Columbia to record forest health disturbances, including bark beetle infestations. Results of the AOS are used to identify areas where more detailed helicopter surveys are needed. In the case of spruce beetle, the AOS and helicopter surveys identify trees killed by the beetle based on the aerial signature, or crown symptoms. Aerial surveys are used to prioritize areas for ground surveys. Ground surveys collect more detailed data, including the locations of trees currently harbouring insects but not yet showing crown symptoms, as well as information on the potential risk posed by infestations. Together, these sequential and complimentary surveys provide the information required to develop an appropriate management strategy for each infestation.

# 5.1.1. Aerial overview survey

The AOS is an efficient method to record a variety of forest health disturbances, including bark beetles, across many forested jurisdictions. The AOS provides current information on forest health and wildfire, as well as a historical record that spans over a century in some regions in Canada. Responsibility for the AOS fell to the provinces after the federal Forest Insect and Disease Survey (FIDS) program ended in the mid-1990s. British Columbia uses the AOS to determine the general locations of disturbances, estimate the gross area impacted, monitor annual damage trends, and identify areas where higher-resolution spatial data are needed to inform management decisions and direct operational activities. The province conducts the AOS between June and October to maximize capture of the major forest health agents that affect forests. The area covered in each region varies annually, based on information needs, priorities, resources available, and other factors such as adverse weather or wildfire smoke that can limit flights. Detailed flight lines and coverage are recorded each year.

The AOS is usually conducted at 500 to 1000 m above ground level in fixed-wing aircraft flying at speeds of 185 to 260 km/h. Typically, two surveyors seated on opposite sides of the airplane sketch the visible current-year damage caused by a variety of forest health agents. Surveyors draw polygons onto topographic maps or satellite images at scales of 1:100 000 to 1:250 000 (Figure 5.1). For each polygon mapped, the forest health agent, the intensity of damage, and the tree species affected are recorded. For spruce beetle, surveyors estimate the percentage of trees displaying newly chlorotic crowns in the polygon and record one of the following intensity classes: trace (< 1%), light (1% to 10%), moderate (11% to 29%), severe (30% to 49%), and very severe (50% to 100%). Paper maps are still used in British Columbia because they are suited to the multitude and complexity of forest health agents, tree species, and damage encountered in the province; however, tablet PC-based digital mapping systems similar to those used in other jurisdictions in Canada may be adopted in

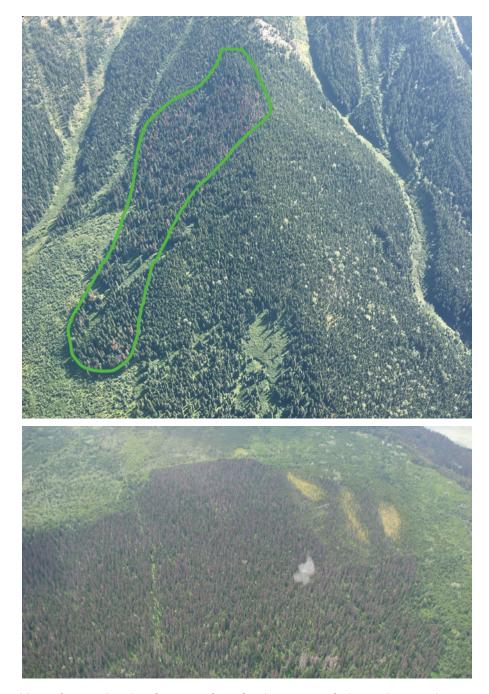


Figure 5.1. View of spruce beetle infestations from fixed-wing aircraft during the annual overview survey. The green polygon in the photo on the top was drawn around a spruce beetle infestation by aerial surveyors. Trees killed by spruce beetle have crown symptoms that can be challenging to detect during aerial surveys (see text). Photos: J. Robert (top); T. Foy (bottom).

the future as mapping technology advances. Some surveyors in British Columbia use a tablet with georeferenced versions of the satellite-based working maps for navigation.

Surveyors record only newly visible chlorotic damage; they do not record cumulative damage. For spruce beetle, a significant delay occurs between attack and the onset of crown symptoms when trees can be identified from the air. The initial onset of crown fade is subtle and can be particularly challenging to see during the high-altitude AOS (see section 5.1.4, Challenges). As a result, trees

attacked by spruce beetle often are not identified in the AOS until the survey year following attack or even the subsequent survey year. Spruce beetle also has a flexible life cycle of one or two years, depending on temperature and microclimatic effects, and a mix of life cycles can occur in the same stand and even in the same tree. As a result, it is difficult to map spruce beetle infestations with a high degree of accuracy during the AOS (see section 5.1.4, Challenges). However, the coverage provided by the AOS makes it a useful tool for identifying emerging infestations, tracking trends through time, and delineating areas where higher-resolution and more detailed helicopter surveys and ground surveys are warranted (BC FLNRORD 2019a, 2019b, 2019c).

# 5.1.2. Helicopter surveys

Spruce beetle infestations of interest identified during the AOS can be more accurately defined using helicopter surveys with a global positioning system. Crown symptoms characteristic of spruce beetle attack are more easily identified during low-elevation helicopter surveys. Areas targeted for helicopter surveys may be based on early results of the current year's AOS; however, often the previous year's AOS results are used to prioritize the areas. Results of the AOS are often not compiled until late autumn, so the previous year's data are used to plan and conduct helicopter surveys, which need to be completed before winter. Helicopter surveys are conducted by one or two trained surveyors per aircraft who define infestation waypoints or draw polygons. All trees with symptoms that have become visible in the survey year are mapped as points or polygons. Points are spot infestations of up to 50 attacked trees within an area of less than three hectares that is more than 200 m from another infestation. The number of attacked trees is recorded for each point. Larger continuous patches are mapped as polygon features and are given an intensity rating in 10% increments, based on the percentage of symptomatic trees within the polygon.

# 5.1.3. Ground surveys

Ground assessment of localized spruce beetle infestations is essential to define the extent, severity, and duration of an infestation and to determine the potential for beetle population increase in an area of concern. As part of the ground assessment, surveyors record observations and provide recommendations that include potential management options and tactics: these on-the-ground observations are valuable for decision-makers, given the challenges associated with spruce beetle detection (see section 5.1.4, Challenges). Other information that may be collected during ground surveys includes: topographic and operability considerations for winter or summer logging; current road access; integrated resource management concerns such as riparian zones, wildlife habitat, and landscape values; comments on the possible origin and history of the attack in the stand; the percentage of the population in a one- versus two-year life cycle; and the likely timing of the next beetle flight (BC FLNRORD 2018). Information is also collected on tree-species composition, tree diameter, and stand susceptibility. This type of information is crucial for planning proactive pest reduction harvesting or mitigation treatments, especially at the early stages of an infestation. The three main types of spruce beetle ground surveys used in British Columbia are grid probes, walkthroughs surveys, and hybrid surveys. Grid probes cover the most area and collect the best information but are the most expensive to conduct. Walkthrough surveys and hybrid surveys are less expensive but collect less information (BC FLNRORD 2018).

#### **Grid probes**

In grid probes, sampling strips that are  $100 \text{ m} \times 10 \text{ m}$  in size and 100 m etres apart are surveyed as a continuous grid until 10% of the target polygon or area has been systematically assessed. Grid probes provide information on the extent, intensity, vigour, and years of beetle attack, as well as on stand species composition, tree diameter, and general stand susceptibility. The information collected in grid probes is used to map the location, shape, and centre of infestations. Bark samples are taken from one currently infested tree in each sampling strip to determine the number of offspring per attack (female); this information is used to assess the relative growth rate of the spruce beetle population in order to help inform management decisions (BC FLNRORD 2018).

#### Walkthrough surveys

Walkthrough surveys use a series of nonsystematic survey lines, sometimes in a "zigzag" pattern, through a contiguous stand type within an infestation polygon that has been identified during aerial surveys. A minimum of 5% of the polygon area is covered during a walkthrough survey. Spruce beetle-infested trees within five metres of the survey line (i.e., in a 10-m-wide strip) are recorded as they are encountered, but the walkthrough survey does not use formal sampling strips like the grid probe does. A walkthrough survey can be completed by one surveyor and is a cost-effective and quick way to assess a small infestation (BC FLNRORD 2018).

#### Hybrid surveys

Hybrid surveys incorporate elements of both walkthrough surveys and grid probes, so that a larger area can be surveyed with fewer resources than can be done through grid probes alone. Hybrid surveys collect some detailed data but use a reduced number of sampling strips, such that there is at least one 100-m representative strip for every 50 ha of polygon. Spruce beetle attack outside of the boundary of a polygon can easily be added to hybrid surveys to assess the full extent of a spruce beetle infestation (BC FLNRORD 2018).

# 5.1.4. Challenges

The nature of the crown symptoms of beetle-killed spruce and the beetle's biology and behaviour present several challenges for detecting and assessing the growth rate of infestations during aerial and ground surveys.

#### Crown symptoms

The foliage of spruce beetle-killed trees first starts to fades to colours that range from a subtle yellow-green to a dull red, usually starting at the bottom of the crown and progressing upwards (Figure 5.2). The entire crown eventually turns a dull red or purple. The needles usually drop the second winter during wind storms after which the trees appear dark red due to the colour of the fine twigs (Figure 5.3). The fine twigs break off after an additional year or two and the trees appear grey. Crown fade, or chlorosis, is more subtle and difficult to see in spruce than in lodgepole pine, subalpine fir, and some other conifer species, that turn a more vibrant red and retain red needles longer than spruce does.



**Figure 5.2.** The start of crown chlorosis on two trees attacked by spruce beetle, where the bottom branches are starting to fade to a dull red (tree on left in foreground) or a greenish-yellow (tree on right). Photo: J. Robert.



**Figure 5.3.** The crowns of spruce trees killed by spruce beetle eventually turn a dull red and then fade to grey (see text). Photo: L. Maclauchlan.

Weather and site conditions can affect the timing and progression of fade. For example, fade may start earlier and progress faster for attacked trees growing on dry sites and severe weather can hasten the fall of needles and fine twigs. In addition, spruce beetle's flexible life cycle and attack behaviour can contribute to variation in crown symptoms (see next section, Beetle population growth rate).

The delay and variable timing in the onset of foliage fade make it challenging to detect trees from the air in the year of attack (Schmid 1976). The colour of fading spruce crowns can be especially challenging to see at the end of the aerial survey season in late autumn because of the low angle of the sun. As a result, current attack is often underreported in aerial surveys and usually lags one year behind actual attack. Such delays in detecting an infestation present challenges for spruce beetle management because control treatments are most effective when applied early to emerging outbreaks, catching them before they build and spread.

Aerial surveys can detect where beetles have recently been, but ground surveys are necessary to locate currently infested trees and assess the risk posed by an infestation. In addition to assessing crown symptoms, ground surveyors can check trees along their transect lines for the presence of pitch tubes (resin), frass, live insects under the bark, and signs of woodpecker feeding on the bole to help them identify spruce beetle-attacked trees. Ground surveys conducted in autumn through early spring can be used to identify currently infested trees, and bark sampling can be used to estimate the proportion of the beetle population that will fly in spring.

### Beetle population growth rate

Assessing the growth rate of a spruce beetle population can also be challenging. Two standard methods are used to assess the status of bark beetle infestations. In the "green to red ratios" method, the impact of an outbreak is measured through tree mortality. The ratio of trees attacked in the current year to the number of trees attacked the previous year is determined from ground and helicopter survey data. Beetle population growth rate is measured directly in the R-values method, where the number of offspring produced per attack (i.e., per female) is determined from bark samples.

Both the green to red ratio and the R-value method can be challenging to apply to spruce beetle due to difficulties in determining the year of attack of a tree and the stage of beetle development based on crown symptoms. In addition to the variable nature of crown fade in spruce discussed above, spruce beetle has a flexible life cycle (one- and two-year cycles) and may repeatedly attack the same tree in multiple years, which can lead to new adults completing development and emerging from the same tree in different years (see sections 2.1 Life Cycle and Life History and 2.3 Regulation of Voltinism). It can also be difficult for surveyors to distinguish between entrance holes (a proxy measure for number of parental females) and ventilation holes made during egg gallery elongation. In addition, a proportion of young adults may also relocate to the base of trees to overwinter (see section 2.1.2, Emergence and dispersal), which can affect R-values based on bark samples taken from the bole at 1.3 m above ground level during the late autumn. Because of the unique challenges associated with spruce beetle, management decisions are often based on a combination of quantitative and qualitative information collected during ground surveys and on past experience. Having access to trained and experienced ground surveyors is critical if spruce

beetle populations are to be accurately assessed, but maintaining that expertise between outbreaks is often challenging.

# 5.2. Strategies and Tactics

In British Columbia, bark beetle management strategies range from population reduction and mitigation of ecological and economic losses to no action (BC FLNRO 2016a). The appropriate management strategy depends on the extent of the infestation, the potential for population growth and impacts, tree and stand susceptibility (see Chapter 6, Decision Support Systems), stand accessibility and operability, the values at risk, and the management objectives for the area.

Tactics for spruce beetle management include measures that remove or kill beetles (traditionally called "direct control") or reduce the amount of preferred breeding material and reduce stand susceptibility to spruce beetle (traditionally called "indirect control"). The main tactics used in British Columbia are harvesting, tree removal or destruction, use of conventional trap trees, and preventative measures (Nagel et al. 1957; Hodgkinson 1985; Bentz and Munson 2000). Other tactics that may be used in certain circumstances include grid baiting stands with aggregation pheromones to "contain and concentrate" beetles before harvest (Dyer and Hall 1983; Shore et al. 1990; Werner and Holsten 1995; Borden et al. 1996; Greenwood and Borden 2000), felling infested trees that can not be extracted before winter to reduce the number of beetles that emerge to relocate (Hodgkinson et al. 2015), mass trapping beetles with semiochemicals (Bentz and Munson 2000), deterring spruce beetle attack with anti-aggregation pheromones (e.g., Lindgren et al. 1989; Holsten et al. 2003; Werner et al. 2006), and reducing spruce beetle attack or success on downed hosts with aggregation pheromones of competing bark beetle species (Poland and Borden 1998; Werner and Holsten 2002). Monosodium methanearsenate (MSMA; Glowon®) was used in British Columbia to create lethal standing trap trees for spruce beetle (Hodgkinson 1985); however, use of MSMA was discontinued after 2008. Other chemical control methods (e.g., insecticide bole sprays, injections) are not used in British Columbia because they are not approved for use in Canada.

# 5.2.1. Strategies

#### Proactive pest reduction

The proactive pest reduction strategy is appropriate for areas with low-density or endemic spruce beetle populations that are primarily infesting downed trees or transitioning to attacking susceptible, stressed standing trees (also see next section, Targeted pest reduction: early intervention). Proactive measures aim to reduce the probability of an outbreak developing by limiting the amount of ideal breeding habitat for beetles and by reducing beetle numbers in the stand. Measures include identifying and removing fresh windthrow, damaged trees, and other susceptible host material before it can be infested, as well as any trees with developing spruce beetles under the bark. Beetles may also be trapped. Tactics used for proactive pest reduction include tree removal or destruction, harvesting, and the use of conventional trap trees.

Early detection of windthrow and emerging spot infestations is often the most challenging aspect of proactive management of spruce beetle. Proactive treatment is the default strategy for any area

where timber resources are the primary objective and hazard mapping has identified susceptible host stands (see Chapter 6, Decision Support Systems).

## Targeted pest reduction: Early intervention

The early intervention targeted pest reduction strategy is used when populations are in the incipient population phase—when beetles are attacking small groups of standing trees—in susceptible stands. The aim of the early intervention strategy is to suppress new, localized infestations through aggressive targeted removal of currently infested stems (i.e., trees with insects under the bark). The proactive tactics described in the section above are also applied. The success of targeted early intervention depends on the early detection of the infestation and a rapid response before populations build.

#### Targeted pest reduction: Reactive

The reactive targeted pest reduction strategy is used to mitigate impacts, limit further spread, protect the mid-term timber supply, and conserve nontimber resources in areas where populations are in the epidemic population phase. The goal of the reactive strategy is to reduce and mitigate widespread bark beetle-caused mortality of host trees. Harvesting efforts focus on stands with active infestations: the objective is to reduce further spread by extracting trees that contain live insects under the bark. Reactive pest reduction harvest tactics can include an array of harvesting methods—including partial cutting, small patches, and even clearcuts—depending on the type and intensity of the infestation. Pest reduction harvesting is most effective when a high proportion of currently infested trees are identified and removed. Stands with the largest number of trees infested with live spruce beetle at the time of harvest are the highest priority for this strategy.

#### Salvage harvest

The salvage harvest strategy is used to mitigate the economic impacts of a spruce beetle outbreak after the outbreak has largely subsided. This strategy seeks to recover economic value by focusing the allowable cut on stands that have a high proportion of trees killed by spruce beetle, while also ensuring a sustainable timber supply for the future by retaining nonimpacted stands. The potential negative consequences of salvage logging after a natural disturbance on understorey vegetation, wildlife, ecosystem processes, and other ecological values must be considered (Lindenmayer et al. 2004; Rogers 2006; Werner et al. 2006). Some of the impacts of salvage harvesting can be mitigated by retaining substantive patches of large-diameter trees, even if they are dead. Specific guidelines have been developed for salvage harvesting beetle-killed stands in spruce ecosystems that are characterized by gap dynamics and uneven-aged stands (BC FLNRORD 2017a). The guidelines promote patch cut, retention, and selection silviculture systems over clearcut silviculture systems.

In order to be economically viable, salvage plans must account for snag decay rates. After spruce beetle has killed a tree, the "shelf life" or "salvage window" for the dead wood is defined as the period during which the wood retains economic value (Lewis and Thompson 2011). As such, shelf life depends on the final wood product; for example, wood used as dimensional lumber has different quality requirements and decay thresholds than wood used for pulp does. Early data collection in northern British Columbia suggests that external symptoms of attack are not always a good proxy measure for time of death but generally are a good indicator of decay. In addition,

site characteristics (e.g., soil moisture regime) may shorten shelf life by three to four years or allow sound standing trees to persist for seven years or more. As a result, British Columbia's government recommends a seven-year stand shelf life as a reasonable estimate for planning salvage operations.

#### No action

The no-action strategy is applied to designated areas where natural disturbances are left unmanaged. This strategy is typically applied to areas where management efforts would be ineffective in substantially reducing beetle populations and impacts, where it is not possible to salvage dead timber in the short term (less than five years), and where access cannot be put in place before substantial merchantable degradation of the dead material for wood products occurs (i.e., economically constrained areas). The no-action strategy also applies to nontimber value areas, such as wilderness areas, parks and ecological reserves, culturally significant areas, and any other areas that are valued for attributes unrelated to timber or wood products. Areas designated for no action should be large enough to permit the full range of ecosystem processes over time.

### 5.2.2. Tactics

#### Harvesting

Harvesting is a tactic used to reduce spruce beetle populations in a stand, remove potential breeding material and lower the susceptibility of stands to attack, and recover economic value from beetle-killed trees that are still suitable for wood products or recuperate value while removing susceptible host material. Spruce beetle populations may be reduced in the forest by removing infested trees and milling the trees before beetles complete development and disperse: spruce beetles developing under the bark are killed during the milling process. Removing trees harbouring developing beetles was previously called "sanitation harvesting", but in British Columbia, the practice is now called harvesting for pest reduction to more accurately reflect the mechanism, intent, and outcome. Removing infested trees reduces beetle numbers; however, populations are unlikely to be eradicated. Harvesting may also be used to manipulate the amount of available host material and the susceptibility of stands to spruce beetle. For example, this may include removing fresh windthrow and damaged trees or altering the basal area and diameter distribution of the spruce component in stands. After an outbreak, salvage harvesting can mitigate economic losses by recovering value from beetle-killed trees that are still suitable for wood products.

Harvesting systems that may be used to manage spruce beetle and mitigate the impacts of an outbreak include clearcut, partial-cut, diameter-limit, and single-tree selection systems. Pest reduction harvesting prioritizes stands with active (current) infestations to reduce beetle populations. A conventional trap-tree program may be used in conjunction with pest reduction harvesting to help reduce the remaining beetle population. Large-diameter logging slash and residue, as well as any windfall that occurs along block edges, must be appropriately managed to reduce ideal breeding material. This includes removing, burning, or peeling slash greater than 10 cm in diameter and ensuring stumps are cut close to the ground (Safranyik and Linton 1988). If harvesting is delayed, trap trees or aggregation pheromone tree baits can be deployed throughout the stand as a temporary holding tactic to reduce beetle emigration until the stand is harvested (BC FLNRO 2016a). Stands with a high proportion of dead timber are prioritized for harvesting, and all harvested stands are replanted. Stands with advanced regeneration and a well-

developed understorey may be left intact (i.e., not harvested) to hasten regeneration and shorten the time to the next stand rotation (BC FLNRORD 2017a; BC FLNRORD 2020). Furthermore, consideration must still be given to the economic and ecological impacts of harvesting regardless of the level of tree mortality. For example, it may be appropriate to retain stands with beetle-killed trees for biodiversity and fish and wildlife values.

#### Single-tree treatment

For inoperable or inaccessible areas, the only current options for direct control of populations are single-tree treatments such as felling and burning individual or small numbers of infested trees or peeling the bark of infested trees to destroy beetles under the bark. These single-tree treatments have been shown to be effective against small spruce beetle infestations (Hopkins 1909; Swaine 1924; Mitchell and Schmid 1973); however, the typically large size of infested spruce trees, worker safety concerns, and the cost of implementing labour-intensive treatments limits the application of these practices today.

#### Conventional trap trees

Conventional trap trees emulate fresh windfall and are extremely attractive to spruce beetle, attracting up to 10 times as many attacking spruce beetles as a standing tree does (Schmid and Frye 1977). Large-diameter living trees are felled in or near infested stands in early spring to ensure the trees are attractive to beetles and are not covered by snow when beetles disperse in May and June (BC FLNRO 2016c). Trees in full shade that do not rest directly on the ground are the most attractive to beetles. Branches are left intact, and trap trees can be felled on top of each other where possible to promote shading and attack. Stumps need to be cut close to the ground to reduce colonization by spruce beetle. Trap trees can be attacked from the base along the bole to a diameter of approximately 10 cm.

After spruce beetle's main dispersal flight, either the entire infested portion of the bole must be removed and milled or the bark must be destroyed if left on-site. This must be done before brood insects complete development and emerge. Failure to go back and remove or destroy trap trees will fuel an infestation. Trees should be removed in late-August or in the autumn of the same year they were felled in case some beetles are univoltine and to increase the probability that the trap trees are indeed collected and processed before the insects complete their development. Late-summer and autumn removal also avoids the challenges of locating and removing trap trees in winter or spring, when they may be covered by snow or frozen in place.

The number and location of trap trees needed to reduce a spruce beetle population depends on the size and growth rate of the population. Approximately one trap tree is needed for every 10 infested standing trees if the population is static, but ratios of 1:4 or even 1:2 may be needed for populations with high growth rates (Nagel et al. 1957; Wygant 1960; Fiddick 1978). Groups or patches of 12 to 25 trees often are felled in standing timber or approximately every 400 m along roads within 800 m of infested trees; however, canopy shading should be maintained to maximize attack (Fiddick 1978). Trees felled as part of road right-of-ways, cutblock strips, and landings can also be used as trap trees if the felling is planned appropriately (Hodgkinson 1985). Too few trap trees can result in spillover attacks on adjacent standing trees. Spruce trees immediately around trap trees must be surveyed

for signs of attack and removed if necessary. Trap tree programs are most effective for localized outbreaks or moderately sized outbreaks with a low to moderate growth rate (see the sections, Proactive pest reduction and Targeted pest reduction: Early intervention, this chapter). Expansive outbreaks with high growth rates are too logistically challenging to control with trap trees.

### Additional preventive measures

A number of preventive measures can reduce spruce beetle spread and susceptible habitat. The most common preventative measures currently used in British Columbia are restrictions on infested timber hauling and storage (BC FLNRORD 2019d). There is a risk that tactics that involve the transport of currently infested trees to mills could lead to spread. Depending on the beetle's life cycle and the time of harvest, infested trees might contain overwintering adults that could emerge during hauling or storage in mill yards or at loading sites. In beetle management units with large areas of susceptible host trees, the extraction, hauling, and storage of infested wood must be planned around spruce beetle's flight period. Forest licensees must have management plans in place for handling and processing infested logs. The Province of British Columbia has developed detailed guidelines for hauling and milling trees infested with spruce beetle (BC FLNRORD 2019d). The guidelines are designed to reduce the probability of beetle spread to uninfested areas.

Harvesting practices can prolong and promote bark beetle infestations. Effective wood use during pest reduction harvesting can reduce ideal breeding material. Spruce beetle can reproduce in stumps, log butts, decked logs, tops, and branches greater than approximately 10 cm in diameter (Schmid and Frye 1977). Cutting stumps low to the ground and using or destroying smaller-diameter pieces can reduce potential breeding habitat (Safranyik and Linton 1988; BC FLNRO 2016a). Harvesting residue can be piled and burned, removed to a pellet-processing facility, or bucked into small pieces and scattered on-site to make it unsuitable for beetles. Other preventative measures include systematically monitoring the edges of harvested areas for windthrow every year for five years after harvest and removing susceptible hosts, as well as using alternative harvest systems (e.g., small patches) that reduce the probability of windthrow. The shallow root system and sail-like crown of spruce makes it susceptible to windthrow. Monitoring and removing fresh windfall from spruce forests reduces the probability of outbreaks developing. Finally, leaving robust retention patches that reflect the composition and diversity of the original stand is crucial for maintaining resiliency of spruce ecosystems into the future.

Preventative measures that involve semiochemicals often have limited applications in forestry in British Columbia due to their high cost and poor efficacy against outbreak populations, but they can be effective under certain conditions. For example, the anti-aggregation pheromone MCH (see section 3.2, Spruce Beetle Pheromones) is sometimes used in British Columbia to protect single or small groups of high-value trees in campgrounds and parks or on private lands from low- to moderate-density beetle populations (BC FLNRO 2016a).

Long-term planning, vigilant proactive monitoring, and tactics to manage susceptible stands across a landscape can reduce spruce beetle impacts. Active and on-going attention to windthrow events in spruce stands, managing age-class distributions, and increasing regenerating stand structure and diversity can effectively decrease the probability of widespread spruce beetle outbreaks into the future.

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# **CHAPTER 6**

# Decision Support Systems

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GIVEN THE COMPLEXITY AND LARGE number of issues facing forest managers, decision support systems are valuable tools, particularly when dealing with uncertainty caused by insect disturbance. Decision support systems refer to knowledge-based tools—computer-based or otherwise—that provide users with information that improves the quality and timeliness of decisions. Decision support systems can support planning, provide rationale for the allocation of scarce resources, allow the exploration of "what if" scenarios, and, in some cases, allow users to compare the effects of different management strategies.

Decision support systems can be relatively simple—for example, numeric hazard rating systems—or they can involve more complex modelling approaches. This chapter reviews several different systems developed to support management of forests affected by spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae), with a specific focus on hazard and risk rating systems, the most commonly developed decision support tools for spruce beetle management.

# 6.1. Risk and Hazard Rating

In the insect management literature, the terms "hazard" and "risk" are sometimes used interchangeably. "Hazard" has been defined in terms of stand susceptibility, based on host tree, site, and stand characteristics, whereas "risk" is the probability of outbreak as a function of insect population and susceptibility (Paine et al. 1984; Shore and Safranyik 1992). Shore and Safranyik (1992) equate "susceptibility" and "hazard" and prefer the former term, because it is less ambiguous. They define "risk" as a function of beetle population pressure and stand susceptibility.

A number of models have been developed to assess spruce beetle risk, susceptibility, or a combination of the two. Some models are simple numeric rating systems, whereas others involve multiple levels of variables or the use of a computer program. Common factors related to stand susceptibility include diameter at breast height (DBH), basal area, tree growth rate, tree age, spruce species, percentage of spruce in the canopy (percent spruce), aspect, weather, elevation, and presence of host material (e.g., windthrow and logging debris). Common factors for assessing beetle population pressure include presence of breeding material, weather during the previous summer (rain and temperature), current population, and stand susceptibility.

Schmid and Frye (1976) combined results of four previous studies on factors that influence spruce susceptibility to create a numeric risk rating system (Table 6.1) with three risk categories: low (1), medium (2), and high (3). Three susceptibility classes identified by Knight et al. (1956) were integrated into a site index created by Alexander (1967) and categorized as physiographic location. Average DBH was categorized based on work by Massey and Wygant (1954). The basal area and percentage of spruce in the canopy were categorized based on earlier work by Schmid and Hinds (1974). The risk is determined by the addition of values from each risk category to give a final number that falls within a numeric range of low (4–5), low-medium (6), medium (7–9), medium-high (10), or high (11–12) risk levels. Holsten and Wolfe (1979) developed a similar numeric risk rating system (Table 6.2) but replaced the basal area and physiographic location categories with stand condition and stand age.

Table 6.1. Risk category system developed by Schmid and Frye (1976).

	Risk value				
Risk category	Average DBH (cm)	Basal area (m²)	Physiographic location	Proportion of spruce in canopy (%)	
High (3)	> 41	> 14	Well drained creek bottoms	> 65	
Medium (2)	30–41	9.5–14	Spruce on sites with a site index of 80–120	50-65	
Low (I)	< 30	< 9.5	Spruce on sites with a site index of 40–80	< 50	

**Table 6.2.** Risk category system developed by Holsten and Wolfe (1979).

Risk category	Average DBH (cm)	Stand age	Stand condition	Proportion of white spruce in canopy (%)
High (3)	> 30	Old growth	Damaged sawtimber Old growth Primary- or second-growth sawtimber not at rotation	> 70
Medium (2)	23–29.9	Second growth	Damaged pole timber  Mature pole timber  Primary- or second-growth pole timber	50
Low (I)	< 22.9	Seedlings and saplings	Seedlings and saplings	_

Paine et al. (1984) created a model that integrated a hazard index (0–1) and a population index (0–1), with risk as a probability. "Risk" was defined as the probability of a bark beetle infestation

starting and growing in any given stand. "Hazard" was defined by an index that is a function of the host tree, site, and stand conditions that are related to threat of outbreak (basal area, stand height, land form and elevation), with a numerical classification system similar to those developed by Schmid and Frye (1976) and Holsten and Wolfe (1979). If the stand is in optimal condition, then the hazard approaches "0"; the risk approaches "0" if the population is also low. A degree of risk always occurs when the population is high. The model includes a threshold for exponential increase in risk, based on the number of beetles needed to kill trees in a certain physiological condition. This model is suitable for short-term predictions because stand resistance varies in a narrow range over the short term, whereas beetle populations can change rapidly.

Reynolds and Holsten (1994) developed a model for risk predictions (Table 6.3) that was designed to provide short-term predictions using Paine et al.'s (1984) definition of "risk". The model includes eight factors categorized into three different levels of influence. Hazard and expected population are the level I factors. The level II factors combine to produce the value for the expected beetle population. Weather and other breeding materials are further broken down into level III factors. Reynolds and Holsten (1996) later created a hazard classification system, defining "hazard" as a measure of damage that would occur to the stand if an outbreak occurred.

	Level I	Level II	Level III
	Hazard		
	Expected population	Current population	
		Weather	Temperature in preceding June
SK		vveatrier	Rainfall in proceeding June, July, and August.
<u>~</u>		Windthrow	
			Right-of-way
		Other breeding materials	Fire debris
			Log decks and logging debris

Table 6.3. Risk model developed by Reynolds and Holsten (1994).

White, Lutz, and Sitka spruce were included in two models for hazard classification—a classification model and an abductive inference model. The variables examined were spruce species, aspect, elevation, mean 10-year radial increment of dominant or co-dominant spruce, total basal area (based on 10-cm-minimum tree DBH), spruce basal area expressed as percent total basal area, basal area of spruce component with a DBH greater than 25 cm and expressed as percent spruce basal area, and basal area of mortality in the last 10 years caused by spruce beetle and expressed as percent spruce basal area. Spruce species were not found to be a significant contributor in the prediction, but that may be due to characteristics and site data reflecting the species and making it redundant. The results of the abductive inference model provided consistent results with the classification model, with neither being superior to the other.

Bebi et al. (2003) developed a multivariate logistic model, which demonstrated that stand-level susceptibility to spruce beetle outbreak was correlated with fire history, amount of spruce in neighbouring stands, and elevation.

# 6.2. Shore and Safranyik Spruce Beetle Risk Rating System

Shore and Safranyik (unpublished) developed a spruce beetle risk rating model similar to that of their mountain pine beetle risk rating system (Shore and Safranyik 1992). The spruce beetle risk rating system was developed over a number of years, based on the collective, published knowledge about this insect, as well as on the authors' own research and experience.

Draft versions of this system have been circulated and used over the past several years, and a number of modifications have been made based on feedback. Most recently, Riel and Safranyik (unpublished) developed further modifications to the system, which are presented in this section.

Research on risk and susceptibility rating systems for bark beetles is ongoing and may be subject to future modifications. Although these systems were developed with special reference to British Columbia and the Yukon, they should be generally applicable throughout the range of spruce beetle.

# 6.2.1. Shore and Safranyik system rationale

This section describes the general rationale for selecting specific variables, models, weights (scores), and limits that are included in the Shore and Safranyik risk rating system. Key references are provided to support the authors' philosophy and methods and to facilitate deeper exploration of the subject.

The general approach taken in the development of this risk rating system was essentially the same as that used by Shore and Safranyik (1992). A heuristic approach, rather than a statistical approach, was used: variables and models were selected based on an assessment of published information and on experience with key factors affecting susceptibility to and risk of the spruce beetle. Weights (scores) and limits were assigned to these factors based mostly on published information described below and, in some cases, based on logic and experience with the beetle and the subject.

The following criteria were used to develop the operational susceptibility and risk rating system:

- Most of the required information should be obtainable from existing forest inventory databases, and the remainder should require minimal field work.
- The system should integrate beetle pressure with stand susceptibility and relate directly to basal area and volume killed by the spruce beetle.
- Susceptibility and risk rating should be at the stand level and should be expressed on a continuous scale.
- Tree and stand variables included in the susceptibility index component of the risk index should be manipulable by silviculture, and those same variables in the beetle pressure component should be manipulable by direct-control pest management methods.

# 6.2.2. Susceptibility index

The following five variables were selected for the stand susceptibility component of the risk rating system: average age of dominant and co-dominant spruce, site quality, stand density and growth rate, relative abundance of larger DBH spruce, and location. Even though in any given stand only one or a subset of these factors may be dominant, all model factors should affect stand susceptibility for the following reason: the five selected model factors—and indeed all factors that had been identified to affect stand susceptibility—are correlated. This implies that their combined effect on stand susceptibility is multiplicative rather than additive. In such systems, the variable or variables that are at or near their lowest weights (scores) often dominate, but the overall index is still affected by all model variables. The weights (scores) for the five variables were determined as described below and then scaled so that the product of the highest possible score of each variable would equal 100%.

Earlier work indicated that development of epidemic infestations of the spruce beetle are related to the following tree, stand, and site factors:

- 1. tree diameter (DBH; Watson 1928; Balch 1942; Massey and Wygant 1954; Werner and Holsten 1983; Safranyik 1985)
- 2. periodic diameter increment (Morris 1958; Holsten 1984; Hard 1985)
- 3. stand age (Massey and Wygant 1954; Morris 1958; Safranyik 1985)
- 4. stand density (Hard et al. 1983; Safranyik 1985)
- 5. spruce composition (Schmid and Hinds 1974; Schmid and Frye 1976; Safranyik 1985)
- 6. site quality (Knight et al. 1956; Safranyik 1985)
- 7. climatic conditions (Massey and Wygant 1954; Dyer and Hall 1977; Safranyik 1985; Hard 1987)
- 8. logging residue (Dyer and Taylor 1968; Schmid and Frye 1976; Safranyik et al. 1983)
- 9. cut, windfelled, weakened, and decadent trees (Schmid and Frye 1976; Dyer and Safranyik 1977; Ostaff and Newell 1981; Unger and Humphreys 1982)

Beetle populations breeding in windfelled or weakened trees and logging residue are often the precursors of epidemics. All recorded outbreaks by the spruce beetle up to the early 1980s occurred following large-scale windfall events and large accumulations of man-made slash (Safranyik et al. 1983). Since then, outbreaks in Alaska, the Yukon, Colorado, Wyoming, and Utah have been mostly linked to the direct effects of climate warming on beetle survival and development (Berg et al. 2006; Bentz et al. 2010) and through the indirect effects of drought on host susceptibility (Fettig et al. 2007; Hebertson and Jenkins 2008; Hart et al. 2014).

Of the five factors used to determine stand susceptibility in the Shore and Safranyik system, four factors—site quality, stand age, susceptible spruce composition, and location—were selected based on the work of Safranyik (1985) in central British Columbia. In addition, a stand density and growth rate factor (Hard et al. 1983) was included to represent stand vigour. In the absence of radial growth rate data, a density factor was developed that approximates the relationship demonstrated in Hard et al. (1983).

Based on an analysis of 166 spruce beetle infestations covering two outbreak periods in a 2800-km² area, Safranyik (1985) determined the relative incidence of infestations (expressed as ratios of observed and expected frequencies of infested stands) for each of three age and site-quality classes and for each of four classes of elevation and percent spruce component. For stand age, site quality, and location, these ratios were used directly to determine susceptibility scores. However, for the location factor, the elevation classes at the study area (the Bowron Forest, near Prince George, British Columbia) of Safranyik (1985) were expanded to other locations, in terms of latitude, longitude, aspect and elevation, using Hopkins's Bioclimatic Law (Hopkins 1919; Shore and Safranyik 1992).

Normally, only a small proportion of spruce trees in susceptible stands are smaller than 25 cm DBH, and during outbreaks, only a small to moderate fraction of these small-diameter trees are killed (Balch 1942; Mielke 1950; Safranyik 1985). The susceptible spruce component of stands was defined as the density of all spruce that are at least 25 cm DBH. This variable was converted to basal area and expressed as a percentage of total basal area of all species with trees at least 12.5 cm DBH within the stand. This conversion was done for two reasons: basal area of large-DBH spruce has been used directly in stand ratings for spruce beetles (Schmid and Frye 1976), and percent susceptible spruce basal area is a reasonable index of host availability in a stand and potential for beetle population growth. The authors used the same approach earlier in defining the susceptible pine component in a susceptibility rating system for mountain pine beetle (Shore and Safranyik 1992).

For a given physiographic site and age, mean radial growth of spruce during the preceding five years is expected to be an inverse function of stand density. Slow-growing trees and higher stocking levels have been associated with spruce beetle attack (Hard 1985). Hard et al. (1983) used a complex function of mean growth rates of spruce over the preceding five years and stand density to model the percentage of spruce mortality from spruce beetle. This model was used to develop relative stand density and growth rate scores corresponding to high, average, and low stand susceptibility classes.

#### Overview of characteristics included in the Shore and Safranyik system

Characteristics related to stand susceptibility:

- 1. Site quality
- 2. Stand age
- 3. Percentage susceptible spruce basal area
- 4. Stand location; i.e., elevation, latitude, longitude, and aspect
- 5. Stand density (growth rate)

Characteristics related to beetle population pressure:

- 1. Standing infested trees
- 2. Windthrow
- 3. Logging
- 4. Fire history

#### Susceptibility rating system

The susceptibility rating model involves assigning scores (or weights) to the characteristics included in the system on the basis of available research and the authors' knowledge of the insect. Some of these scores have been adjusted to conform to the constraints of the system design (e.g., the relative weights of each characteristic in the system and the imposed constraint that the susceptibility index should range between 0 and 100). When mean radial growth is available, it is incorporated into a density factor. In its absence, a simplified density factor is used.

#### Calculation of stand susceptibility

Determine the scores for the following five variables:

1. Site quality (Q)

	Site class			
	Good	Medium	Poor	
Score (Q)	1.0	0.53	0.24	

#### 2. Stand age (A)

	Age of dominant/co-dominant spruce (years)			
	> 120	100-120	< 100	
Score (A)	1.0	0.61	0.06	

3. Percentage susceptible spruce basal area (P)

This value is expressed as a percentage and is calculated as follows:

$$P = \frac{\text{basal area of spruce} \ge 25 \text{ cm}}{\text{basal area of all species} \ge 12.5 \text{ cm}} \times 100$$

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#### 4. Location (L)

This is a complex variable incorporating elevation, latitude, and longitude. In addition, extra weight has been given to stands with a northerly aspect.

	Value of Y				
Score (L)	Y 0	0 > Y -400	-400 > Y -900	Y < -900	
North	1.0	0.94	0.65	0.37	
Other	0.94	0.87	0.56	0.19	

#### 5. Stand density (**D**)

When radial growth is available

Both stand density and growth rate are important characteristics influencing spruce beetle epidemics. These variables have been combined in the following equation:

$$Y = e^{(-0.53 - 1.92 \times \ln(X) + 0.006 \times N)}$$

where:

- Y equals the estimate of percentage of spruce trees killed,
- X equals mean radial growth of spruce during the preceding five years (mm),
- N equals the number of **spruce** trees per hectare that are at least 12.5 cm DBH, and
- e equals 2.718, the base of natural logarithms.

Y is interpreted as follows:

	Y ≥ 0.69	0.69 > Y ≥ 0.26	Y < 0.26
Score (D)	1.0	0.60	0.19

When radial growth is unavailable

In situations where mean radial growth is unavailable, the following can be used to determine the density factor (D),

	SPH < 350	700 < SPH ≥ 350	1000 < SPH ≥ 700	1500 < SPH ≥ 1000	SPH ≥ 1500
Score (D)	0.2	0.4	0.6	0.8	1.0

where SPH equals stems per hectare of all species greater than 12.5 cm DBH.

The five scores are combined as described below to calculate stand susceptibility:

$$S = 10 \times (Q \times A \times P \times L \times D)^{0.5}$$

#### Beetle population pressure factors

A number of factors can be used to indicate the beetle population pressure on a given stand. Unlike the mountain pine beetle system, where only infested standing trees are included, the spruce beetle system includes some sources of preferred host material such as windfall, logging debris, and fire-killed trees. Although these may not initially be beetle population sources, experience has shown that because of the ubiquitous distribution of this insect, this material likely will become infested quickly.

Endemic populations breed in windfall, logging residue, and trees with impaired vigour from advanced age, physical injury, drought stress, or disease. Population buildup in such host materials preceeds outbreaks.

#### Windfall

Spruce windfall that has been down from one to three years and is scattered within the stand or is small-patch blowdown is an especially important host material for spruce beetle: the stand overstorey and snow cover tend to moderate subcortical temperatures within the downed trees. Because of this, the inner bark of windfall inside the stand tends to remain suitable for attack for longer periods than it does in windfall in the open. In addition, during winter, snow cover protects broods from woodpecker predation and low temperature extremes. On a per-tree basis, sheet windfall often may be less suitable breeding material than scattered windfall is, due to reduced shading, increased stem breakage, and the resulting increased deterioration of the inner bark. Large concentrations of sheet windfall, however, represent a high potential for infestation in adjacent stands where the shading is greater.

The windfall density limits of the beetle pressure rating were largely based on Safranyik et al. (1983) and his experience with sampling stand windfall for a seven-year period in central British Columbia as part of a spruce beetle population dynamics study. Safranyik et al. (1983) found that densities of spruce windfall along stand edges and inside stands were linked. Windfall densities of less than approximately 19 trees per hectare along stand edges and 10 trees per hectare inside stands did not result in significant change in numbers of infested trees. Two and five trees for each 100-m line transect represent about 10 trees per hectare and 25 trees per hectare, respectively, assuming an average attacked tree length of 30 m and a random orientation angle of interception of the windfall and the transect. Therefore, the highest windfall scores are given to situations in which, given the appropriate conditions of tree and stand susceptibility, development of an infestation was deemed likely. Medium scores of 0.5 and low scores of 0.2 were assigned to the average and below-average windfall densities observed in the study referred to above.

Due partly to the concentration of host material, coupled with the timing of sheet windfall, often only a small to moderate proportion of the downed trees are infested, especially in the interior regions of the affected area. Experience suggests that beetle pressure increases with the size (area) of sheet windfall, probably because of increased stand edges and increased probabilities of windfall inside the stand and host predisposition due to wind sway. In addition to producing beetles, sheet

windfall can absorb beetles for two to three years because a substantial proportion of downed trees remains alive with functional roots. Therefore, sheet windfall of moderate to large size often generates beetle populations of sufficient size to pose an infestation threat to nearby stands. Sheet windfall of 50 ha or greater was designated the highest relative beetle pressure (score = 1). The relative score for the medium and small windfall size class was assigned based on the ratio of class mean size (30 ha) and upper size class boundary (10 ha), respectively, to 50 ha (30 ha/50 ha = 0.6 and 10 ha/50 ha = 0.2).

#### Standing infested trees

The score for standing infested trees is determined by estimating the number and proximity of infested trees affecting the stand being rated. Under endemic conditions, an infested tree density of up to one tree per hectare frequently occurs in mature stands (Safranyik et al. 1983). On the other hand, over the entire period of a low-intensity infestation, average mortality may not exceed 10% of the spruce component that is at least 20 cm DBH (Safranyik 1985), which represents a range of approximately two to six trees per hectare under normal conditions in mature, spruce-dominated stands in central British Columbia. Thus, small, medium, and large infestation sizes were defined as corresponding to per-hectare infested tree densities of less than one, two to six, and greater than six, respectively. The scores corresponding to combinations of the three infestation size classes and distance to the nearest infestation were established in the same manner as given in Shore and Safranyik (1992). This was done because it was assumed that the capacity of dispersal for the mountain pine beetle equalled that of spruce beetle (Schmid 1970; Safranyik et al. 1992; Werner and Holsten 1997).

#### Logging

Logging residue created within the previous two years adjacent to the stand being rated is a source of spruce beetles because stumps and large-diameter cull logs and tops are normally infested (Dyer and Taylor 1968; Schmid 1977; Safranyik and Linton 1978) and brood development takes one to two years. Safranyik and Linton (1987) reported that the bark area per hectare of logging residue suitable for attack by spruce beetle was equivalent to the bark area of approximately six average-sized trees. The average population increase in stumps in central British Columbia was 1.7, and up to about one-half of the broods developed on a one-year cycle (Safranyik and Linton 1999). Considering this information and that only part of the total bark area of trees is attacked, the six trees per hectare represent, on average, at least 10 potential attacked trees per year for each of the next two years. For a stand size of 100 ha, which is a medium-sized stand in central British Columbia, the potential attack trees represent the highest beetle pressure based on standing infested trees described earlier. Hence, a beetle pressure index of 1 was assigned to logged areas 100 ha in area or greater, and the relative scores corresponding to the smaller size classes were made proportional to the average size (area) of the classes, rounded to the nearest decimal.

#### Fire injury

Recent fires, occurring within the previous two years, provide breeding material for spruce beetle. Depending on fire intensity, the bark of the main bole of trees may be scorched to various degrees. Heavily scorched bark is not usually attacked. On the other hand, trees showing no or slight scorching are readily attacked. Brood production in either case may not be at its optimum, due to the deterioration of the inner bark, mainly from drying in the former case and water-logging in the

latter. For these reasons, beetle pressure from burned stands was treated in the same way as logging. Hence, the same size classes and scores were assigned to burned and logged areas.

#### Calculating the beetle pressure index

The effects on population build-up of the various sources of infested host material are neither mutually exclusive nor independent. Therefore, we do not have a framework for combining the various beetle pressure scores. For this reason, even when beetle pressure originated from more than one type of host material, a single score corresponding to the highest value of the alternatives was designated as the overall score for beetle pressure.

#### Windfall (W)

Choose the score associated with the description that best describes the windfall conditions in the stand.

Table 6.4. Windfall score

Score	Description of windfall
1.0	Mature spruce windfall, down one to three years, scattered in stand, or small-patch blowdown averaging more than two trees per 100-m transect across the opening or more than five trees per 100-m transect along the stand edges.
0.5	Same as above, but averaging between one and two trees per 10-m transect in opening or between 2.5 and five trees per 100-m transect along stand edges.
0.2	Same as above, but averaging less than one tree per 100-m transect in opening or less than 2.5 trees per 100-m transect along stand edges.
1.0	Sheet windthrow greater than 50 ha in the stand being assessed or in adjacent stands.
0.6	Same as above, but 10-50 ha.
0.2	Same as above, but less than 10 ha.

#### Standing infested trees (I)

The standing infested tree score is determined by estimating the number and proximity of infested trees affecting the stand being rated. To arrive at the score for this section, first determine the size category (small, medium, or large) of the infestation from Table 6.5. After you have determined the size category of the infestation, use Table 6.6 to determine the score for that size category.

**Table 6.5.** Use this table to determine the relative size of a spruce beetle infestation within three kilometres of the stand being rated.

	Number of infested trees inside stand		
Number of infested trees outside stand within 3 km	< 2 per ha	2–6 per ha	> 6 per ha
≤ 6 per ha	Small	Medium	Large
> 6 per ha	Medium	Large	Large

Table 6.6. Use this table to determine the standing infested tree score (I).

	Standing infe	Standing infested tree score (I)				
	Distance to r	Distance to nearest infestation (km)				
Relative infestation size	In stand	0-1	I-2	2–3	3–4	4+
Small	0.4	0.3	0.2	0.1	0.08	0.05
Medium	0.7	0.6	0.5	0.3	0.2	0.08
Large	1.0	0.9	0.7	0.5	0.2	0.10

#### Logging (L) / fire history (F)

Recent logging (L) and/or fire history (F) within the previous two years in stands adjacent to the stand being rated will provide breeding material for the spruce beetle.

Table 6.7. Use this table to determine the fire and or logging score

Score	Size of cutblocks/fire (ha)
1.0	> 100
0.5	50-100
0.3	20-49
0.2	5–19
0.1	< 5

The Beetle Pressure Index (B) is calculated as the highest value of W, I, L, or F.

# Combining the susceptibility index and beetle population pressure scores into a risk index

A risk index (R) is determined as a function of stand susceptibility and beetle population pressure following a similar form as the Shore and Safranyik (1992) mountain pine beetle risk function:

$$R = 2.74[S^{1.77} e^{-0.0177S}][B^{2.78}e^{-2.78B}],$$

where:

- e equals 2.718, the base of natural logarithms,
- S equals the susceptibility index, as calculated above, and
- B equals the beetle pressure index, as calculated above.

# 6.3. Other Decision Support Models

Although hazard and risk rating systems are the most common decision support tools for spruce beetle management, some other approaches have been developed.

### 6.3.1. Expert systems

SBexpert, a computer program designed as a knowledge-based decision support system, was developed by the Pacific Northwest Research Station and Forest Health Management, USDA Forest Service, for south central Alaska (Reynolds et al. 1994; Reynolds and Holsten 1997). The most current version, SBexpert, version 2.0, includes white, Lutz, and Sitka spruce species and uses a tree classification model for hazard classification developed by Reynolds and Holsten (1996), with 13 possible outcomes (Reynolds and Holsten 1997). Overall, the decision support system consists of four separate but integrated programs. The programs include an introduction with help topics, a literature search program, a textbook program that provides background information, and the main analytical program, which acts as an advisory system for spruce beetle management. The analytical program provides recommendations to reduce risk and hazard based on model results. The risk model, designed by Reynolds and Holsten (1994), includes prioritization of factors based on the proportional contribution they make to the overall risk rating.

# 6.3.2. Connectivity analysis

A significant spruce beetle outbreak in the Yukon that ran from the 1990s to the mid-2000s led to the development of a spruce beetle habitat connectivity analysis tool (Fall et al. 2008). Connectivity is defined as the degree to which pattern impedes or facilitates movement (Taylor et al. 1993). The connectivity analysis was based on an approximation of the Shore and Safranyik spruce beetle susceptibility rating, but it incorporated spatial information by examining how high-susceptibility stands are spatially connected across the landscape and then evaluated the cost of spruce beetle movement through that landscape (Shore et al. 2008). The model is based on an extension to graph theory (Harary 1994), called "spatial graphs", that captures features relevant to geospatial ecological analysis (O'Brien et al. 2006; Fall et al. 2007). This approach has also been applied to assess mountain pine beetle habitat connectivity in several studies (Shore et al. 2008; Riel et al. 2010; Fall et al. 2012).

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