REVIEW OF INSECT AND DISEASE CHALLENGES TO ALBERTA CONIFEROUS FORESTS

IN RELATION TO RESISTANCE BREEDING AND CLIMATE CHANGE

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Abstract

Increasing temperatures with climate change during the coming decades are predicted to drastically alter forests and forest ecosystem dynamics. These changes will impact forest insects and diseases in many ways through changes in host tree distributions, population dynamics, moisture and nutrition, tree defence compounds, and through effects on natural predators, parasites, and mutualist feeders. Predicted changes in Alberta's forests with climate change provide many new challenges for the integrated management of forest pests. To explore the scope of these challenges, a list was developed of insect and disease species considered to be currently the most economically important pests of concern in the management of Alberta's coniferous forests, based on their past historical presence. Each of the 20 pest species identified is rated in relative economic importance according to management priority and on potential levels of damage impact they cause to forest values. The biology of each of the 20 species is briefly reviewed, their damage impacts are described, and information is summarized on likely interactions and potential responses to the changing climate.

The science of genetics and tree breeding for pest resistance is reviewed to examine and explore possible opportunities that could have application in the management of future forests and pest populations in the province. Case history studies of four high-profile pests, including white pine blister rust (*Cronartium ribicola*), white pine weevil (*Pissodes strobi*), dwarf mistletoe (*Arceuthobium americanum*), and mountain pine beetle (*Dendroctonus ponderosae*) are reviewed in detail. Information is provided on life histories, populations, epidemiology, damage impacts, current management practices, climate relationships, and emphasis on genetics and tree breeding for pest resistance.

The information in this report is intended to serve as a guide to help select and prioritize opportunities for genetic tree resistance breeding as part of climate change adaptation strategy, and to incorporate any new strategies into integrated pest management practices for protecting the health, productivity, and diversity of Alberta's coniferous forests.

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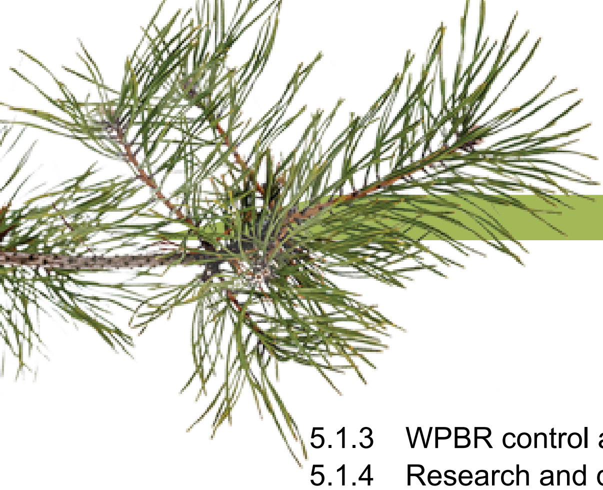
Table of Contents



List of Tables

1.0 Introduction

The world's climate is changing and has resulted in a global average temperature increase of an estimated 0.7° C during the past 100 years, and is expected to increase further during future decades (Moore and Allard 2008; Johnston *et al.* 2009; Williamson *et al.* 2009). In Canada, the average projected temperature increase is somewhat higher at 0.9° C (Mortch 2006). This warming trend, along with increasing concentrations of greenhouse gases, is predicted to influence varying changes in tree species distribution patterns and forest ecosystems. The earliest consequences of the changes in Canada are likely to occur in Alberta and western Saskatchewan where some changes are already apparent (Johnston *et al.* 2009; Mbogga *et al.* 2009; Williamson *et al.* 2009). The climate change effects are predicted to drastically alter forest and forest ecosystem dynamics through increased heat and moisture stresses on trees, affect changes in growth patterns due to higher concentrations of atmospheric carbon dioxide, cause changes in moisture availability, increased evapotranspiration, result in longer and warmer growing seasons and changes in phenological development of tree functions, growth and development (Hogg and Bernier 2005; Volney and Hirsch 2005; Johnston *et al.* 2009).

Direct and indirect interactions of these climatic changes will impact forest insects and diseases in a variety of ways, some negatively and some positively (Hogg and Bernier 2005; Rouault *et al*. 2006; Moore and Allard 2008; Dukes *et al*. 2009). A main objective of this paper is to identify currently important forest pests affecting coniferous species in Alberta, review their known and likely interactions in a changing climate, and examine challenges and opportunities for tree breeding for pest resistance as a means of reducing damages by incorporating genetic resistance into integrated pest management.

Since its start in 1975, the forest genetics and tree improvement program of Alberta Environment and Sustainable Resource Development (ESRD), has participated in numerous surveys and research projects to identify and screen for traits that confer resistance to stem rusts in lodgepole and jack pine (Yanchuk *et al*. 1998; Yang *et al*. 1997, 1998, 1999) and white pine weevil in white spruce (ASRD 2004). With concerns for reductions in forest productivity predicted to occur as a result of climate change, and the current threats of depleting pine resources from mountain pine beetle (MPB) infestations, work is now underway to strengthen the genetics and tree breeding program for increased tolerance to drought, insects and diseases (AFGRC 2006; ASRD 2008a; Hansen *et al*. 2009). Other major provincial challenges include increased impacts of forest insect and disease outbreaks (Volney and Fleming 2000; Moore and Allard 2008; Kliejunas *et al*. 2009; Woods *et al*. 2010; Sturrock *et al*. 2011), and conservation and restoration of limber and whitebark pine. These two species have been declared endangered in Alberta due to mortality and serious population decline caused by mountain pine beetle and severe infection by white

pine blister rust (ASRD and ACA 2007a; ASRD and ACA 2007b; King *et al*. 2010; Gould 2011; Jones 2011).

As a first step toward developing programs to deal with these challenges, a planning meeting was held by Alberta Environment and Sustainable Resource Development (ESRD) in April 2008 to establish a strategy and guidelines for management of forest pests through genetic selection and breeding while also considering impacts of future climate change on forest health. The following prioritized assignments were established that provide the framework and informational content of this report.

1) Review important forest pests of conifers in Alberta;
2) Review the science pertaining to the mechanisms of resistance/tolerance to insects and diseases and their applicability to tree breeding;
3) Review the role of climate change on important conifer pests, their life histories and potential future impacts on forest health;
4) Review case histories of selected pests to identify resistance breeding strategies that can be practically integrated into Alberta forest pest control programs;
5) Prepare a prioritized list of important pests to be managed through forest genetics and tree breeding; and
6) Develop information on the interaction of insects and diseases with climate change as a basis for identifying future opportunities for pest resistance selection and breeding.

Overall, this report provides scientific information on the above topics to develop a better understanding of insect and disease challenges to Alberta's coniferous forests. The report identifies 20 economically important insects and diseases of concern in the management of Alberta's coniferous forests. Literature sources pertaining to the science of genetics and tree breeding for pest resistance are reviewed to examine and explore possible opportunities that could have application in Alberta. Case history studies of four high profile pests are reviewed in detail, two of which have been the subject of intensive research to develop trees genetically resistant to these pests. Important climate change issues pertaining to Alberta's forests and forest pests are summarized to indicate predicted changes that are expected to occur in the coming decades. Each of the 20 insects and pathogens is reviewed with information on life history, behaviour, damage impact and their likely responses to the effects of a changing climate. Possible opportunities for resistance breeding are discussed for its potential role in contributing to the diversity, productivity and health of Alberta's forests and in the management of insects and diseases. This information will be helpful to guide the strengthening of insect and disease resistance breeding programs in Alberta. In addition, discussion on important pests that need to be addressed through genetics and breeding in Alberta and conclusion sections are added to the report.

It should be noted that deciduous forests, particularly aspen and balsam poplars are a very important component of the Alberta forestry landscape. However, these are not discussed in this report except for a limited review in relation to climate change.

2.0 Review of Important Forest Pests of Conifers in Alberta

Table 1 identifies and rates ten species each of coniferous insects and diseases considered economically most important in Alberta based on their historical presence and impact on provincial forest resources (Brandt 1995; Brandt and Amirault 1994; Hall and Moody 1994; Cerezke and Volney 1995; Moody and Amirault 1992; Cerezke *et al.* 2011). The ratings are subjective and were arrived at by consensus from the above reference sources based on the long-term survey records of the former Forest Insect and Disease Surveys carried out by the Canadian Forestry Service in Alberta over the past few decades. Each pest is rated by management priority and its potential impact on forest resources is given to indicate their relative importance. It should be noted that, while these pests are appropriately designated as being currently important, their status and relative importance could change in the future because of warming climates, the introduction of new invasive pests or because of major land-use changes (Yanchuk 2006a).

Table 1. List of important forest insect and disease pests of conifers in Alberta and their current relative management priority and potential impact ratings on the forest resource values in the province.

	Insect and Disease Pest	Management Priority	Potential Impact on Forest Values
Insects species:			
Mountain pine beetle	*(Dendroctonus ponderosae)*	Very High	Severe
Spruce budworm	*(Choristoneura fumiferana)*	High	High
Spruce beetle	(*Dendroctonus rufipennis)*	Moderate	Moderate
White pine weevil	*(Pissodes strobi)*	Low	Low-Moderate
White spotted sawyer beetle	*(Monochamus scutellatus)*	Low	Low-Moderate
Yellow headed spruce sawfly	*(Pikonema alaskensis)*	Low	Low
Western spruce budworm	*(Choristoneura occidentalis)*	Low	Low
Douglas-fir beetle	*(Dendroctonus pseudotsugae)*	Low	Low
Warren rootcollar weevil	*(Hylobius warreni)*	Low	Low
Spruce cone maggot	*(Strobilomyia neanthracina)*	Low	Low
Disease species:			
Armillaria root disease	*(Armillaria ostoyae)*	Moderate-High	Moderate
White pine blister rust	*(Chronartium ribicola)*	Moderate	Severe
Comandra blister rust	*(Chronartium comandrae)*	Moderate	Moderate
Western gall rust	*(Endochronartium harknessii)*	Moderate	Moderate
Tomentosus root rot	*(Inonotus tomentosus)*	Low	Low
Red ring rot	*(Phellinus pini)*	Low	Low
Dwarf mistletoe	*(Arceuthobium americanum)*	Moderate	Moderate
Pine needle cast	*(Lophodermella concolor)*	Low	Low
Atropellis canker	*(Atropellis piniphilia)*	Low	Low
Stalactiform blister rust	*(Cronartium coleosporioides)*	Low	Moderate

3.0 Review of Science Pertaining to Genetics and Breeding Applicability

This section considers the role genetics and tree breeding can play in the management of insects and diseases of Alberta's major conifers. Based on the insects and diseases identified in Table 1, the relevant conifers to be considered include white spruce, lodgepole pine, jack pine, Douglas-fir, whitebark pine and limber pine. Pest species (from Table 1) associated with each of these tree hosts (Table 1) are listed below. The pest species that are underlined indicate that the particular tree species is a primary host associate.

White spruce: spruce budworm, spruce beetle, white pine weevil, white-spotted sawyer beetle, yellowheaded spruce sawfly, spruce cone maggot, armillaria root disease, tomentosus root rot, red ring rot, Warren rootcollar weevil

Lodgepole pine: mountain pine beetle, white pine weevil, white-spotted sawyer beetle, Warren rootcollar weevil, armillaria root disease, comandra blister rust, western gall rust, stalactiform blister rust, red ring rot, dwarf mistletoe, pine needle cast, atropellis canker

Jack pine: mountain pine beetle, white pine weevil, white-spotted sawyer beetle, armillaria root disease, comandra blister rust, western gall rust, stalactiform blister rust, red ring rot, dwarf mistletoe, atropellis canker, Warren rootcollar weevil

Douglas-fir: western spruce budworm, Douglas-firbeetle, armillaria root disease, red ring rot

Whitebark pine: mountain pine beetle, white pine blister rust, atropellis canker

Limber pine: mountain pine beetle, white pine blister rust

The use of insect and pathogen resistant plant varieties is an important part of integrated pest management in agriculture and is well established. In forestry, however, the breeding of trees for resistant traits is a relatively new science that has been developing rapidly over the past several decades (Hanover 1980; Larsson 2002; Yanchuk 2006a). Forest trees have been extensively bred for growth, yield, wood characteristics, morphology and physiological traits, and the literature is abundant in this area. In contrast, breeding for insect and disease resistance, and eventual reforestation with insect and disease resistant varieties, is limited (Heidger and Lieutier 2002; Kamata 2002; Larsson 2002; Yanchuk 2006a).

Where wide-scale deployment of genetic resistance in forestry has been used in recent decades, the application has almost entirely been against diseases. Robison (2002) suggests that the relative lack of genetic resistance development and deployment for insects compared to diseases in forestry may be due to the following reasons: (1) there is a greater apparency and persistence of disease impacts in time and space when they occur as a problem; (2) disease resistance appears to be easier to screen for in the field and laboratory; (3) as a general rule, diseases tend to be more specialized on particular hosts than are insects; and (4) there are fewer ecologically or environmentally viable pesticide and biological controls for tree diseases. Also, according to Yanchuk (2006a), operational deployment of resistant material in forestry is limited by its requirements for a large research effort to reliably screen many genotypes for resistant traits, and whether or not the observed resistance is silviculturally useful. There needs to be an institutional commitment for genotypic resistance research, which in part depends upon the perception of the developed resistance being repeatable and durable in the field.

The objectives of a tree improvement program may include one or more of the following key objectives: (1) improving aspects of forest health and productivity, (2) conserving genes and forest biodiversity, (3) providing an adapted seed supply for reforestation, land reclamation and species restoration, and (4) meeting demands for wood products (Mahalovich 1995). The development of tree genetic resistance can be deployed against two types of stress that affect forest health and survival: abiotic stress factors such as drought, cold temperatures, heat, and mineral toxicity; and biotic stress factors such as insects and diseases.

Seasonally predictable abiotic factors such as cool season temperatures exert strong natural selection pressures, which through survival and reproduction, allow natural populations of forest trees to accumulate higher frequencies for genes that confer tolerance to frost and heat stress. Likewise, low moisture caused by either low annual precipitation or high moisture loss due to heat and/or rapidly drained soils exert natural selection pressure on trees leading to evolution of drought tolerant populations, familes and clones. Biotic factors such as insects and fungi have coevolved with forest trees. Where sustained damages by insects and pathogens exist, tree populations evolve genetic resistance/tolerance against these insects and pathogens. Thus, even without breeding, wild populations, families and clones which exhibit wide genetic variability within natural populations could be found that are genetically tolerant to abiotic and biotic forest damaging agents. Where natural tolerance is lacking, or is present but weak, articificial selection and breeding can be applied to develop insect and disease tolerant varieties.

The nature of interaction between trees and pests is complex, involving genetic, environmental and multi-trophic interactions and pest life history characteristics (Robison 2002). In discussing the current status of pest resistance tree breeding programs, Yanchuk (2006a) outlined three general trends that have negatively

impacted operational deployment of resistant material. (i) The high resources needed to undertake a viable genetic screening program combined with doubts of finding major resistance genes, means that the economic potential of resistance breeding has to be weighed against the potential of managing insects and disease through pestcides, silviculture and other non-genetic methods; (ii) For some conifers, resistance may be expressed in a complex way such as in bark reactions, low levels of infection, or slow developing infection. These complex responses may indicate that resistance is controlled by several minor genes, or they could be due to several major genes interacting with various pathotypes. (iii) Quantifying genetic gains from resistance requires field trials in a variety of ecological sites and different degrees of natural pest exposure to allow for normal infection and full expression of pest symptoms and impacts to development. This process may take a long time to complete. Yanchuk (2006a) has suggested that the development of a tree resistance response for a given pest organism may take up to 10 to 20 years.

Although historically, tree improvement programs have focused on increasing wood productivity per hectare, there is increasing emphasis on developing those traits that contribute to improving forest health. The ability to make progress in developing resistance traits depends upon the genetic variation in host trees and whether uniform and high enough infection or infestation levels will occur that allow detection of differences in the absence of artificial inoculation and infection procedures (Mahalovich 1995).

Carson and Carson (1989) and Mahalovich (1995) have suggested a logical sequence of steps or guidelines that can be taken toward developing and incorporating insect and disease resistance into tree species to improve forest health:

1) Generate a list of pest problems (e.g., list of important insect and disease pests in Alberta as indicated in Table 1);
2) Prepare an inventory of the forest land-base, based upon the presence or distribution of a pest and its host tree, or a hazard assessment of the pest associated with its tree hosts;
3) Determine the cause and effect of the pest on its host;
4) Review effective control measures available and their likely cost-benefits;
5) Select for few important traits of genetic interest, rather than many. Also, resistance breeding can use tree populations that are already screened and improved for other traits (e.g., white pine weevil incidence on white spruce, western gall rust on lodgepole pine or growth and yield);

6) Apply screening techniques to assess the amount and rate of disease development or incidence and damage level of an insect pest. Since the intrinsic genetic component of disease or insect resistance cannot be measured directly, the traits that are measured will reflect this;

7) Develop methods for screening candidate trees either in field trials or in operational forest plantations (Carson and Carson 1989).

Many different disease-resistant mechanisms have been suggested for conifers with respect to rust diseases and include the following signs and symptoms (Carson and Carson 1989):

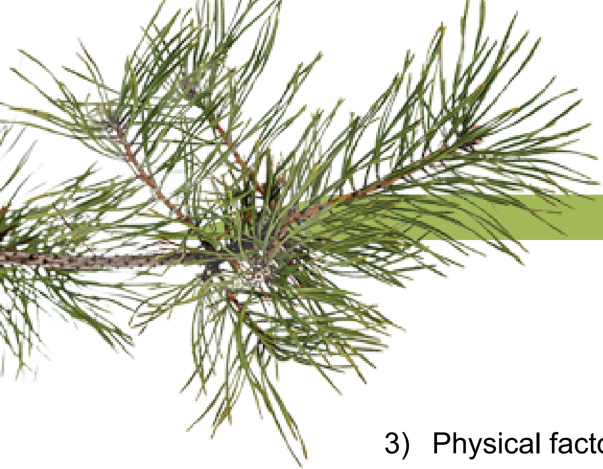
1) Hypersensitive reactions to needle tissues;
2) Premature shedding of infected secondary needles;
3) Reduced receptivity to infection;
4) Slow fungal growth in bark tissue;
5) Hypersensitive reactions in bark tissue, and
6) Ontogenetic or age-related resistance.

Traditionally, disease resistance has been considered to be more genetically determined than insect resistance, where environmental factors are considered to play a greater role in infestation success (Larsson 2002). According to Larsson (2002), resistance mechanisms of tree/insect interactions constitute the tree’s response to an attack by the insect.

Tree resistant traits known to influence insect preference (e.g., feeding and oviposition) and performance (e.g., behaviour) include the following four characteristics (Larsson 2002):

1) Primary metabolites such as nitrogen and carbohydrates, which are nutritional requirements for the insect’s growth and development;

2) Secondary metabolites such as terpenoids, phenolics and alkaloids, many of which are toxic to insects thus impeding infestation. Some of secondary metabolites are constitutive (always present in the plant) or induced (produced as a response to an insect’s initial attack). These metabolites may also serve to guide the insect to the right host, such as in host plant specificity, while deterring other insects not adapted to the host. Metabolites such as terpenoids and phenolics may be increased in concentration as host tree defensive response following attack and feeding by bark beetle species;



3) Physical factors such as bark thickness, hardness of plant tissues, presence of surface hairs, viscosity of resin, etc. Some of these traits may be difficult to separate from chemical traits; and

4) Timing of the host's annual shoot growth and development cycle (phenology) also affect infestation. The feeding, oviposition and development of many insects are often highly synchronized with the seasonal development (e.g., bud burst and bud set that indicates initiation and termination of growth) of the host plant. Variation in the timing of these events can have serious consequences for the growth and survival of insects. Such insect groups as bud and foliage feeders, gall- forming insects and many seed and cone feeders are highly specialized with the development of the host. It has been suggested that exploiting asynchrony between tree and insect pests could be an important component of integrated pest control. Tree phenology and its seasonal development imply that there are accompanying changes taking place in plant tissue chemistry (Larsson 2002; Yanchuk 2006a) that may support or impede infestation.

Resistance to bark beetles may be both constitutive and of an induced type such as with the formation of traumatic resin ducts and polyphenolic parenchyma cells that occur within a few days or weeks after bark beetle attack and associated fungi colonization. This rapid induced resistance following bark beetle attack has been referred to as "hypersensitive reaction" (Larsson 2002; Lieutier 2002; Sobrosa and Martins-Corder 2001) and may be a common response induced by both insect and pathogen attacks. The induced resistance is generally triggered when the insect attacks and certain genes are activated by tissue damage, resulting in increased synthesis of specific compounds such as the secondary metabolites (Lieutier 2002). The hypersensitive reaction plays a role in conifer resistance and is the most important mechanism of resistance to bark beetle species. This reaction is completed by the formation of wound periderm, which contains an impervious layer of cells surrounded by the formation of traumatic resin ducts that build up in the sapwood (Lieutier 2002).

For insect defoliators such as spruce budworm, Clancy (2002) and Heidger and Lieutier (2002) noted several mechanisms that could be operative in the resistance of trees to this insect group:

1) Phenological asynchrony between host trees and insect;
2) Host tree compensatory photosynthesis and growth; i.e., the tree responds by increased rate of photosynthesis and growth, which helps the tree recover more quickly;

3) Toughness of leaves and needles, which can negatively impact feeding ability;
4) Low nutritional quality of foliage;
5) Some foliage may contain defensive compounds that are either toxic, distasteful or act in other negative ways;
6) Formation of defensive compounds induced by insect feeding;
7) In many cases, the feeding by defoliator species may trigger increased susceptibility to attack by associated predatory and parasitic insects.

For shoot attacking insects such as the white pine weevil, several resistance mechanisms were identified (Alfaro *et al* 2002):

1) Resin toxicity to larvae;
2) Low gustatory or olfactory stimuli to feeding source;
3) Variation in the chemical composition of feeding stimulants and deterrents;
4) Variation in resin canal density associated with bark thickness;
5) High density of scleried cells;
6) Production of traumatic resin;
7) Differences in the physical and chemical properties of resin; and
8) Phenology of bud break and shoot elongation.

It was noted that the resistance of white pine weevil on Sitka spruce and white spruce relies upon dense constitutive resin canals for defence. According to Alfaro *et al.* (1996, 2002, 2004), traumatic resin in Sitka and white spruces may be formed in response to weevil wounding and has a higher monoterpene to resin acid ratio, is less viscous, and more easily floods over newly laid eggs and young larvae than does constitutive resin.

For wood boring insects that primarily colonize freshly killed and dying trees, the physical and nutritional factors associated with bark and wood may be the most important in contributing to tree resistance (Paine 2002).

Early reviews of forest tree breeding for pest resistance have been provided by Bjorkman (1964), Gerhold *et al.* (1966), and Hanover (1980). More recent reviews have provided important advancements and guidance in breeding for resistance in forest trees (Carson and Carson 1989; Mahalovich 1995). The importance of maintaining genetic diversity in breeding programs has been emphasized by a number of authors, including Burdon (2001), Burley (2001), Johnson *et al.* (2001), Namkoong (1991) and Yanchuk (2001, 2006a, 2006b). Gene resource populations have traditionally been categorized as either *in situ* (in the population's native location) or *ex situ* (transplanted outside the population's native location or preserved in other forms such as seed and tissue banks). Management of gene resources,

both *in situ* and *ex-situ*, is important for maintaining genetic diversity in a breeding program (Johnson *et al*. 2001; Namkoong 1991). Namkoong (1991) discussed the nature of heritable resistances, their distribution, types of breeding programs, how breeding is related to gene-conservation programs, and also the size and design of gene-conservation programs. In managing for genetic diversity to combat disease, Burdon (2001) stressed the importance of knowing and understanding the pathogen-tree system (i.e., pathosystem), but noted that very few forest tree pathosystems are understood very well (the fusiform rust on slash/loblolly pines and white pine blister rust [WPBR] on western white/sugar pines pathosystems appear to be exceptions). Another consideration is the size of the breeding population and its role in maintaining sufficient genetic variation to allow for continued genetic gain over many generations (Johnson *et al*. 2001; Namkoong 1991; Yanchuk 2001, 2006b). Insects and disease tolerances controlled by many genes with small effects provide a stable genetic system for managing insects and diseases in forestry (Burdon 2001). Environmental conditions can influence the level of tree resistance, and the application of silvicultural practices can be a potentially beneficial tool to enhance tree resistance (Heidger and Lieutier 2002; Yanchuk 2006b).

Sobrosa and Martins-Corder (2001) reviewed disease resistance and provided an overview of the types of resistance, resistance mechanisms, aspects of classic genetic breeding, and the use of biotechnology to accelerate tree-breeding. Sniezko (2006) reviewed resistance breeding against non-native pathogens in forest trees and outlined some current successes in North America. A similar review outlining the challenges and opportunities of host-pathogen interactions and pathogen damages to Canadian forest tree species were discussed by Ekramoddoullah and Hunt (2002). They stressed that understanding host-pathogen interactions is important in managing yield loss and can aid in the identification of disease resistant trees.

Looking to the future, Burley (2001) and Yanchuk (2006a) noted that forest managers must also contend with future genetic changes in insect and disease pests and of the likelihood of new introductions of nonnative pests as well as the over-riding influences of a warming climate. Some of these aspects provide an element of uncertainty for the long-term breeding of tree-pest resistance and point to the need of maintaining ongoing and continuing effort in pest resistance breeding programs.

4.0 Review of the Role of Climate Change on Identified Pest Species, Their Life Histories, Damage Impacts, and Prediction of Future Changes of Pests and Impact on Forest Health

4.1 Overview of Climate Change Issues in Alberta

The world's climate is changing; the global average temperature during the past 100 years has increased by an estimated 0.74° C, and is expected to increase further over the next 80 years in the estimated range of 1.8° C to 4.0° C (La Porta *et al.* 2008; Moore and Allard 2008; Johnston *et al.* 2009; Williamson *et al.* 2009; Bentz *et al.* 2010). Temperature increase projections in Canada tend to be higher (presently at 0.9° C) than the current global average (Mortsch 2006). The greatest warming is expected to occur in the central and northern parts of Canada, and is predicted to influence varying changes in tree species distribution patterns and forest ecosystems. The earliest consequences of the changes are likely to occur in Alberta and western Saskatchewan, some of which is already occurring (Johnston *et al.* 2009; Mbogga *et al.* 2009; Williamson *et al.* 2009).

Increasing emissions of greenhouse gases (e.g., CO_2, CH_4, N_2O, O_3) into the earth's atmosphere are generally acknowledged as a major cause of rising global temperatures as well as influencing the global mean hydrological cycle (Allen *et al.* 2010). The effects of climate change on trees and forest ecosystems include positive aspects (e.g., a longer growing season, increases in forest vigor and growth due to CO_2 fertilization, and increased water use efficiency) and negative aspects (e.g., increases in stress and mortality, reduced growth and other habitat changes due to heat stress and drought) (Rouault *et al.* 2006). There are also forecasts of increased frequency and intensity of other disturbances such as severe storms, wild fire activity and insect and disease outbreaks (Hogg and Bernier 2005; Petzoldt and Seaman 2005; Volney and Hirsch 2005; Allen *et al.* 2010). Weber *et al.* (2008), specifically address climate change and biophysical impacts likely to affect Alberta's forests and document some of the major vulnerabilities of Alberta forests.

Temperature changes are predicted to drastically alter forest and forest ecosystem dynamics. These changes could include increased heat and moisture stresses on trees, changes in moisture availability, increased evaporation and evapotranspiration, longer and warmer growing seasons, and changes in phenology, tree growth and development. Interactions within and among plant species will vary, and will likely lead to tree distribution changes including a general northward shift in species natural ranges and a shift to higher elevations (Norby *et al.* 2005; Johnston *et al.* 2009; Mbogga *et al.* 2009; Chen *et al.* 2010; Gray and Hamann 2011). Climate

affects forest insects and pathogens through its influence on their tree host species; i.e., through changes in the hosts' distribution, population dynamics, nutrition, defence compounds, and through effects on predators and parasites and other mutualist feeders (Dukes *et al.* 2009).

A number of trends expected in climate change are already occurring in Canada during the 20th century (i.e., from 1900 to 1998), and are summarized from Mortsch (2006). All of these climate changes can directly or indirectly influence the development and life cycles of forest pests. In addition, Mbogga *et al.* (2009) predict that Alberta will receive up to 20 per cent less annual precipitation in future decades. In summary, these changes include:

- There has been an increase in mean annual temperature of 0.9° C;
- Warming has occurred in all seasons and in all regions in Canada;
- Greatest warming has occurred in winter and spring, somewhat less in summer and the least in the fall. This warming has been most prominent in the Arctic and in the southern and central Prairies;
- Increased temperatures have resulted in a lengthened growing season, increased growing degree days, a significant trend for an earlier spring, and a longer frost-free growing period;
- Daily minimum temperatures have risen more than daily maximum temperatures, decreasing the spread between the two extremes;
- The warmer temperatures have enhanced the rate of evaporation and evapotranspiration, which decreases available soil moisture content and causes drying. Consequently, most of Canada, especially the Prairies, will experience decreases in soil moisture and higher soil temperatures;
- There have been increases in annual precipitation with some changes in seasonality, especially during the summer period when some areas have experienced decreases. Precipitation in winter is likely to increase;
- Most of Canada south of 60° latitude has experienced an increase in precipitation of 5 per cent to 30 per cent, but the proportion falling as rain has increased while the proportion falling as snow has decreased;
- Winter and early spring snow depths in Canada have decreased, coincident with an increase in air temperatures, and the snow cover season is ending earlier and reaching an earlier date of maximum snow cover;
- There have been frequent fluctuations of temperature around 0° C due to a late winter and early spring warming, which have resulted in increased frequency of thaw-freeze events.

4.2 Review of Potential Climate Change Effects on Insects and Diseases

For insects generally, temperature is the single most important abiotic factor, directly influencing insect behavior, development, survival, distribution and reproduction. Predictions of insect life stage development are most often calculated on the basis of accumulated degree-days from a base temperature and a biofix point (Petzoldt and Seaman 2005; Dukes *et al.* 2009). Therefore, an increase in temperature could speed up development time as well as increase the number of generations per season for some insect species. Changes in moisture and CO_2 may also be an important consideration for insect behavior and development (Petzoldt and Seaman 2005). Warmer winter temperatures may increase overwinter survival, influence diapause, change generation time, and contribute to rapid population build up to epidemics for some species. On the other hand, decreased snow cover could increase exposure to cold temperature and lead to higher overwinter mortality (Ayres and Lombardero 2000; Bale *et al.* 2002; Battisti 2008; Moore and Allard 2008; Dukes *et al.* 2009; Hicke *et al.* 2011).

The magnitude of impacts of temperature on insects will differ among species, depending upon habitat conditions, life history, interactions with other organisms and tree hosts, and the ability to adapt to environmental changes (Moore and Allard 2008). Some species unable to adapt could be driven to extinction, while some other species not known to be present or present in a significant amount, may expand their populations. Insect physiology is highly sensitive to temperature, and thus a warming climate could accelerate feeding activity and movement, including dispersal, and thereby influence population dynamics through changes in fecundity, generation time, dispersal and survival. There are growing examples of insect distributions extending farther north and to higher elevations due to a warming climate (Carroll *et al.* 2004; Battisti 2008; Moore and Allard 2008; Dukes *et al.* 2009; Bentz *et al.* 2010).

Temperature change may influence the synchrony of insect life cycle development dependent upon phenological development of host trees as well as with natural predatory and parasitic species, thus adding to the complexity of predicting species survival and population change (Battisti 2008; Moore and Allard 2008; Dukes *et al.* 2009). For example, population synchrony is important to insure mass attack on host trees by several bark beetle species (Hicke *et al.* 2011).

There are fewer studies of the effects of precipitation on insects than with temperature. Excess moisture is often detrimental to insect life stages and may contribute to mortality by drowning, washing off foliage, or by interfering with feeding, mating and dispersal behaviors. Precipitation changes may also indirectly affect insects by influencing their predators and parasites and other mutualist feeders (Petzoldt and Seaman 2005; Moore and Allard 2008). Precipitation may have a profound effect on the health of the trees and their resistance mechanisms that protect against both insect and pathogen attacks. Changes in both temperature

and moisture or drought have been associated with insect and pathogen outbreaks (Hicke *et al.* 2011; Jactel *et al.* 2012).

The effects of CO_2 on insect pests generally operate indirectly by affecting changes in host trees. Higher atmospheric CO_2 levels result in improved growth rates and water use efficiency of many plant and tree species. The increased growth results in lower nitrogen concentrations in trees as the carbon:nitrogen ratios rise. This results in reduced nutritional value for feeding insects (Moore and Allard 2008). Some insects may respond by feeding more. Increased CO_2 levels may alter plant structures such as increased leaf area and leaf thickness, alter defensive chemicals, influence palatability, or modify nutritional properties (Battisti 2008; Petzoldt and Seaman 2005; Moore and Allard 2008; Peltonen *et al.* 2010; Pinkard *et al.* 2011). For different groups of herbivorous insects, Battisti (2008) noted that defoliators generally increased leaf consumption by about 30 per cent in response to elevated CO_2 levels, whereas leaf miners consumed at a lower rate, and phloem–sucking insects such as aphids appeared to benefit considerably from elevated CO_2, since they grew larger in a shorter time frame (Petzoldt and Seaman 2005; Moore and Allard 2008). In a 9-year experiment reported by Pinkard *et al.* (2011) examining plant-insect interactions under elevated CO_2, there was reduced abundance of leaf miners. This was attributed to increased mortality from natural enemies and from greater ingestion of tannins. Phloem feeders in general appear to be the main guild of insects that show increased development and reproduction under elevated CO_2 (Pinkard *et al.* 2011).

The effects of biotic disturbances, including forest pest disturbances, on forest carbon cycling were reviewed for North American forests (Hicke *et al.* 2011). The review examined major insect and pathogen disturbance species that cause significant damage across large areas of forests; their interactions with other disturbance agents, and documented the influence of insects and pathogens on carbon cycling. They concluded that these large biotic disturbances impact several aspects of carbon cycling through damages resulting in reduced tree productivity, growth reductions and mortality. Consequently, there is decreased primary productivity and excess dead organic material, with the end result of a forest switching from a carbon sink to a source. Important factors involved include the number of affected trees, type of disturbance agent (e.g., growth reducer or tree killer), and duration of attack. Since both forest insect and disease pests are strongly influenced by climate and weather, future warming is likely to increase the severity and extent of pest outbreaks (Hicke *et al.* 2011; Pinkard *et al.* 2011).

Overviews of potential climate change effects on tree pathogens include reviews by Ayres and Lombardero (2000); Boland *et al.* (2004); Petzoldt and Seaman (2005); Desprez-Loustau *et al.* (2006); Parker *et al.* (2006); Moore and Allard (2008); Dukes *et al.* (2009); Kliejunas *et al.* (2009); Hicke *et al.* (2011), Kliejunas (2011) and Sturrock *et al.* (2011). Forest pathogens are taxonomically a diverse group and include fungi, bacteria, phytoplasmas, viruses, nematodes and parasitic higher plants (Hicke *et al.* 2011; Sturrock *et al.* 2011). Fungal pathogens are the most common cause of forest diseases and are primarily in the phyla Basidiomycetes and Ascomycetes (Hicke *et al.* 2011). Most of the important functional groups of fungal pathogens affecting trees include bark and stem cankers, foliar pathogens such as needle casts and rusts, root diseases that infect mostly underground, rust fungi that infect stems and cones, wood decays and stains, and parasitic vascular plants such as dwarf mistletoe (Kliejunas *et al.* 2009; Hicke *et al.* 2011; Sturrock *et al.* 2011).

The two most important environmental factors affecting the development of plant disease epidemics are temperature and moisture. Other contributing factors are atmospheric CO_2 and O_3 concentrations, nitrogen deposition, ultraviolet radiation, and insects that weaken trees or act as vector carriers of fungal spores (Boland *et al.* 2004; Dukes *et al.* 2009).

Several authors stress the fact that predictions and uncertainty are two major concerns for assessing future response and the impact of forest pathogens, and that pathogens could respond negatively or positively under the influence of climate change (Boland *et al.* 2004; Desprez-Loustau *et al.* 2006; La Porta *et al.* 2008; Dukes *et al.* 2009; Kliejunas *et al.* 2009; Sturrock *et al.* 2011). This is because climate change will affect the geographic distribution of vegetation types, ecosystem processes such as primary production, and the distribution and abundance of individual tree species and other plants. Interactions between plant species and host-pathogen interaction systems are complex and may be altered in different ways. For example, rising temperature and CO_2 will impact various functions such as seasonal phenology, biochemistry, photosynthesis, and other physiological traits. Climate warming will also act directly on fungal pathosystems that are already present in a forest and will favor the emergence of new diseases because of distributional range and temporal activity; community structure of pathogens will be modified (Desprez-Loustau *et al.* 2006; La Porta *et al.* 2008). Global climate change is ultimately expressed at the microclimate level; i.e., the level at which plant pathogens infect their hosts, reproduce, and disperse (Kliejunas *et al.* 2009; Sturrock *et al.* 2011). Although there is great uncertainty as to how specific forest pathogens will respond, some general predictions can be made (Kliejunas *et al.* 2009; Sturrock *et al.* 2011):

- Climate change will affect the pathogen, the host plant and the interaction between them, resulting in changes in disease epidemiology and disease impact;
- Changes in interactions between biotic and abiotic stresses may represent the most significant drivers of disease outbreaks;

- Changes in temperature and precipitation will influence changes in distribution of host and disease organisms, allowing them to expand their latitudinal and elevational ranges;
- Pathogens that especially affect water-stressed trees are likely to have an increased impact on forests in regions where precipitation is reduced;
- The ability of pathogens to adapt to new climatic conditions faster than their long-lived tree hosts will likely increase their potential role as disturbance agents;
- Most pathogens will be able to migrate to locations where climate is suitable for their survival and reproduction at a faster rate than tree species;
- Climate change will affect the life cycles and synchronicity of many tree species and pathogens that could effect changes in the distribution and phenology of events such as bud break, spore release and activity of insects that serve as vectors of pathogens;
- Climate change may facilitate invasion by new non-native pathogenic species, resulting in new epidemics;
- Many pathogens currently are limited by cool winter temperatures: rising winter temperature could favor increased overwinter survival of pathogens and disease severity.

In addition to the above predictions, Sturrock *et al.* (2011) predict that under a climate change scenario of warmer and drier future conditions, diseases that are caused by pathogens directly affected by climate (e.g., dothiostroma needle blight) will have a reduced or unchanged impact on their hosts, but will have an increased impact under a scenario of warmer and moister conditions. For pathogens indirectly affected by climate such as Armillaria root disease, and for tree decline diseases in general, these authors predict an increased impact on hosts if the climate scenario is warmer and drier, and a reduced or unchanged impact under warmer and wetter conditions. Many of the most important forest diseases such as root rot diseases, stem diseases, and decline diseases require a stressed host before infection or disease expression occurs (Hogg and Bernier 2005; La Porta *et al.* 2008). Additionally, from their analysis of the literature, Desprez-Loustau *et al.* (2006) noted that most published studies referred to a positive association between drought and disease that applied to both broadleaf and coniferous trees.

Kliejunas (2011) developed a risk assessment analysis of eight important forest diseases of western United States and Canada with the objective of estimating the likelihood that each disease will cause increased damage to forest ecosystems as a result of climate change projected to 2100. The risk assessments project the effects under two climate change scenarios: that the future environment will be warmer and dryer than at present, and that the environment will be warmer and wetter than at present. Risk values for each disease were assigned as either high, moderate or low, based on available biological information and subjective judgement. Diseases of particular concern to Alberta include foliar diseases, stem rusts, dwarf mistletoe, and root diseases. The results suggest that climate change will affect forest health, although the projections are masked by considerable uncertainty.

Rising temperatures, moisture and pH can favor soil-inhabiting pathogens that cause root rots; all of these variables will influence pathogen growth and reproduction. Floods, drought, increased mean winter temperature and seasonal shifts in precipitation pattern may trigger epidemics of some pathogens. Moisture is essential for many pathogens in determining survival and sporulation, while the duration, frequency and timing of rain events during the winter play a key role in inoculation production (Kliejunas *et al.* 2009; Sturrock *et al* 2011). Rust diseases such as white pine blister rust require high humidity conditions for basidiospore germination and pine needle infection, and at temperatures below 20° C.

Pathogens that are indirectly affected by climate may often be associated with drought-stressed trees. Disease types associated with drought generally include canker/dieback (e.g., Hypoxylon canker of aspen) diseases as well as some rusts. Obligate parasitic pathogens such as rusts and mildews do not appear to be positively associated with drought (Desprez-Loustau *et al.* 2006; Sturrock *et al.* 2011).

In large areas of Colorado and Wyoming, a recent event of “sudden aspen decline” occurred in stands of trembling aspen. A severe drought and record high temperatures during 2002 are suspected as the cause. The decline is characterized by rapid, synchronous branch dieback and tree mortality on a landscape scale, and without the apparent involvement of aggressive, primary pathogens or insects (Worrall *et al.* 2007, 2010). A similar phenomenon at a landscape scale of aspen decline and mortality has occurred along the southern edge of the boreal forest in the Prairie Provinces. This decline is attributed to severe drought that occurred during 2001-2002 (Hogg and Bernier 2005; Hogg *et al.* 2008; Michaelian *et al.* 2011).

Increased atmospheric CO_2 concentrations can impact both the host tree and pathogens in multiple ways. Responses to elevated levels of CO_2 may vary between species. The elevated CO_2 concentrations can affect changes in plant structure such as increased leaf area and thickness, greater amount of foliage, leaf waxes, and larger diameter stems and branches. The increased growth rate of foliage could result in denser canopies with higher humidity that favors some pathogens. Also, longer periods of high humidity conditions resulting from more frequent and extreme precipitation events could enhance pathogen environments.

Increased leaf growth from elevated CO_2 levels could result in lower plant decomposition rates that could increase crop residues on which disease organisms overwinter, resulting in higher inoculum levels in the following spring (Petzoldt and Seaman 2005). Other observations have suggested that elevated CO_2 levels could affect host-pathogen interactions by initially delaying the establishment of a pathogen and by causing increased fecundity of pathogens (Boland *et al.* 2004; Dukes *et al.* 2009; Pinkard *et al.* 2011). On the other hand, increases in water use efficiency of host trees exposed to elevated CO_2 levels may improve plant water status, and thereby reduce susceptibility to root and stem pathogens (Pinkard *et al.* 2011).

Limited experimental studies to date to evaluate the effects of elevated concentrations of atmospheric CO_2 on plant diseases have provided variable results. For example, Lake and Wade (2009) showed that stomatal density, guard cell length, and trichome numbers on leaves developing post-infection are increased under elevated CO_2 levels, and that pathogen aggressiveness was also increased. However, there were large inherent differences in epidermal responses to elevated CO_2. Furthermore, it has been speculated that elevated levels of CO_2 will have differing effects on diseases caused by obligate versus facultative pathogenic fungi (Runion *et al.* 2010).

In another study, two southern forest diseases (fusiform rust fungus, *Cronartium quercuum* f. sp. “*fusiforme”* and pitch canker fungus, *Fusarium circinatum*) were induced experimentally to infect loblolly pine seedlings under elevated CO_2 levels. The results indicated that fusiform rust infection was unaffected by increased CO_2 concentrations, and that infection by pitch canker was lower on pine seedlings compared with controls. The reasons for reduction or no effect in disease incidence or disease severity of the two pathogens were not determined but may have been related to the high CO_2-induced alterations in pine tissue chemistry such as a reduction in nitrogen concentration or increased carbon-based defence compounds (Runion *et al.* 2010). Although the results of this study were indicated to be preliminary, the study did suggest that disease incidence, regardless whether obliate or facultative, might be reduced as atmospheric CO_2 concentrations continue to rise.

Leaf size and surface characteristics of paper birch were examined after exposure to elevated levels of atmospheric CO_2 and O_3. After 9 years of tree exposure, CO_2 and O_3 increased epidermal cell size and reduced epidermal cell density, but did not affect leaf size or stomatal density. The stomatal index, however, was increased under elevated $C0_2$. The combination of elevated CO_2 + O_3 resulted in different responses than expected under exposure to CO_2 and O_3 alone (Riikonen *et al.* 2009).

4.3 Review of Potential Climate Change Effects on Important Insect and Disease Pests in Alberta

4.3.1 Mountain pine beetle (*Dendroctonus ponderosae* Hopkins)

The current outbreak of the mountain pine beetle (MPB) in British Columbia and Alberta has affected over 14 million hectares of lodgepole pine forests, representing the largest and most severe epidemic in recorded history for this insect in western Canada (Kurz *et al.* 2008; Woods *et al.* 2010). MPB is the most destructive biotic agent of mature pine in western North America (Safranyik and Carroll 2006). Until recently, the natural range of this bark beetle in western Canada was restricted to interior British Columbia (Safranyik and Carroll 2006). However, because of a warming climate, especially higher winter temperatures, and existing landscape conditions of extensive mature lodgepole pine forests, beetle populations expanded rapidly to epidemic levels and spread northward in British Columbia, to higher elevations, and eastward into Alberta (Carroll *et al.* 2004; Woods *et al.* 2010). This spread was well beyond its previous known range (Safranyik and Carroll 2006).

Although the principal tree host in British Columbia and Alberta is lodgepole pine, the beetle's advance to higher elevations in both provinces has resulted in major destruction of the two soft pine hosts, limber and whitebark pines (Cerezke 1995; Bentz *et al.* 2010) which are also listed as endangered species in Alberta. In west-central Alberta, infestations of this beetle have advanced to the eastern edge of the range of lodgepole pine where forest composition shifts to a lodgepole-jack pine hybrid zone. It has been speculated that the hybridization could allow future successful transit of the beetle eastward into boreal jack pine forests, which extend continuously eastward to Nova Scotia (Safranyik *et al.* 2010; Cullingham *et al.* 2011).

Bentz *et al.* (2010) provide a synthesis of climate change effects on native bark beetle species, including the MPB. They concluded that this bark beetle's response will be characterized by a high degree of complexity and uncertainty, since populations are influenced directly by shifts in temperature, and indirectly through

climatic effects on host trees and community associates. However, future predictions suggest that rising temperatures will be conducive for mountain pine beetle success and its expansion into new habitat areas, both northward and to higher elevations (Carroll *et al.* 2004; Bentz *et al.* 2010). Woods *et al.* (2010) have suggested that future advancement of this beetle may not occur at an epidemic rate, but that a similar wide-scale outbreak could occur again in British Columbia within 70 years after forest recovery of the current outbreak.

An emergency risk assessment sponsored by the Government of Canada to assess the potential of MPB establishing and persisting in the boreal forest east of the Rocky Mountains with the potential to exploit jack pine forests and expand to eastern Canadian provinces was undertaken by a team of scientists (Safranyik *et al.* 2010). Their assessment reviewed and analysed key components of the interactions of MPB with its biotic and abiotic environments and had the following objectives: (a) examine the effects of weather and climate on MPB populations and project the distribution of suitable climatic conditions for the period 2001-2030; (b) review the critical aspects of MPB life history and epidemiology to identify its potential to establish and persist in new habitats; and (c) assess susceptibility and connectivity of potential host trees (e.g., jack pine) within the boreal forest. The authors applied three climate suitability models to assess the present and future climate suitability of the boreal forest for the establishment and spread of MPB populations.

Some conclusions of the risk assessment include the following:

1. MPB can breed successfully in a variety of pine hosts, including jack pine and will be accompanied by their necessary mutualistic organisms;
2. There appear to be no major biological impediments to MPB's establishment, persistence, and spread in the boreal forest zone;
3. Jack pine stands are less susceptible to outbreaks than are lodgepole pine because of their relatively lower pine volume, smaller trees, and less contiguous stands; hence rate of MPB population increase and spread will likely be reduced;
4. Direct and indirect effects of weather and climate control the main limits to MPB range expansion and define areas of suitability for rapid spread and population increases. Climate suitability for MPB is rated moderate in central Alberta east to Saskatchewan, and decreases steadily eastward to a low in northern Ontario, but increases again as volumes and contiguity of pine forests increase northwest to the Great Lakes and in the Maritime provinces;
5. The greatest potential risk of MPB lies in the high likelihood to establish persistent endemic populations outside of the normal range since these

populations could expand under favourable weather conditions to epidemic levels, and thereby increase the potential to spread eastward into more susceptible pine forests.

4.3.2 Spruce budworm (*Choristoneura fumiferana* [Clemens])

The spruce budworm (SBW) is a native defoliator species of primarily balsam fir and white spruce hosts. It is considered the most important insect disturbance in Canada's boreal forest (Volney and Fleming 2007). Severe infestations of the SBW in Alberta have occurred in practically all mature white spruce forests in the past, except for the foothills region (Volney and Cerezke 1992; Cerezke and Volney 1995).

Most severe damages have occurred in the northern half of the province, coinciding with extensive stands along major river drainages (Cerezke and Volney 1995). In eastern Canada, historical records of SBW outbreaks extend over the past 270 years and indicate an outbreak cycle lasting 5 to 15 years and recurring on average every 35 years (Volney and Fleming 2007).

In Alberta, and areas farther north, outbreaks have persisted over several years and appear not to be cyclic in nature (Volney and Fleming 2000). Its current northern distribution is generally limited by the range of white spruce (Juday *et al.* 2010). Cold winter temperatures do not appear to be an important source of mortality since this insect overwinters as an early instar larva in a deep diapause state (Régniére 2009). Also, its distribution is restricted to lower elevations, above which summers are too cool for its eggs to hatch before winter. Under climate change, the budworm's distribution is predicted to advance toward more northerly latitudes and to higher altitudes (Régniére 2009).

Weather factors (temperature, moisture, etc.) are critical in determining budworm distribution. This insect generally persists in the forest in low endemic numbers and erupts to epidemic levels often following periods of drought and also after hot, dry summers. Periods of drought cause stresses of the host tree populations,

lowering their resistance, and higher summer temperatures can increase budworm reproductive output (e.g., female moths' lay 50 per cent more eggs at 25° C than at 15° C). Higher temperatures and drought may also shift the timing of budworm reproduction, and therefore decrease the effectiveness of natural parasitoids and predators (Juday *et al.* 2010).

Initial spring larval feeding on new reproductive and vegetative buds and needles is highly synchronized with the phenological development of the host tree. The young larvae may therefore starve to death if a late spring frost occurs and kills the new shoot growth (Volney and Cerezke 1992). The synchronization with the host tree is critical to initiating outbreaks, and ultimately, in determining the intensity of defoliation damage (Volney and Fleming 2007; Moore and Allard 2008). Wind is an important factor during dispersal of first instar larvae (disperse on silken threads) and during the moth stage. Excess moisture during mating and oviposition may also be an important factor (Candau and Fleming 2011). Climate in general will impact the SBW defoliation dynamics both directly and indirectly. Potential direct effects include changes in insect phenology, in the spatial extent of the populations, and in the frequency and duration of outbreaks. Indirect effects will be largely mediated through changes in the distribution and phenology of host trees, in the population dynamics of natural enemies, and in the interaction with other disturbances (Candau and Fleming 2011). In their examination of the responses of SBW defoliation to climate change in Ontario, Candau and Fleming (2011) used various climate change models that project an extension of the northern limit of defoliation, a decrease in the frequency of defoliation in the historical central defoliation belt, and a persistence of defoliation in the southern limit of defoliation areas. Similar analysis by Gray (2008) in eastern Canada predicts that in future decades, outbreaks of the SBW will likely be longer and more severe.

4.3.3 Spruce beetle (*Dendroctonus rufipennis* [Kirby])

The spruce beetle, a native bark beetle species, attacks white and Engelmann spruces as its primary hosts, and may rarely attack black spruce. It is widely distributed across Canada and is one of the most destructive insects of mature spruce (Safranyik 1995). Endemic populations are always present and exist in wind-felled trees, logging debris, as well as in injured, diseased, decadent or other severely stressed trees. The abundance of these materials provides favourable conditions for rapid population build-up to epidemic levels, allowing excess populations to spill over and attack adjacent live, healthy trees. All known outbreaks of the spruce beetle in Alberta have occurred following large-scale accumulations

of windthrow, cull logs, felled trees along right-of-way logging operations, and from trees weakened with broken tops resulting from severe storms of high winds and heavy wet snow (Cerezke and Brandt 1993; Cerezke and Volney 1995).

The spruce beetle predominantly has a 1-year life cycle in the warmer parts of its range, but most often requires 2-years or rarely 3-years to complete development. For a 1-year cycle, over wintering occurs in the adult stage, whereas during a 2-year cycle, both larvae and adults over winter (Safranyik 1995). Adult emergence and dispersal to seek new hosts occurs in late spring to mid summer. Occasionally some brood adults emerge in late summer and early fall, but they then move to the base of their brood trees to over winter (Safranyik 1995).

The important factors that affect generation survival include host resistance, climatic events, especially temperature, deterioration of the sub-cortical habitat, competition from other sub-cortical feeders, various natural parasitic and predacious enemies, and especially woodpecker predation (Safranyik 1995). Studies in Alaska have indicated that the relationship of spruce beetle to climate involves two direct temperature controls over populations of this insect, and an indirect control affecting host tree resistance, such as in drought-stressed trees (Juday *et al.* 2010). Direct temperature control is exerted during the over wintering stage when cold temperatures can reduce survival, and thereby reduce the risk of outbreak potential for the following season. The spring and summer development periods are driven largely by temperature. Abnormally warm summers can allow the beetle to complete its life cycle in 1-year, which can dramatically increase its potential for population expansion. Tree health increases host resistance by providing increased growth reserves, resin flow and higher turgor pressure, making it difficult for successful beetle attacks. Host trees under heat or moisture stresses succumb more readily to spruce beetle attacks (Berg *et al.* 2006; Juday *et al.* 2010).

Several temperature-dependent physiological processes help to insure synchronicity for adult beetle emergence and life cycle timing, as well as to promote adult longevity, prolong adult emergence and flight (Bentz *et al.* 2010). These processes

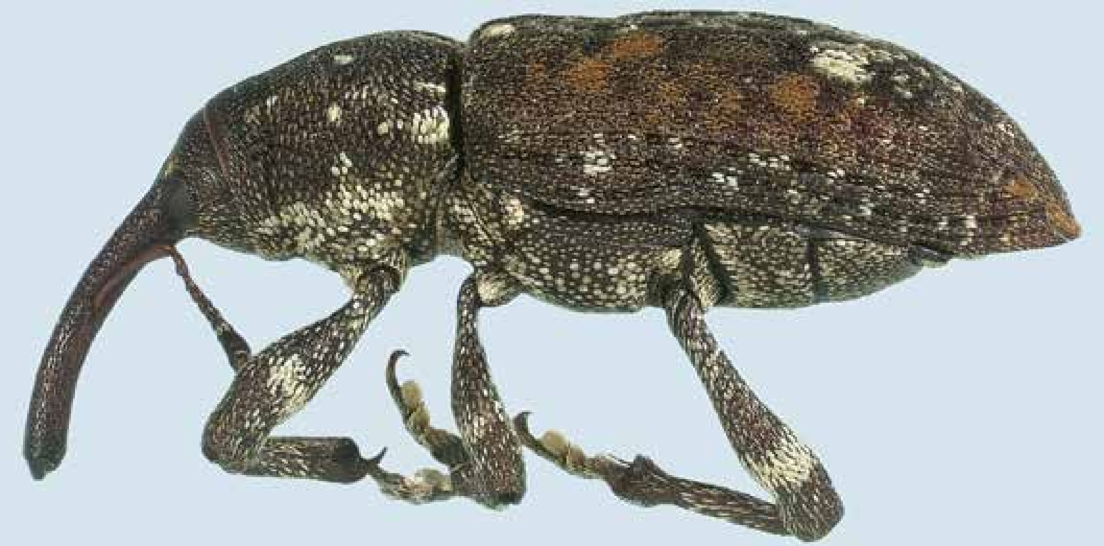
are important to facilitate winter cold tolerance and diapause, which provide safety for the beetle against environmental extremes and help to synchronize with food availability (Bentz *et al.* 2010).

Recent large-scale spruce beetle outbreaks studied in Yukon and Alaska, and in south western United States, indicated that these outbreaks originated during the early 1990's and were different in their origin from previous outbreaks in that they did not result from a clearly identifiable disturbance (Berg *et al.* 2006). Results of these studies indicated that the outbreaks were initiated and sustained by periods of 5 to 6 years of warm summer temperatures, which began in 1987 (Berg *et al.* 2006; Garbutt *et al.* 2006). The outbreak periods were associated generally with warm fall and winter temperatures. A dramatic increase in summer temperatures during the late 1990's appears to explain these recent massive outbreaks of the spruce beetle. It is predicted that outbreaks are likely to increase in the coming decades if the warming trend continues and may even increase in frequency and intensity. Outbreaks are also expected to expand to new areas (Berg *et al.* 2006; Juday *et al.* 2010). Other disturbance events predicted to occur with increasing frequency and severity in relation to a warming climate include wildfires and severe storms with high winds. These events will likely increase the risks for future spruce beetle outbreaks and add to the complexity of predicting these events.

4.3.4 White pine weevil (*Pissodes strobi* [Peck])

The life history, seasonal development and damage impact on host trees of this weevil are reviewed in section 5.2 of this report. The white pine weevil is considered one of the most damaging insect pests of young spruce plantations (e.g., Sitka, white and Engelmann spruces) in western Canada (Hiratsuka *et al.* 1995; Woods *et al.* 2010). Its main hosts in Alberta are white and Engelmann spruces, but it also commonly attacks blue and Norway spruces, and less commonly black spruce and pine hosts such as lodgepole, jack and Scotch pines. Incidence of its attack may be found throughout Alberta, both as a forest pest and in rural and urban environments on shelterbelt and ornamental trees (Ives and Wong 1988).

The life cycle of the white pine weevil is 1-year. Adults emerge in early spring, most commonly during warm sunny days throughout April. They crawl up the stems to the previous years leader where feeding, mating and oviposition occurs. Eggs are deposited in small punctures in the leader bark during May and early June, and the larvae feed under the bark, progressing downward as they develop and mature (Retnakaran and Harris 1995). The resultant feeding girdles and kills at least two years of leader growth (current and previous year's) (Hiratsuka *et al.* 1995). Pupation



occurs in August and the new adults may feed for a period before entering the duff material at the tree base. They enter diapause and remain over winter, emerging again in early spring.

The success of the weevil from spring emergence to fall entry into duff is strongly regulated by heat accumulation (Woods *et al.* 2010). Reduced winter snow fall and rising temperatures could allow earlier spring emergence, feeding and mating behavior, while reduced snow cover during the over winter months could increase over winter mortality. Natural mortality during over wintering can be very high and ranges from 50 per cent to 80 per cent (Retnakaran and Harris 1995). Drought stressed trees may have shorter leader length for larval growth and development, and this may require larvae to extend their feeding below the previous year's leader, resulting in up to three years of leader kill.

Resistance mechanisms of the host tree may also be lowered in moisture stressed trees, allowing more successful oviposition and brood development (King and Alfaro 2009).

In British Columbia, accumulated spring and summer heat units provided the basis for delineating weevil hazard zones. As climate warms, therefore, areas currently delineated as low to moderate hazard, could become increasingly more suitable to the weevil (Woods *et al.* 2010). Also, with climate warming, there will likely be a distributional shift to new habitats northward and to higher elevations. Woods *et al.* (2010) have suggested that the identification and propagation of weevil-resistant spruce genotypes will help mitigate the impacts of the weevil in regenerating white and Engelmann spruces.

4.3.5 Whitespotted sawyer beetle (*Monochamus scutellatus* [Say])

Woodborers are a taxonomically diverse group of insects of many species that include ambrosia beetles, roundheaded woodborers, flatheaded woodborers, wood wasps, powder post beetles, carpenter ants, and others (Safranyik and Moeck 1995). However, only one species is considered here because it has consistently contributed most of the economic losses through downgrading of timber products. The species considered here is the whitespotted sawyer beetle, a large 2-3 cm long beetle and member of the roundheaded woodborer group (Safranyik and Moeck 1995). This species is present in all forested areas of Alberta and attacks all conifer species. It is attracted to weakened or dying conifer logs and causes economic losses from its tunnelling into the sapwood and heartwood of logs, which results in "worm hole" defect in finished wood products. The tunnels are excavated mostly by larvae, and a small portion by adults when they emerge from logs.

Trees at risk to sawyer beetle attack include those weakened and dying from root and stem decays, other insect attacks, competition, wind and storm damages, and wildfires, as well as freshly-cut green logs (Cerezke 1977, 1999). Economic losses from this beetle arise during the harvesting or salvaging of borer-attacked trees, and later at the mill site during the manufacturing and processing of logs into lumber or other wood products. The presence of wormholes and tunnels can result in increased handling and fibre loss during plywood production, rejection of logs for power poles, and downgrading of dimension lumber with a corresponding value loss. The presence of wormholes in finished products may restrict their saleability, both domestically and for export. The wormholes can also provide entry for moisture that will promote the development of fungal stains and decays (Cerezke 1999).

Most economic losses caused by sawyer beetle damages occur in fire-killed timber, especially in large burns where salvage operations extend over one or more years. The beetle's life cycle extends over 1-year, but most commonly over 2-years and occasionally 3-years. Within-log damage caused by the larvae increases as they grow and extend their feeding tunnels. Within burn areas, risk of sawyer beetle damage may relate especially to the intensity of the burn as well as season of burn. For example, April to June fires coincide with adult emergence and flight periods, and therefore carry a higher risk of attack than late summer or fall fires. Burn intensity relates to the degree of scorching on the tree and is usually classified into different levels of burn intensity for convenience of sawyer beetle assessment. A medium class of burn is usually the most common in burn areas where trees are scorched around the base and up the stem several meters; foliage is killed, but the inner bark remains white and succulent. This condition provides the preferred medium for adult oviposition and food source and protection for young larvae (Cerezke 1999). Trees characterized with a medium level of burn intensity are immediately attractive post-fire for sawyer beetle attacks. Wind-blown trees resulting from severe storms may also contribute large sources of breeding material and contribute to subsequent downgrading of salvaged wood products (Gardiner 1975).

Climate change is predicted to produce increased frequency, duration and intensity of wildfires and greater extremes in climate and weather events such as intense precipitation, drought, windstorms and lightning. Additionally, climate change may increase the annual area of forest burned and also increase the length of the fire season (Johnston *et al.* 2009; Williamson *et al.* 2009). These events will all provide increased breeding materials for the sawyer beetle as well as for many other secondary feeding bark and woodborer species. The increased frequency, duration and extent of burns will help to insure relatively high populations of woodborer species are maintained. Wildfires that burn with greater than medium intensity, however, will result in greater charring of tree stems and bark. Consequently, this will reduce suitable sawyer beetle breeding habitat (Cerezke 1999).

4.3.6 Yellowheaded spruce sawfly (*Pikonema alaskensis* [Rohwer])

The yellowheaded spruce sawfly is a native species in Canada and occurs throughout the distribution of white spruce. It has occasionally been a problem in young forest stands of white and Engelmann spruce and occasionally black spruce, but is more commonly a pest of ornamental, shelterbelt and plantation grown spruce. Other species commonly attacked include blue and Norway spruces. This sawfly rarely attacks mature spruce, but prefers young open-grown trees, often in a sunny exposure, and occasionally has become a pest in cutover areas of young natural regeneration (Martineau 1984; de Groot 1995). All damage is caused by larvae of this sawfly since they feed initially on current-year needles, then on older needles. Trees die if defoliation is complete for one or more years. Trees that are partly defoliated commonly suffer top kill and radial stem growth reduction. Infestations in a plantation, for example, may selectively occur on certain trees and may persist for one or more years, re-attacking the same trees (Martineau 1984).

The yellowheaded spruce sawfly has one generation each year and is well synchronized with the phenological development of its spruce hosts and with local weather conditions. Adult sawflies emerge from the soil during late May to mid-June, coinciding with the opening of spruce buds. Eggs are deposited in slits on current-year needles or in bark between needles. After hatch, the young larvae feed openly on the new needles, and later as they deplete the new needle growth, they move to older needles to complete their development. By July, they are mature and drop to the ground, form cocoons in the soil and remain as prepupae during the overwintering period (Martineau 1984). Defoliation is most intense in the top part of the tree crown and progresses downward with each year's repeat defoliation.

There appear to be no studies available linking yellowheaded spruce sawfly with aspects of climate change. However, it can be surmised that this defoliator will respond similarly to other defoliator species. Warmer temperatures and sunny exposures during the larval feeding period will promote faster development and possibly greater survival. Warm springs will also benefit adult sawfly dispersion, mating and oviposition. Increased atmospheric concentrations of carbon dioxide could be beneficial to the sawfly if it results in increased growth rates and water use efficiency of the host (Moore and Allard 2008). Reduced snow cover could have a negative effect on the overwintering prepupae and result in increased mortality. Late instar larvae and the overwintering cocoons are prone to a large number of insect parasitic and predaceous species as well as to predation by voles and shrews. One study reported predation of overwintering cocoons as high as 66 per cent (de Groot 1995). These predaceous and parasitic species will likely be influenced by climate change as well, but their role and interactions are unknown.

Juday *et al.* (2010) reported that during the period 1991 to 1996, forest areas defoliated by the larch sawfly in Alaska increased substantially and were attributed in part to warmer summers and winters. The yellowheaded spruce sawfly has a similar life cycle and behavior pattern to that of the larch sawfly and may benefit similarly to a warming climate.

4.3.7 Western spruce budworm (*Choristoneura occidentalis* Freeman)

Douglas-fir is the primary host for western spruce budworm, although it may feed on true firs and occasionally on spruce. As a defoliator, its larvae feed on the buds and needles of Douglas-fir and cause similar damage to that of the eastern spruce budworm. Tree damage consists primarily of radial and height growth reductions, top tree dieback and stem deformity. However, tree mortality mostly occurs in the understory, below large heavily infested trees (Shepherd *et al.* 1995). This damage is most serious in multi-storied older stands. The larvae may also feed on cones and seeds (Furniss and Carolin 1977).

The western spruce budworm is native to Douglas-fir forest ecosystems and is distributed throughout the range of this host in British Columbia (Heppner and Turner 2006). In Alberta, this insect has historically remained endemic and no major

infestations had been reported prior to 1988 (Ives and Wong 1988). However, the first report of a major infestation of this insect in Alberta indicated that an outbreak developed after 2000, and by 2007 it had spread and caused severe defoliation over an estimated 16,000 hectares in the Porcupine Hills of southwest Alberta (ASRD 2008b).

The moths lay their eggs in masses on the underside of needles in July. These hatch in August, but the young larvae do not feed at this time but move to protective niches on branches or tree stem where they spin silken shelters in which to hibernate during winter. The larvae emerge in the following spring and may mine into buds or in 1-year old needles. Their synchronization with host expanding buds is important to insure maximum protection and nutrient quality of young larvae. After bud flush, the larvae continue to feed on foliage and their survival decreases rapidly thereafter as they complete their development in late June and early July. Pupation occurs on the residual foliage and moths appear about 10 days later, mate, disperse and commence oviposition (Shepherd *et al.* 1995).

Climate models were recently applied in British Columbia to project future distribution shifts for Douglas-fir forests. These models suggest that during the 21st century, new areas of climate suitability for Douglas-fir are projected to shift toward more northerly latitudes and to higher elevations (Murdock and Flower 2009). These authors also modelled the risk of future outbreaks of the western spruce budworm and concluded that outbreaks are projected to increase considerably in central and northwestern British Columbia, particularly under a warm/wet scenario of climate change. This insect has a long history of outbreaks in the dry Douglas-fir dominated forests of interior British Columbia. Outbreaks that have been monitored in British Columbia have generally lasted 3-5 years (Heppner and Turner 2006). The current outbreak, monitored since 1995-2010 in this province, is distinguished from previous outbreak patterns by the fact that infestations have expanded into higher elevations and have advanced northward into Douglas-fir forests that had no prior record of infestation (Woods *et al.* 2010). These authors also noted that the climate has become more favourable for this budworm, and that stand structure is at a higher hazard/susceptibility risk than in the past. They predict that as climate warms, the western spruce budworm will continue to expand its range.

These projections of future trends of outbreak pattern in British Columbia may suggest similar predictive trends for this insect in Alberta. Provincial surveys of the current outbreak suggest that it likely commenced in about 2002 (ASRD 2008b), and was possibly triggered by severe drought conditions reported during 2001-2002 (Hogg *et al.* 2008). The composite area of infestation was estimated at

17,679 hectares in 2007, and expanded to nearly 31,000 hectares by 2009 (ASRD 2010), but declined sharply to less than 3000 ha in 2010 (ASRD 2008b, 2009a, 2010, 2011a). However, extensive top kill and some tree mortality had already occurred by 2007 (ASRD 2008b).

Projections of future habitat suitability of Douglas-fir distribution in Alberta carry large uncertainties according to Gray and Hamann (2011), and therefore projections of the western spruce budworm beyond 2020 could be highly speculative at this time.

4.3.8 Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins)

The Douglas-fir beetle, a species similar to the spruce beetle, attacks Douglas-fir and occasionally felled or freshly cut western larch in British Columbia. Infestations in Alberta have occurred in the Porcupine Hills and in Banff and Jasper national parks. The most recent outbreak in Jasper National Park occurred from about 1986 to at least 1992 (Cerezke and Volney 1995). This bark beetle normally breeds in felled, injured or diseased trees. Drought-stressed and fire-killed trees are also highly attractive, and can allow populations to expand and attack apparent healthy trees that are mostly mature and overmature (Furniss and Carolin 1977). When abundant, the Douglas-fir beetle will attack and kill adjacent vigorous trees. The adult beetles carry blue-stain fungi into the tree when they attack, which contributes to tree decline and mortality (McMullen 1984). When attacking live standing trees, small groups of trees are normally killed by the beetle. Tree mortality becomes more extensive during outbreaks when tree losses can be substantial (Schmitz and Gibson 1996). Outbreaks in standing trees have generally lasted from 2 to 4 years, but can be prolonged during periods of drought. Bentz *et al.* (2010) have indicated that the Douglas-fir beetle has the potential to cause landscape-scale tree mortality. Endemic populations appear to thrive in scattered windfall, fire-scorched trees, or trees injured

by other agents (Parker *et al.* 2006). Vigorous trees can be resistant to this beetle's attack if resin exudation is sufficient to prevent adult beetles from constructing under bark galleries.

The Douglas-fir beetle develops through one generation each year. Both adults and late instar larvae overwinter under the bark of tree stems. This allows early emergence and initial flight of adults during April to June. Adults from the overwintering larvae mature in June and July and emerge and attack trees in July and August. Spring attacks exceed the late summer attacks, which may only account for 20 per cent of all attacks in one season (Schmitz and Gibson 1996). The eggs are deposited in groups alternating on opposite sides of the female galleries and hatch in 1 to 3 weeks. Young larvae mine the inner phloem and extend galleries latterly from the main adult gallery. They develop through four stages of growth, form pupae and young adults by fall. Emergence, dispersal and growth and development are all temperature driven. Outbreaks of the Douglas-fir beetle in British Columbia are often associated with weather-related events such as drought and windthrow (Woods *et al.* 2010). These authors have suggested that, with climate change forecasts of more frequent summer drought periods and winter wind storms, episodes of increased tree mortality by this beetle will increase in frequency. The beetle also responds to trees stressed from prolonged periods of defoliation caused by the western spruce budworm. Woods *et al.* (2010) further suggest that this trend is already occurring in interior British Columbia.

Direct effects of climate change on Douglas-fir beetle population dynamics is expected to operate through the influence of temperature and its controlling effect on life history strategies, such as in maintaining adaptive developmental timing for synchronized population emergence and life cycle development. Temperature effects also have a controlling influence on the development of cold tolerance as a strategy to enhance overwinter survival of adults and larvae. This strategy helps to initiate diapause as a mechanism to keep this beetle synchronized with its environment and food availability (Bentz *et al.* 2010).

Climate models applied to Douglas-fir forests in British Columbia (Murdock and Flower 2009) and in Alberta (Gray and Hamann 2011) suggest there will be shifts in suitability of Douglas-fir to higher elevations and latitudes than in its current range. A similar pattern of shift is likely to occur with the Douglas-fir beetle.

4.3.9 Warren rootcollar weevil (*Hylobius warreni* Wood)

Warren rootcollar weevil is a native insect widely distributed in Alberta's forests. Its prime hosts include lodgepole and jack pines, but other pine species such as Scotch pine are readily attacked. Spruce species are also hosts but are less commonly attacked than pine species in Alberta (Cerezke 1994). This weevil attacks healthy trees from a few years old to maturity, but its injury has greatest impact in stands less than 30 years old. Feeding damage by larvae occurs in the root collar zone, either on the lower stem or on main lateral roots, and results in various circumferential amounts of partial girdling of the tree stem or roots (Cerezke 1994). Weevil-caused tree mortality occurs in natural stands up to about the age of 30 years, but appears to peak between 5 and 10 years (Ives and Rentz 1993). Accumulated tree mortality from girdling injury often ranges from 5 per cent to 10 per cent, but can exceed 15 per cent in intensively managed stands and plantations (Cerezke 1994). Trees that survive various levels of partial girdling have slightly reduced radial growth, while height growth reductions are more significant, and can range from 10 per cent to 30 per cent post-attack (Cerezke 1994).

Within natural lodgepole pine forests, *H. warreni* is distributed in predictable patterns: weevil numbers are positively correlated with increasing tree size, indicating preferential selection for attack of dominant and codominant size trees. Weevil numbers are also correlated positively with increasing duff depth materials (depth to mineral soil) around the tree base, indicating its preference for a moist environment. In mature stands, maximum weevil population estimates occurred in stand densities between 900 and 1300 stems per hectare (Cerezke 1994). Studies of weevil-caused tree mortality in west-central Alberta indicated that the incidence of mortality was highest on high productivity sites, compared to low and medium productivity sites (Ives and Rentz 1993).

The life cycle of *H. warreni* is commonly 2-years, but can extend to 3-years, depending upon latitude, elevation and degree of shade. In both Alberta and British Columbia, this weevil has not been found above 1585 meters elevation (above sea level), probably because of cooler temperatures and shorter growing seasons that impact synchrony of its life cycle development. The weevil's oviposition period extends from late May to early September, with a peak period in June and July. Egg hatch occurs during the summer months and the larvae feed in the bark, extending resinous feeding galleries during two summer periods. After the second overwinter period, the mature larva prepares a special soil-resin chamber in which pupae and young adults are formed (Cerezke 1994). The adult weevil is long-lived, up to 5 years, and both it and the larvae survive overwintering.

The effects of climate change on *H. warreni* populations and survival are likely to be detrimental in much of its current habitat. Warming temperatures and a longer growing season will probably allow increased migration and survival at higher elevations than its current distribution and allow it to exploit new habitats. At the same time, increased drought conditions will decrease suitable habitats at lower elevations, and perhaps decrease suitable areas now classed as high productivity sites.

Heineman *et al.* (2010) investigated the influence of climate, site, location, and stand treatment factors associated with *H. warreni* damage to young lodgepole pine in interior British Columbia. They reported that this weevil was present on 13 per cent of the sites surveyed, of which the average proportion of affected trees ranged from 0.7 per cent to 8.3 per cent, and that the only factor associated with increasing risk of this weevil was moisture.

One indirect effect of climate change that relates to the mountain pine beetle outbreak in British Columbia is the apparent higher levels of weevil incidence in young pine stands that are adjacent to mature beetle-killed lodgepole pine. There is evidence that *H. warreni* populations that survived on the beetle-killed trees migrated to the adjacent young pine, and subsequently resulted in increased invasion and tree mortality in the young stands (McCulloch *et al.* 2009).

4.3.10 Spruce cone maggot (*Strobilomyia neanthracina* Michelsen)

The spruce cone maggot is distributed widely across Canada throughout the range of white and Engelmann spruces, its primary hosts (Hedlin *et al.* 1980). Of the several species of seed and cone insects that attack spruce, the spruce cone maggot is the most common and damaging, and is often the most abundant. Seed losses from its maggot feeding stage have ranged up to 100 per cent (Turgeon and deGroot 1992). Surveys of white spruce cones collected from seed orchard plantations in Alberta over a 10-year period (1995 to 2004) indicated estimated seed losses varied from less than 2 per cent to over 70 per cent. Highest levels of seed loss usually occur in a light cone crop year that was preceded by a heavy cone crop year (Cerezke 2004). Attacked cones are usually shorter than non-attacked cones; the presence of only one larva per cone can destroy an estimated 55-65 per cent of the seeds (Turgeon and de Groot 1992). Spruce cone maggot seed and cone damages tend to be higher in seed orchards than in natural stands (Anon. British Columbia Ministry of Forests, Lands and Natural Resource Operations).

The life cycle of the spruce cone maggot is 1-year. Adult flies emerge during late May until mid-June. Females lay eggs singly between cone scales during the time of conelet pollination. Egg hatch occurs 5-10 days later. The timing of adult emergence, mating and oviposition are highly synchronized with the phenological development of the female strobili. After hatch, the young larva tunnels around the central cone axis, feeding on scale tissue and seeds. Upon maturity, about mid-July, they tunnel to the cone surface, drop to the ground and form a puparium. They then pupate in late summer or fall, enter diapause and overwinter in the litter. Normally, a portion of the overwintering population may enter a “prolonged diapause” for an additional year or more. This strategy is characteristic of many obligatory seed/cone insects such as the spruce cone maggot. The obligatory restriction of this insect indicates that its feeding stage is spent exclusively within the young cone, and it cannot feed and develop elsewhere (Miller *et al.* 1995). The prolonged diapause is a unique strategy that allows the insect to survive annual fluctuations in cone crop size, ranging from nil crop in some years to light to heavy crops in other years (Miller *et al.* 1995). Levels of cone attack and maggot population levels appear to relate directly to annual cone crop size and to the frequency of cone production years.

It can be speculated that climate change will influence several aspects of the spruce cone maggot life cycle, its physiology and development. For example, a warming climate could interfere with the prolonged diapause and may result in asynchrony with host cone development. Low snowfall during winter months could increase mortality of overwintering puparia. Other critical periods of the life cycle coincide when the adult flies emerge in the spring, during their mating behavior, and during their search for oviposition sites. Cool temperatures, rainy or wet conditions, and strong winds may disrupt all of these behaviors. Climate change effects may affect spruce cone crop production, and this could impact the population dynamics of the spruce cone maggot, either negatively or positively.

4.3.11 Armillaria root disease (*Armillaria ostoyae* [Romagn.] Herink)

Armillaria root disease is caused by a fungal pathogen in the Basidiomycetes phylum, and infects both conifers and hardwoods. About 12 species have been collected in Canada, two of which have been collected in Alberta (Mallett 1992; LaFlamme 2010). The species in Alberta are *A. sinapina* and *A. ostoyae*, of which the latter is most common, accounting for over 85 per cent of collections (Mallett 1992). *Armillaria ostoyae* is also the most common species found in the boreal forest, even though it may or may not be the most aggressive (LaFlamme 2010). *Armillaria sinapina* is considered a weak pathogen and primarily occurs on broadleaf hosts in British Columbia and in Alberta, and rarely on coniferous hosts (Mallett 1992; Morrison 2011). This review focuses only on *A. ostoyae*.

Armillaria ostoyae inhabits the soil and subterranean parts of trees. It spreads to lateral roots of live trees by means of its subterranean rhizomorphs (brown to black shoestring-like structures) produced during the saprophytic phase of the fungus. The saprophytic phase inhabits woody tissue on cut stumps or dead trees which provide a food base for sustaining the fungus, and from which its rhizomorphs are produced and grow radially from the food base. The fungus can persist for decades on this food base as a normal component of many ecosystems. As the rhizomorphs grow they may attach to healthy roots and penetrate the bark. If successful, the fungus colonizes the root and initiates infection by establishing a white fungal mycelium (referred to as a mycelial fan) in the cambium. This infection disrupts water and nutrient absorption by the tree, and in turn affects its growth. As the pathogen progresses further into the tree it causes root decay and subsequently the decay may spread into the base of the tree stem. When this occurs, the tree is prone to windthrow, either by uprooting or by stem breakage. The tree usually dies after 20 or more years of Armillaria infection (LaFlamme 2010).

Trees of all ages can be infected, but there is wide variation in expression of disease symptoms, the temporal development of pathogenicity, and in the epidemiology of the fungus. The development of Armillaria root disease may kill small young trees within a few months, but in older trees, mortality may occur after decades of infection (Mallett 1992). *Armillaria ostoyae* has been described as an aggressive opportunistic pathogen waiting for stress conditions to develop in trees. The pathogen can remain saprophytic on site in dead roots and stumps for decades until conditions become conducive for successful infection of roots.

Visible symptoms of Armillaria root disease include foliar discoloration, stunting of tree growth, stress crop of cones, resinosis around the lower stem and root or butt rot or both. Crown foliage may appear visibly thin. Basidiocarps (mushrooms) of the fungus are often found at the base of dead or dying trees and stumps in late August or early September. Dead and dying trees can be found in “disease centres”, or they can occur as individual dead or dying trees scattered throughout the stand. Disease centres in mature stands may appear as openings in which many infected trees have died and have fallen over during many years (Shaw and Kile 1991; Mallett 1992; Morrison and Mallett 1996; Mallett and Volney 1999).

Numerous surveys have been conducted in young coniferous stands to assess mortality caused by Armillaria root disease. Surveys in immature lodgepole pine in Alberta and British Columbia have shown that Armillaria is a major cause of tree mortality, especially in the 5 to 10 year age class, and that mortality may continue to at least age 25 (Mallett 1992; Ives and Rentz 1993; Cleary *et al.* 2008; Heineman *et al.* 2010; Mather *et al.* 2010). Morrison *et al.* (2000) have noted that mortality

caused by *A. ostoyae* in juvenile stands can be as high as 2 per cent per annum, with cumulative mortality reaching 15-20 per cent by age 20 years. Similar surveys in young lodgepole pine stands in interior British Columbia reported mortality in the range of 2.3 per cent to 22.8 per cent, and that the risk of Armillaria presence increased from west to east and with increasing soil moisture regime (Heineman *et al.* 2010).

Morrison (2011) studied the temporal and spatial development of *A. ostoyae* in young Douglas-fir plantation trees (7 to 15 years after establishment) in interior British Columbia and recorded cumulative mortality 35 years after planting as high as 30.5 per cent. He showed that the time from first root infection until tree death increased from an average of 2 years at age 7, to about 11 years at age 25, and then to 20 years at age 32. Tree mortality began close to the primary inoculum at a nearby food base or colonized stump. Rhizomorphs were the cause of nearly all infections that were located on or close to the taproot or root collar. Tree mortality declined with age: it was postulated that the decline in mortality rate results from increasing host resistance that includes resinosis, callusing of lesions, formation of adventitious roots, and to reduction in inoculum potential. The host tree-pathogen system was described as a dynamic process with host defences being overcome at one stage and being re-established at another, resulting in a high percentage of trees with basal root lesions. The Armillaria pathogen is viable in many of these lesions but remains in check by host resistance. However, this equilibrium can be upset in favor of the pathogen by a number of abiotic and biotic factors (e.g., fire, drought, insect, disease) (Wargo and Harrington 1991; Kliejunas *et al.* 2009). The result can be an active Armillaria root disease centre with dead and dying trees (Morrison and Mallett 1996; Morrison 2011).

Woods *et al.* (2010) noted that there is at present no conclusive study linking climate change to increased root disease activity in British Columbia. They point out, however, that drought stress caused by climate change predisposes host trees to root diseases, and that Armillaria root disease will increase significantly for interior forested areas as these sites become warmer and drier. Other reviews (Boland *et al.* 2004; Moore and Allard 2008; Kliejunas *et al.* 2009; Klopfenstein *et al.* 2009; Sturrock *et al.* 2011) report that Armillaria becomes more aggressive as host trees become stressed from rising temperatures and decreasing moisture. They suggest that climate change will increase the pathogen's incidence and spread. Climate change may also alter the relative fitness of various mycorrhizal fungi and other soil microbes that currently help to suppress root disease (Kliejunas *et al.* 2009). Some of these host-pathogen changes will be difficult to predict because of diverse pathogenic responses in relation to different climatic scenarios, the rise in atmospheric carbon dioxide, and increased growth of tree roots (Kliejunas *et al.* 2009).

Armillaria root disease may have interactions with bark beetle and defoliator species and fire. For example, trees weakened by bark beetle attacks or from defoliators may induce stress and trigger development of root infection, or the reverse situation may also occur (Parker *et al.* 2006; Kliejunas *et al.* 2009; LaFlamme 2010). Mallett and Volney (1990) reported a significant association between Armillaria root disease and jack pine budworm damage on jack pine in Saskatchewan. Fire may inhibit Armillaria root disease on or near the soil surface, but prescribed fire had no affect on Armillaria populations at depths of 30 cm (Parker *et al.* 2006).

4.3.12 Tomentosus root rot (*Inonotus tomentosus* Karst.)

Tomentosus root rot is a fungal disease that occurs across Canada and causes root and butt rot mainly in spruce (e.g., white, black, Engelmann, Norway). It may occasionally be found infecting other conifers such as balsam fir, subalpine fir, jack, lodgepole and whitebark pines and Douglas-fir (Hepting 1971; Myron *et al.* 1994; Allen *et al.* 1996; LaFlamme 2010). Studies in white spruce stands in Saskatchewan and Manitoba indicated that this pathogen was the cause of “stand opening disease” and was associated with 80 per cent of the dead trees and 58 per cent of the diseased trees in these openings. The disease organism caused considerable losses in the white spruce stands, and growth reduction began about 15 years prior to tree death ((LaFlamme 2010). Similar pattern of infection was observed in a 50-year old white spruce plantation in Quebec where 85 per cent of the trees were infected. Tree mortality occurred 12 to 15 years after growth reduction had begun. Dissection of some of these trees indicated a much more advanced pattern of decay. Stress created by competition appeared to be a predisposing factor of *I. tomentosus* (LaFlamme 2010).

Lewis (1997) and LaFlamme (2010) have provided reviews of the impact and epidemiology of *I. tomentosus*. The fungus spreads by root contacts and also by spore infections that can initiate new disease centres. Lewis (1997) noted that the tree volume yields of infected trees are reduced in four ways: mortality, increased

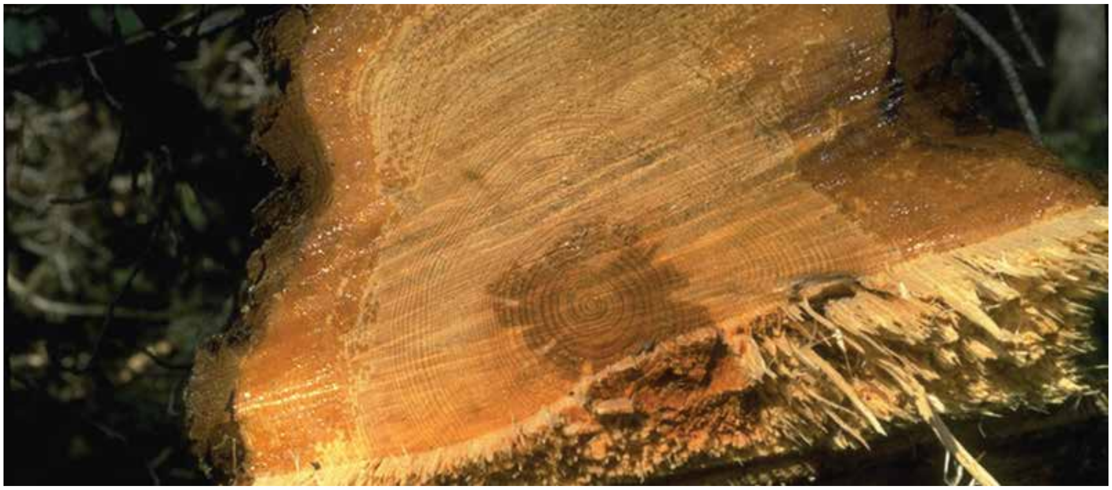
windthrow, butt cull due to lower stem rot, and to growth reduction. This pathogen appears to cause a more gradual tree decline than does *A. ostoyae*, and that the impact of the disease is dependent upon the size of root system. Crown symptoms of foliage chlorosis may first appear when at least 50 per cent of the roots are infected with advanced decay. Growth reductions during the last 5-year growth period on infected black and white spruces have been estimated at 5 per cent and 12 per cent, respectively. Trees growing in a stand with a high density of spruce appear more likely to be infected at an earlier age because of the greater potential of root contacts. Hence, decline may be more rapid in these trees relative to healthy trees. Severity of disease, expressed as butt rot, may also be greater in dense stands.

Studies by Lewis (1997) in east-central British Columbia of white spruce with light to severe classes of infection indicated declines in volume increment, primarily in the most severe class, and the decline was significant during at least the last 15 years of stem growth. Earliest stages of infection were shown to develop in the heartwood of larger roots, eventually advancing into the sapwood. Site and soil characteristics were related to the incidence of *I. tomentosus* in the Sub-Boreal Spruce in central British Columbia. The most important variables postulated to be influencing the disease appeared to be oxygen availability as regulated by moisture and slope, rooting depth and the number of root contacts (Bernier and Lewis 1997).

Studies of insect relationships with tomentosus root rot infected white spruce trees have involved the spruce beetle and spruce budworm. In British Columbia, observations of spruce beetle attack incidence indicated that the beetle may actually avoid severely infected trees. However, the general consensus was that tomentosus root disease helps to maintain endemic levels of the spruce beetle (Lewis and Lindgren 2002). LaFlamme (2010) reported that tree mortality in old spruce plantations in Quebec had been attributed to the spruce budworm, however, he questioned this and suggested that the cause of mortality was more likely due to tomentosus root rot, but that the budworm defoliation effects accelerated the mortality.

The fruiting bodies of *I. tomentosus* are usually less than 10 cm, are shelf-like, are stalked and occur on the ground around infected trees or on dead roots and at the base of infected stems. These fruiting bodies are annual and commonly develop in August and September. The earliest stages of decay are characterized by red-brown discoloration in the heartwood (incipient decay). Advanced decay may show larger elongated or rectangular spindle-shaped pits that weaken the stems and make them more prone to windthrow (Allen *et al.* 1996). The fungus is known to survive in stumps for 30 years or more (LaFlamme 2010).

Trees under stress from various causes are likely to increase the incidence and spread of this pathogen. Boland *et al.* (2004) in Ontario predict a moderate increase of tomentosus root disease with climate change, that the fungus will benefit from warmer temperatures and drought stress, and that the increased frequency of wind and heavy rain will make forests more susceptible to breakage and mortality, as well as to decay organisms. Wood *et al.* (2010) concur with this view for this pathogen in British Columbia spruce forests.



4.3.13 Red ring rot (*Phellinus pini* [Brot. Fr.] Ames)

Red ring rot fungus in western Canada infects many coniferous hosts including white, black, and Engelmann spruces, jack and lodgepole pines, balsam fir, tamarack and Douglas-fir, and elsewhere in North America, it is known to attack several hardwood species (Myron *et al.* 1994; Allen *et al.* 1996). This pathogen is classed as a heartwood decay-causing disease and produces a white pocket rot in the lower stem of its hosts. It does not usually kill its hosts but performs as a heart rot, and is considered one of the major causes of volume loss in conifers in North America. Several early surveys in Alberta of stem decays and stain-causing fungi have indicated that *P. pini* is often the major cause of cull and stem decays and stains of Engelmann, white and black spruces, lodgepole and jack pines, Douglas-fir and tamarack (Hepting 1971).

Red ring rot is not usually considered a butt rot, but often causes considerable volume loss to the middle and upper parts of the butt log and may also advance higher up the stem (Myron *et al.* 1994). While the most extensive decay occurs in the trunk, the pathogen commonly extends into the tree base and roots (Manning 2007).

Infection occurs through live branches, stem wounds and broken tops, and usually when conditions are wet and cool in late fall and early spring (Allen *et al.* 1996). Most active spore production occurs in the spring and fall. Wind, and possibly moisture disperse spores. Once infected, a reddish stain develops in the heartwood and is incipient at this stage and contributes little toward reduction of wood strength. The decay can progress from the heartwood to sapwood and cause tree death. Sporophores (spore-producing structures) of the pathogen are produced on living trees and are variable in size and appearance. They often develop adjacent to branch stubs and usually along the length of the infected bole (Allen *et al.* 1996).

No specific climate change relationships were found for red ring rot. However, it is likely that drought stress and other forest disturbances will help to promote infections or allow more rapid development of the pathogen. Increased wind activity in the spring and fall will enhance the likelihood of successful spore dispersal. Also, increased storm activity, resulting in broken stems and branches, and other stem wounds, will provide an increased number of potential infection sites.

4.3.14 Stalactiform and comandra blister rusts (*Cronartium coleosporioides* Arthur and *C. comandrae* Peck)

Stalactiform and comandra blister rust diseases are caused by rust fungi. Both species infect hard pine species including lodgepole, jack, ponderosa and Scotch pines. Both have similar complex life cycles involving five spore stages, and both require alternate herbaceous plant hosts to complete life cycle development. Alternate host plants for stalactiform blister rust include Indian paintbrush and cow-wheat, and for comandra blister rust, the alternate hosts are bastard toadflax and northern bastard toadflax (Hiratsuka 1987; Allen *et al.* 1996). Both rust species occur widely in Alberta within the ranges of pine hosts, but their distributions may be restricted to sites where pine and alternate hosts co-exist. Both rusts attack pine hosts of all ages but cause most mortality on seedlings and saplings.

The life histories and epidemiology of both rusts are similar. Basidiospores produced on alternate host plants are airborne and infect healthy young pine shoots in late summer. Cankers develop from these infections within two years. As the cankers grow, they produce characteristic powdery orange-colored aeciospores from late May to the middle of July. These spores become windborn and are dispersed to leaves of alternate host plants where they may initiate new infections. They develop through other spore stages before again producing basidiospores. The development period requires one year (Hiratsuka 1987; Allen *et al.* 1996).

Stalactiform blister rust

Comandra blister rust

The life cycle of the two rust species are strongly influenced by environmental conditions, particularly moisture and humidity during the growing season. When the optimal conditions are met, peaks in new rust infections or "wave years" occur, which may, on average, occur about once every 10 years (Woods *et al.* 2010). Both stalactiform and comandra blister rusts require cool, moist conditions in mid to late summer for optimum infection potential. Woods *et al.* (2010) have suggested that the frequency of wave years appears to have increased in recent years in interior British Columbia.

Cankers of stalactiform rust may form in the bark of branches and on the stem. On trunks of more mature trees, cankers are diamond-shaped, often sunken and grow faster vertically on the stem than tangentially. Most mortality occurs on seedlings and young saplings as a result of the cankers completely girdling the stem. The cankers grow annually up the stem as long narrow lesions and are often several meters in length. Though they may not kill the tree, the cankers can result in considerable stem deformation and resinosis (van der Kamp 1994). Some trees may have multiple bole infections.

Canker development from comandra blister rust infections develop similarly as that of stalactiform rust, except that growth of comandra in the bark is much faster tangentially, and somewhat slower vertically on the stem. Consequently, bole

infections by comandra rust girdle and kill trees much more quickly. Most comandra rust infections are restricted to the lower crown of young lodgepole pine (van der Kamp 1994). Geils and Jacobi (1990) noted that the development of comandra blister rust infections on lodgepole pine occurred throughout the lower 80 per cent of the crown of sapling trees, and were uncommon at the top of the crown. Cankers on branches tend to advance toward the main stem. These authors noted that the number of years required for a canker to girdle a host tree was about equal to the stem diameter in centimetres. The incidence of both rust species increased in young lodgepole pine stands after thinning treatment (Heineman *et al.* 2010).

The influence of climate, site, location, and stand treatment factors on damage to young lodgepole pine in southern interior British Columbia was examined by Heineman *et al.* (2010) and Mather *et al.* (2010). They reported that stalactiform was present on 22 per cent of the sites examined and that 78 per cent of the infected trees were rejected as potentially productive. According to the risk model they used, the risk of stalactiform rust presence increased with latitude, elevation, stand age, pine density, a temperature factor, and also where mechanical site preparation or pruning treatments had been applied. Comandra rust was present on 21 per cent of the sites and 96 per cent of the infected trees were rejected as potentially productive trees. Risk of this rust increased with decreasing slope and with increasing latitude, northness, eastness, and with stand age. Pruning treatment increased the risk and brushing decreased the risk. These projected risks are consistent with the moist, cool summer conditions that the rusts require to successfully infect lodgepole pine. The two rust pathogens require these conditions in late spring to early summer to coincide with the period of spore release (Heineman *et al.* 2010). The data also suggested that recent hot, dry summer conditions resulted in drought–stressed trees, which may have increased their susceptibility to rust infections.

Studies by Ives and Rentz (1993) in west-central Alberta in immature lodgepole pine stands indicated relatively low incidence of infections by stem rusts (stalactiform and comandra blister rusts were not differentiated in this study) of mostly <1 per cent; the data suggested there was an increasing trend of infection with stand age class up to 25 years.

In studies by Mather *et al.* (2010), both stalactiform and comandra rusts were dominant mortality factors identified in 66, 15-30-year old lodgepole pine plantations that had been declared as free-to-grow by provincial standards. However, the study revealed that 27 per cent of the plantations no longer met the free-growing criterion. Their study showed that free-growing and stocking status are linked to climatic conditions, and that shifts in precipitation and winter temperature with climate change could enhance damage and reduce yield of lodgepole pine. It is possible that climate may become too hot and dry in some areas for rust pathogen spread and infection, thus acting negatively on rust diseases (Desprez-Loustau *et al.* 2006).

The potential influence of atmospheric carbon dioxide concentrations on rust pathogens is largely unknown. Some pathogens have shown more rapid growth rate following invasion of host tissue, and pathogen fecundity and aggressiveness have increased under elevated carbon dioxide levels (Kliejunas *et al.* 2009; Pinkard *et al.* 2011). Ecological interactions with other species, especially insects, may affect the severity of rust disease impact such as in the association of pitch moths attraction to resinosis associated with rust cankers (Rocchini *et al.* 1999). These interactions may have direct or indirect climate influences and biotic responses. In addition, lodgepole pine trees severely cankered by comandra rust have lower sugar levels, which increase their susceptibility to bark beetles such as the mountain pine beetle (Kliejunas *et al.* 2009).

4.3.15 White pine blister rust (*Cronartium ribicola* J.C. Fischer)

White pine blister rust (WPBR), an invasive introduced rust disease of Asian origin attacks all five needle or soft pine species in North America (Zeglen *et al.* 2009). In Alberta, infections by this pathogen occur widely throughout the distribution of the two native soft pine species, whitebark pine (*Pinus albicaulis*) and limber pine (*P. flexilis*) (see Section 5.1 of this report for more detailed information on the genetic resistance of white pine blister rust). It is the most serious of all tree rust diseases. *Cronartium ribicola* is an obligate parasite that requires live host plants to survive. Its life cycle development requires two hosts (heteroecious) and the rust is macrocyclic in that it has five spore stages: pycnial and aecial on *Pinus* and uredinial, telial and basidial on the alternate host *Ribes* species (current and gooseberry). In northern Idaho, alternate hosts also include *Pedicularis* spp. (housewort) and *Castillega* spp. (paintbrush).

Infection on the pine host begins when wind-dispersed basidiospores from alternate host plants are transported in autumn to pine foliage and germinate. The pathogen enters through stomata and subsequently colonizes the needle tissue, then progresses into phloem and bark tissues. Infection may occur on the main stem or commonly on branches, and branch cankers may often advance toward the main stem (Zeglen et al, 2009; Geils *et al.* 2010; Kliejunas 2011). Visible symptoms appear after a 3-year latent period when the infected tissue swells forming a visible canker, which blisters and contains orange aeciospores. The aeciospores are wind-dispersed in the spring and land on leaves of alternate host plants where they infect, again through stomata. Branch and stem cankers may be diamond-shaped, may have pitch oozing, roughened bark, and expand annually. Stem cankers grow faster vertically than circumferentially (Zeglen *et al.* 2009). Branch and stem infections ultimately result in “red flagging”, branch dieback, reproductive failure, and tree mortality (Kliejunas 2011; Sturrock *et al.* 2011). Areas of high mortality of whitebark pine and limber pine have resulted from the synergistic effects of WPBR, drought, increasing temperatures, and mountain pine beetle attacks (Kliejunas 2011; Sturrock *et al.* 2011).

Infections of *C. ribicola* have typically occurred in “wave years” when ideal environmental conditions of temperature and moisture prevail, which directly affect pathogen reproduction, spread, infection and survival. *Cronartium ribicola* is a cool weather disease, with basidiospore germination and infection occurring within the temperature range 0 to 20° C. Spread of infecting spores is driven mostly by moisture, air temperature and air circulation. Basidiospore germination on the pine host requires 48 hours of 100 per cent relative humidity and temperatures less than 20° C. Therefore, changes in temperature and the frequency of 100 per cent air humidity will influence the epidemiology of the WPBR pathosystem (Kliejunas 2011; Sturrock *et al.* 2011).

Climate is currently not considered a limiting factor in WPBR distribution in British Columbia, and probably also in Alberta; the only effective limits of its spread may be isolation from suitable *Ribes* species (Kiejunas 2011). In western United States under a future climate change scenario of warmer/drier, Kliejunas (2011) considers the risk of increased disease damage to be low with a moderate risk potential, and similarly under a future scenario of warmer/wetter. Sturrock *et al.* (2011) predict a similar decrease in impact of WPBR under a warmer/drier scenario with a low level of uncertainty, and under a warmer/wetter scenario, they predict no change in impact with a moderate level of uncertainty. In Ontario under a future warming climate, Boland *et al.* (2004) anticipate a decrease in WPBR disease establishment, rate of disease progress and potential duration of an epidemic on eastern white pine.

4.3.16 Western gall rust (*Endochronartium harknessii* [J.P. Moore] Y. Hiratsuka)

Western gall rust disease occurs widely across Canada and infects lodgepole, jack and ponderosa pines in natural forests in western Canada. It occurs throughout the range of these host species. The rust infects trees of all ages and causes woody swellings (globose galls) on branches and stems. During late May to July, orange-colored spores form on blisters beneath the bark of galls. The spores are dispersed by wind or rain and land on young elongating shoots of pine hosts where infection takes place. This rust does not require an alternate host plant, so infection occurs from pine to pine, thereby shortening the life cycle, compared to other stem rusts. Small galls appear a few months after infection but do not produce spores until one year later (Hiratsuka 1987; Allen *et al.* 1996). The galls are perennial and enlarge each year, and may produce spores (inoculum) every spring for many years.

Galls formed on the main stem may cause stunting of the trees, stem deformity and tree mortality, especially on young trees. Branch galls can have little effect on tree growth; however, they contribute annual sources of inoculum. Rust infections occasionally occur in wave years when climatic conditions are optimal for spore dispersal, infection and germination. For example, in a survey of a 7-year old lodgepole pine plantation in northern British Columbia, 49.1 per cent of trees were infected with western gall rust, of which 90 per cent of all infections occurred in a single year (van der Kamp et.al. 1995). In this survey, average percentage of stem galls varied from about 3 per cent to 10 per cent and the number of gall rust infections per tree was linearly related to tree height. Blenis and Li (2005) artificially inoculated young lodgepole pine and showed that the number of gall infections decreased with tree age from 2 to 10 years, suggesting that tree resistance increases as trees age. Many trees with stem galls do survive; in one study, 45 per cent of the trees with stem galls were expected to survive to age 80 (Wolken *et al.* 2006).

In surveys of biotic agents causing mortality of young 15-30 year old lodgepole pine stands in interior British Columbia, Heineman *et al.* (2010) reported that western gall rust was present on 100 per cent of all sampled sites and affected about one-quarter of all pine stems. They considered that over half of the occurrence of western gall rust-infected trees was serious enough to reject as potentially productive trees. Their model indicated increasing risk of gall rust presence with increasing latitude and longitude, with decreasing soil moisture, lower slope position, and with decreasing northness of aspect. There was also a higher risk of presence of gall rust on unburned versus burned sites, and on sites after juvenile spacing, brushing or pruning treatments. Some increased risk was also associated with higher temperature and decreasing degree-days above 5° C. A positive correlation between the presence of western gall rust and an increasing moist climate was also reported by Mather *et al.* (2010).

In west-central Alberta, Blenis and Duncan (1997) surveyed 26 to 32-year-old lodgepole pine stands that had been thinned at ages 15 to 23 years. Their results indicated that 43 per cent of all trees had stem galls, and that the number of stem galls increased with tree age and height, reached a maximum at age 18, then declined. Similar surveys of immature lodgepole pine stands on cutover areas in west-central Alberta showed that percentage trees with stem and branch galls increased steadily from age 5 to 25 years, reaching almost 70 per cent on some sites (Ives and Rentz 1993). Mather *et al.* (2010) concluded that the various surveys in British Columbia and Alberta all agree that western gall rust is the most important disease in young unthinned lodgepole pine stands. A volume loss of 15 per cent of lodgepole pine was estimated due to western gall rust over a 20-year period in west-central Alberta (Bella and Navratil 1988).

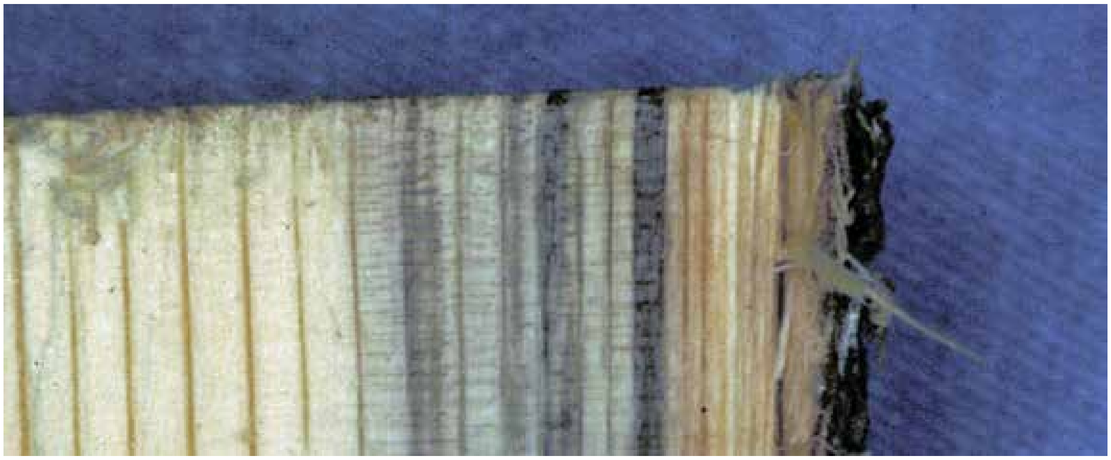
In two lodgepole pine progeny trials established at higher elevations in west-central Alberta, Yang *et al* (1998) reported that, at age six, mean family western gall rust infection at one site was 24.9 per cent (range 0-76 per cent) while at the second site, mean family infection was 1.6 per cent (range 0-27 per cent). At the first site only 1 per cent of families were uninfected while 73 per cent of families were free from infection at the second site. Infection severity followed a similar pattern with lower severity at the second site. Strong site X family interactions for western gall rust infection occurred across the sites which, along with the differences in infection frequency and severity, suggest contrasting patterns may be the outcome of environmental or genetic causes or both. Both individual and family estimates of heritability for western gall rust infection were comparable to those of other studies for lodgepole pine for both individual and family at $hi^2 = 0.41$ and $hf^2 = 0.53$ at the first site and at $hi^2 = 0.14$ and $hf^2 = 0.23$ at the second.

Patterns of western gall rust infection based on 15-year measurement of four field trials established with Alberta populations of lodgepole pine, jack pine and their hybrids were studied by Rweyongeza and Yang (2005a). For all four sites, western gall rust infection was greatest for lodgepole pine and least for jack pine. Across sites (three foothills and one boreal) average infection was 32.7 per cent for lodgepole pine, 24.7 per cent for hybrids and 7.9 per cent for jack pine. Variation in infection rates among populations across sites and genotype by site interaction were significant. Among population infection rates for lodgepole pine ranged from 69.1 per cent (a high elevation population from the Highwood Pass) to 7.9 per cent for a population from the Cypress Hills. For jack pine, the range was 29.2 per cent (Wandering River population) to 0.0 per cent for populations from the Stoney Mountains and south of Ft. Vermillion. The hybrid range of 43.0 per cent to 2.5 per cent was intermediate but overlapping with that of the parent species.

Heineman *et al.* (2010) predict that lodgepole pine mortality is likely to increase as environmental factors such as drought predispose trees to pathogens such as western gall rust. They suggest that increasing temperature of the warmest and coldest months made strong contributions to risk assessments. Cool moist conditions during the growing season and especially during late spring, are necessary requirements for successful spore release, dispersal and infection on young host shoots (Hiratsuka 1987; Woods *et al.* 2010).

Rising atmospheric carbon dioxide levels may also influence western gall rust infection, but studies of this aspect are unknown (Kliejunas *et al.* 2009; Pinkard *et al.* 2011). Several insect associations with rust galls are known and may have direct or indirect ecological interactions that can affect the severity of gall rust impact (Roccini *et al.* 1999; Kliejunas *et al.* 2009).

4.3.17 Atropellis canker (*Atropellis piniphilia* [Weir] Lohman & Cash)



Atropellis canker is a fungal pathogen that attacks primarily lodgepole pine in Alberta and British Columbia, but may occur on jack and ponderosa pines. It is considered an important disease of lodgepole pine and occurs sporadically over most of the range of this pine in Alberta, and has a high incidence of infection in several areas (Hopkins 1963; van der Kamp 1994). This pathogen causes perennial stem and branch cankers, which may occur on a high proportion of trees within a stand. There may be multiple cankers (e.g., up to 40 to 60) on severely infected trees. Trees 15 to 30 years old appear to be most susceptible.

Most stem cankers start as infections on undamaged bark in the vicinity of branch whorls. The canker develops into the bark and sapwood causing extensive resinosis, sunken areas, severe deformity of stem, and a blue-black stain in the sapwood and heartwood. Cankers that are centered around a branch stub, elongate at an annual rate of about 5 cm vertically and 0.6 cm tangentially, and potentially grow to 3 m in length (Hopkins and Callan 1992). Most cankers develop below the live crown (van der Kamp 1994).

There may be two types of fruiting structures produced on the cankers; pycnidia and apothecia. Pycnidia usually appear first in young cankers, prior to apothecia and are globose in shape and produce conidia in a mucilaginous mass when wet. Apothecia are stalked, black and saucer-like, and form singly or in groups in the center of the canker. The apothecia are present throughout the year and produce ascospores, which are dispersed by wind or rain, and are responsible for spreading the disease (Hopkins 1963; Allen *et al.* 1996).

Tree mortality can occur when cankers become large and expand tangentially to encircle the stem, or when multiple cankers occur. Stem growth reductions are variable, depending upon the severity and longevity of canker development (Mather et al 2010). The presence of the sunken bark areas, resinosis and blue-black stain may interfere with manufacturing processes such as bleaching, debarking or penetration of preservatives. Infections and canker development may be most severe in dense stands, and especially those stands growing on dry sites (Hopkins and Callan 1992; Allen *et al.* 1996). High levels of infection have been observed after fire in lodgepole pine regeneration that was infected by residual diseased trees that survived the fire. Such infected regeneration may result in stand stagnation. No infections have been found on tissues younger than 5 years, and new infections are rare on tissues older than 40 years. However, large stem cankers 40 to 50 years old have been found occasionally in vigorous trees (Hopkins and Callan 1992). Atropellis canker tends to be more common in unthinned stands than in thinned stands (van der Kamp 1994).

Studies by Hopkins (1963) indicated the importance of high precipitation or extended periods of high humidity required to swell apothecia and to allow ascospore release. The ascospores are disseminated by wind for distances up to 100 m. However, because the apothecia are present throughout the year, spore release, dispersion and infection appear not to be restricted to seasonal time periods, and may therefore benefit from increased storm and wind events for initiating new infections. Desprez-Loustau *et al.* (2006) suggested that the climatic conditions necessary for ejection and germination of ascospores could have negative effects on some stem diseases, suggesting uncertainties for predicting climate change effects.

The incidence of atropellis canker has been predicted to increase in densely stocked stands, and especially on drought-stressed sites (van der Kamp 1994). In the southern interior of British Columbia, Heineman *et al.* (2010) surveyed 15 to 30 year old lodgepole pine stands and reported this disease was present on 27 per cent of the sites surveyed. Percentage of infected trees at different sites ranged from 0.2 per cent to 29.1 per cent. Application of their model suggested that the risk of Atropellis increased with increasing latitude and decreasing northness and eastness, and was higher where broadcast burning and juvenile spacing had been applied. Increasing mean temperature of the coldest month was associated with increasing Atropellis risk. These authors predicted that as climate change progresses, young lodgepole pine stands will be at a high risk of continuing damage by stem diseases generally. Both increasing temperatures of the warmest and coldest months appear to favor increasing risk of Atropellis. Kliejunas *et al.* (2009) have suggested that climate change may increase the incidence of many canker-causing diseases, partly because they benefit from heat and drought stressed trees. Specific information on possible relationships between Atropellis and climate change are lacking. As well, the possible influence of atmospheric carbon dioxide on Atropellis disease has not been examined (Pinkard *et al.* 2011).

4.3.18 Pine needle cast (*Lophodermella concolor* [Dearn.] Darker)

Pine needle cast is a virulent fungal pathogen causing disease of needles of lodgepole, ponderosa, jack and Scotch pines. Several species of needle casts infect lodgepole pine in Alberta, of which *L. concolor* appears to be one of the most common and damaging. Two other common species of needle casts are *Elytroderma deformans* and *Davisomycella ampla* (Hiratsuka 1987). However, *L. concolor* has been reported most often, and has generally caused severe infections over large areas, particularly along the Alberta foothills, Rocky Mountain National Parks, Cypress Hills, and occasionally in the north western part of the province (Cerezke *et al.* 1991; Cerezke and Gates 1992; Cerezke and Brandt 1993).

Current-year needles are infected during the spring and summer; the infected needles turn reddish-rust in the following spring, and by July they fade to a straw color. At this stage spore-producing fruiting structures (apothecia) are produced on the dead needles. The dead needles are shed about this time resulting in partly defoliated branches. The fruiting bodies appear as shallow depressions on infected needles and may be difficult to observe since they are the same straw color as the needles. The apothecia bodies mature only on the current-years infected needles. Release of the ascospores from the apothecia requires periods of high humidity, and the spores are disseminated by wind mostly over short distances. Infection likely takes place through needle lenticels. This completes the 1-year life cycle of *L. concolor* (Hunt 2000).

During periods of severe infection, and especially if present for more than one year, considerable defoliation and growth reduction may result especially on young trees. Tree mortality may also occur, although it is relatively uncommon (Cerezke and Gates 1992). Trees of all ages may be affected.

Epidemics of *L. concolor* tend to be sporadic but can be widespread and severe in a year following a wet spring. Hunt (2000) reported that a severe epidemic occurred in interior British Columbia during 1993 and 1994 following a series of wet springs. Conditions that are optimal for fungal sporulation and infection are critical; a high humidity is a major requirement. Needles are susceptible for infection only during the period from spring bud break until maturity (Hunt 2000).

Many pathogens causing needle diseases such as *L. concolor* are sensitive to precipitation and humidity and their rates of reproduction, spread and infection tend to be greater when conditions are moist (Sturrock *et al.* 2011). Hence, predictions of climate change impacts on this foliar pathogen are highly uncertain. Increased drought could reduce the severity and occurrence of the disease (Kliejunas *et al.* 2009; Woods *et al.* 2010). However, increases in precipitation and in overnight minimum temperatures and the potential for greater overwinter survival of foliar pathogens could be favourable for spread of this disease (Woods *et al.* 2010). Elevated concentrations of atmospheric carbon dioxide can increase the growth and pathogen fecundity, and have an influence on foliar disease interactions (Kliejunas *et al.* 2009; Pinkard *et al.* 2011). The incidence and severity of foliar diseases in general are likely to increase if late winter and spring become wetter and warmer, but may decrease if summers become drier (Kliejunas *et al.* 2009).

In young lodgepole pine sites in interior British Columbia, *L. concolor* was present on 45 per cent of sites surveyed, and the average proportion of affected pine ranged from 1.1 per cent to 50 per cent (Heineman *et al.* 2010). Their logistic model suggested that risk of pine needle cast increased with increasing elevation and soil moisture, with decreasing stand age and pine density, and with an increasing temperature factor and number of frost-free days. Risk also increased with broadcast burn and juvenile spacing, but brushing and pruning decreased the risk. Site, stand treatment and climatic factors contributed more strongly than location factors.

4.3.19 Dwarf mistletoe (*Arceuthobium americanum* Nutt.)

The biology of dwarf mistletoe on lodgepole and jack pines is described in Section 5.3 of this report. This section therefore only covers notes primarily on climate change relationships. The damage caused by *A. americanum* results in increased tree mortality and susceptibility of its tree hosts to attack from other pathogens and insects (Hawksworth and Wiens 1970). Heavy brooms that are often present can add to the stress of the host tree. Infected trees stressed by drought are likely to die more quickly than noninfected trees and are predisposed to bark beetle, woodborer attacks and root pathogens (Mallett and Volney 1990; Kliejunas *et al.* 2009). Dieback of infected branches may reduce inoculum and spread of the disease (Hawksworth and Wiens 1996; Brandt *et.al*. 2004b).

Climate limits the range of *A. americanum*, and a warming of temperatures will likely result in extensions of its range northward and to higher elevations (Brandt *et al.* 2004b; Woods *et al.* 2010). Heineman *et al.* (2010) reported that *A. americanum* was present on 9 per cent of the sites they surveyed in young lodgepole pine stands in interior British Columbia. Their model suggested that increasing risk of mistletoe was associated with decreasing latitude, elevation, slope and northness, and with increasing soil moisture and eastness. Risk of dwarf mistletoe was also associated with increasing growing degree-days, which are important because its pollen germination in the spring can be limited by late spring frosts. Boland *et al.* (2004) have forecasted an increase in *A. americanum* with climate change on jack pine in Ontario and a similar forecast was expressed for increased infections on lodgepole pine in interior British Columbia (Woods *et al.* 2010). These authors point out that the extensive mountain pine beetle-caused mortality of mature lodgepole pine has reduced some of the current risks of mistletoe infections and spread.

Wildfire has been an important factor in determining the distribution, abundance and spread of dwarf mistletoe in western North America. However, the natural fire-dwarf mistletoe ecological relationship has been partly disrupted by fire suppression. The disruption has subsequently resulted in an increase in the severity and distribution of dwarf mistletoe (Parker *et al.* 2006). Increased wildfire predicted with climate change may act as a controlling effect on the overall distribution and spread of this parasitic pathogen. The presence of dwarf mistletoe infections on tree crowns can also increase live-tree consumption during wildfires because the dead branches and brooms are highly flammable fuels. This behavior will tend to reduce a source of early re-infection in young regeneration post-fire because of a more complete elimination of residual live parasitic plants (Parker *et al.* 2006).

5.0 Review of Some Case Histories of Successful Programs and Approaches

5.1 Case History 1: White Pine Blister Rust (*Cronartium ribicola* J.C. Fisch.)

In Alberta both native white pine species, limber (*Pinus flexilis*) and whitebark (*P. albicaulis*) are in serious decline due to a number of human-caused and natural factors (ASRD and ACA 2007a, 2007b; Burns *et al.* 2008; Kearns and Jacobi 2007; Schoettle 2004; Smith *et al.* 2008; Stuart-Smith *et al.* 2002; Zeglen 2002). In this regard, on the 24th of October 2008, both pine species were recommended for listing as "Endangered Species" under Alberta's *Wildlife Act* and the listing was approved in 2009 (Fish and Wildlife Division 2010). The identified factors contributing to decline included fire exclusion and resulting competitive replacement by more shade tolerant tree species, MPB (*Dendroctonus ponderosae*), global climate warming and infections caused by the fungal pathogen, WPBR (*Cronartium ribicola*). Both pine species are highly susceptible to attacks by MPB, which has caused extensive mortality in the past as well as during the current outbreak (Alberta Forests, Lands and Wildlife 1986; Campbell and Antos 2000; Cerezke 1995; D. Lux, personal communication; Schwandt 2006; Zeglen 2002). Species recovery plans for both species are currently in preparation.

5.1.1 Taxonomy of pine susceptible species to WPBR

Limber pine and whitebark pine are members of the family Pinaceae in the genus *Pinus*. Three Subgenera within the genus *Pinus* are recognized and include *Strobus* (includes white or soft pines), *Ducampopinus* (pinyon, lacebark and foxtail pines), and *Pinus* (yellow or hard pines). “White or soft pines” are further subdivided into two Subsections (Sniezko *et al.* 2004) that include:

- **Subsection Strobi**: includes several soft pine species including the three North American commercial species, eastern white pine (*P. strobus*), western white pine (*P. monticola*), and sugar pine (*P. lambertiana*), as well as the non-commercial limber pine;
- **Subsection Cembrae**: includes the non-commercial whitebark pine. “Hard Pine” species such as lodgepole pine, jack pine and Scotch pine are classified in the Subgenus *Pinus* and have defining morphology of cone scales with a dorsal umbo and a sealing band; seed wings are usually articulate or easily removed; and needles possess two fibrovascular bundles per needle.

The defining morphology of the white or soft pines is that cone scales have a terminal umbo and no sealing band. Seed wings are absent, and there is one fibrovascular bundle per needle. Additional features are: needles occur in clusters of 5 and are in fascicles of 5; bark is generally smooth; wood is generally white and soft with smooth-walled tracheids and relatively few resin canals. Cones of limber pine tend to be long and narrow and open at maturity, where as cones of whitebark pine do-not open at maturity. Both species have large seeds that are collected and dispersed by Clark’s nutcracker (*Nucifraga columbiana*), which also utilizes the seeds as an important food source.

5.1.2 Distribution, infection and disease development of WPBR

Both whitebark and limber pines are long-lived species and have a long maturation period for reproduction, and therefore, may not adapt as readily as competitor species under changing climates. Limber pine, however, shows considerable drought tolerance, and this trait may enhance its potential to spread and survive under future climate changes, as suggested in ASRD and ACA (2007a). Warming trends could feasibly play a role in displacing whitebark pine as competing vegetation invades (ASRD and ACA 2007b). Also, as Schwandt (2006) has suggested, a warmer and moister weather pattern would likely favour white pine blister rust (WPBR) by creating more favourable conditions for “wave year” infections. Milder winters and drought periods predicted to occur with global warming also may alter fire regimes, add stress to trees, as well as favour higher overwinter survival of MPB and its survival at higher elevations. All of these changes could negatively impact these two pine species. A WPBR hazard model developed for Colorado also predicts that the rust disease incidence will be higher in areas with longer frost-free periods and warmer night time temperatures in September and higher levels of precipitation in July (Burns *et al.* 2008).

White pine blister rust is a non-native, invasive pathogen, possibly originating from Siberia, and was discovered in Alberta in 1952 on limber pine growing on Table Mountain (Bourchier 1952). Its presence and spread in the province has, therefore, continued unabated for over 50 years. During this period, WPBR has spread throughout most of the range of both pine species in the province and has caused variable infection levels, often exceeding 70 per cent in many areas of its northern range (Burns *et al.* 2008; Kinloch 2003). Surveys of infection in Alberta on limber pine were conducted in 1996 (Kendall *et al.* 1996) and again in 2004-05 (ASRD and ACA 2007a). Average tree mortality during the 2004-05 survey was about 27 per cent (range 7 per cent to 49 per cent) and was attributed mainly to WPBR, but also to MPB and possibly other causes. In Waterton Lakes National Park, the percentage mortality between the 1996 and 2004-05 surveys had increased from 46 per cent to 56 per cent, while the proportion of infected trees declined from 92 per cent to 82 per cent. Farther north in the Porcupine Hills area, the percentage tree mortality increased from 14 per cent to 43 per cent during the same survey interval, while the proportion of living trees sustaining infections increased from 55 per cent to 65 per cent (ASRD and ACA 2007a).

WPBR infects trees of all ages (Burns *et al.* 2008; Kearns and Jacobi 2007; Schoettle and Sniezko 2007). Pines are infected through needle stomata in late summer and early fall by basidiospores produced on infected leaves of its alternate plant host, *Ribes* species (*Pedicularis* spp. and a *Castilleja* sp. have also been identified as alternate hosts [Burns *et al.* 2008]). Following infection, the pathogen develops down the needle and into the bark where a canker forms. In subsequent years, blisters form at the margins of cankers and are packed with orange-colored aeciospores, which can then disperse to infect susceptible *Ribes* plants. WPBR cannot spread from pine to pine, but is transmitted to pine only via the basidiospore stage. Once infected, mature white pines are able to survive for several years, but typically experience decline in cone production resulting from the killing of upper branches where most cones are produced (Kearns and Jacobi 2007). Eventually, as the infections invade the main stem, tree mortality usually occurs. WPBR also readily infects seedlings, thus decreasing the opportunity for regeneration and natural stand renewal (Burns *et al.* 2008; Mahalovich and Dickerson 2004). Infected seedlings usually die within three years (Smith *et al.* 2008).

A recent discovery that the WPBR pathogen naturally hybridizes with comandra blister rust (*Cronartium comandrae*), which is a native rust that infects hard pine species in western Canada, raises some new concerns for the WPBR pathosystem on limber pine and needs further examination (ASRD and ACA 2007a; Joly *et al.* 2006).

WPBR infections on whitebark pine in Alberta extend throughout the range of this species (ASRD and ACA 2007b; Smith *et al.* 2008). In surveys conducted by Smith *et al.* (2008), percentage infection rates throughout the range of whitebark pine, ranged from an estimated 73 per cent near the Canada-US border to about 16 per cent in Banff National Park, with an increase to about 60 per cent in Jasper National Park and westward toward McBride, BC. This survey, conducted in 2003-04, examined whitebark pine seedlings and older trees in 170 plots scattered throughout the south-north range of the species: WPBR infections occurred in all but four of the plots (Smith *et al.* 2008). Results of a previous survey of WPBR conducted by Kendall (2003) in Waterton Lakes National Park indicated that infection levels had increased from 43 per cent to 71 per cent by 2003-04, and that tree mortality had increased from 26 per cent to 61 per cent during the same interval. Whitebark pine has been listed as the least resistant to WPBR of seven North American white pine species evaluated (Wilson and Stuart-Smith 2002; Zeglen 2002).

WPBR has been described as a cool weather disease having exacting environmental requirements for completion of its complex life cycle (Kinloch 2003). Critical requirements include cool, moist conditions of at least two days to produce, disseminate, germinate and establish basidiospores on pines. These spores are vulnerable to desiccation and sunlight and are usually transported only over short distances (up to 300 m), but may be carried over longer distances if ideal conditions prevail. Such ideal conditions, which are only partly understood, have contributed to “wave years” of infection when increased rates and intensities of infection have occurred (Burns *et al.* 2008; Kinloch 2003).

5.1.3 WPBR control and limber/whitebark pine restoration strategies

WPBR is now recognized as the most important threat to the long-term survival of white pine species in western North America (Kinloch 2003; Smith *et al.* 2008; Sniezko 2006; Geils *et al.* 2010). There is a long history of attempts to control and eradicate WPBR, with the focus primarily on the important commercial species (eastern white pine, western white pine and sugar pine) (Bingham 1983, King *et al.* 2010). Less attention, until recently, has been given to the non-commercial species such as limber and whitebark pines (Burns *et al.* 2008; Kinloch 2003; Sniezko 2006). Because of severe blister rust infections, along with MPB-caused mortality, some local extinction of these pine species are predicted to occur. Smith *et al.* (2008) and Zeglen (2002) have suggested that these extinctions will narrow the genetic gene pool and render attempts to breed WPBR-resistant whitebark pine more difficult. As well, extinctions will limit any management actions to maintain these communities in the future.

Attempts using different control methods against WPBR, such as *Ribes* eradication, antibiotics and silvicultural treatments including stand thinning, pruning, site hazard alignment and scribing of WPBR cankers, have all had some practical application in restricted situations, but for the most part they have only provided short-term mitigation effects (Bingham 1983; Burns *et al.* 2008; Kinloch 2003; Schwandt 2006). In the Rocky Mountain National Parks, Parks Canada has initiated a trial program using prescribed fire in high elevation sites to provide exposed soil for Clark’s nutcracker to cache seeds and to decrease fire exclusion in selected whitebark pine habitats. This program is meant to assist restoration and conservation of these sites (Stuart-Smith *et al.* 2002; Zeglen 2002). A conservation

strategy plan has also been prepared for the restoration of whitebark pine for the Rocky Mountain National Parks and promotes a holistic approach for whitebark pine ecosystems with multi-agency cooperative input (Wilson and Stuart-Smith 2002). As a consequence of this restoration strategy, seed conservation collections of both limber and whitebark pines have been made from apparent rust-resistant trees to build seed reserves and include in rust resistance screening trials. Once seed reserves are sufficient, putatively resistant stock from these parents will be grown for restoration outplanting on selected sites. Some initial whitebark planting in Waterton Lakes National Park using putatively resistant stock has occurred with seedlings sourced from Glacier National Park, MT (pers. comm. Cyndi Smith). Additionally, phenotype-identified rust-resistant parent trees are being protected for cone production from MPB attack with the deployment of an antiaggregant pheromone (Quinlan 2008; Jones 2011).

5.1.4 Research and development of WPBR-resistant trees

Research and development of genetic resistance against WPBR on white pines appears to offer the best long-term prospect for control (Burns *et al.* 2008; Kinloch 2003; Schoettle and Sniezko 2007; King *et al.* 2010). A genetic program for whitebark pine restoration has been started in British Columbia and involves identifying potential parent trees for breeding purposes and cone collections to supply seed to grow seedlings for reforestation (Zeglen 2002). More recently, Alberta in cooperation with British Columbia and Parks Canada has been working under cooperative agreements to make population bulk and individual tree seed collections for both limber and whitebark pine in preparation for WPBR screening trials and restoration outplanting. Resistance breeding work is proposed (ESRD *in prep*). Smith *et al.* (2008) suggest that active management involving supplemental planting of seeds or seedlings may be necessary to ensure restoration of the severely damaged whitebark stands. They suggest that the seeds should only be collected from potentially blister rust resistant trees. Parent trees selected for cone collections may require protection from MPB attack such as by the deployment of the semiochemical Verbenone. In Alberta, a program of conservation collections of cones from whitebark and limber pines has been ongoing to help conserve variation within and among populations of these species and for maintaining their adaptability in their natural environments (ASRD 2008a). The program is part of the new Gene Conservation Plan for Native Trees of Alberta (ASRD 2009b).

Relatively successful breeding programs have been established for the three (eastern white pine, western white pine and sugar pine) North American commercial white pine species (Bingham 1983; Daoust and Beaulieu 2004; Kinloch 2003;

Sniezko 2006). A comprehensive review of genetic approaches to the management of blister rust in white pines is provided by King *et al.* (2010). These programs were established to provide resistant trees to use in reforestation and restoration. This research effort has also provided considerable progress toward understanding the biological basis of resistance and application for these commercial species. Bingham (1983) summarized 25 years of early (1950-1975) research and development work by U.S. Forest Service co-operators in the breeding of WPBR resistant western white pine. This knowledge base and the successes achieved will aid in the research of pathogen resistance of the non-commercial white pine species. Considerable geographical variation exists in the resistance observed for sugar pine and western white pine, and similar variation likely exists for other white pine species (Schoettle 2004). According to Schoettle and Sniezko (2007), all of the North American white pine species have some heritable resistance to WPBR, however, the frequency of resistance is low in all species. Current restoration strategies and management for the non-commercial species are based on increasing the genetic resistance, and will focus on the most severely infected stands (Burns *et al.* 2008; Mahalovich and Dickerson 2004; Schoettle and Sniezko 2007).

Kinloch and Dupper (2002) reported that major genes for resistance against WPBR have been found in low frequency in both sugar pine and western white pine. These resistant genes have been designated Cr1 and Cr2 (R-genes), respectively for the two species and express similar phenotypes; i.e., the response is a classical “hypersensitive reaction” produced when needle tissues are artificially inoculated with WPBR spores. However, both alleles have been neutralized by blister rust inocula from certain locations, suggesting that these inocula of WPBR harbour alleles with specific virulence to Cr1 and Cr2 (i.e., gene-for-gene pathosystem characteristic). These authors suggest, on the basis of observations of resistant phenotypes, that the same R-genes may also exist for other white pine species such as limber and whitebark pines. In inoculation tests on seedlings conducted by Kinloch and Dupper (2002), a hypersensitive reaction occurred on limber pine at a relatively high frequency in one of five bulk seed lot sources from Colorado. While formal proof of a Cr gene was not confirmed, its existence was strongly suggested. Similar tests did not reveal a hypersensitive reaction in seedlings of whitebark pine although the sample size may have been too small (Kinloch and Dupper 2002; Zambino and McDonald 2003).

Individual trees of both species growing in areas of high WPBR infection have been commonly observed free of or with a low incidence of WPBR cankers, indicating the likely presence of natural resistance (Kinloch 2003; Sniezko 2006). Several mechanisms of complete (R-gene or major gene) and partial or multi-gene resistance are reported as common in several white pine species. In western white pine, for example, 2-year old seedlings inoculated with WPBR inocula have shown an array of resistant responses (Ekramoddouallah and Hunt 2002; Sniezko 2006; Zambino

and McDonald 2003). These have included a longer period for stem symptoms to appear, higher levels of bark reaction to canker inactivation, lower incidence of stem symptoms, and a higher survival of tree symptoms. Artificial inoculation of 2-year old seedlings has been the principal method of assessing resistance in all programs of white pine species (Sniezko 2006). Details of procedures used to test seedlings for resistance against WPBR inocula and for successful inoculation procedures were described by Ekramoddoullah and Hunt (2002). Kinloch *et al.* (2004) suggested that for single (major) resistant genes identified in sugar and western white pines, that these could be neutralized rapidly in individual stands by WPBR virulent genes. They suggested that this effect could be dampened silviculturally by removing alternate hosts *Ribes* spp. to reduce inoculum potential, and genetically by buffering major genes controlling partial or horizontal resistance traits, since these are not likely to be specifically vulnerable to matching virulence genes in the pathogen. Mechanisms of partial resistance (polygenic) to WPBR may therefore provide the foundation for establishing durable resistance over time in future generations of white pines (Jermstad and Neale 2007; King and Hunt 2004; Kinloch *et al.* 2003; Sniezko *et al.* 2004; Woo *et al.* 2001). Currently in British Columbia, no virulent pathotype of WPBR to the Cr2 gene has so far been demonstrated in western white pine over 15 years (Hunt *et al.* 2004). These authors suggested that the Cr2 gene could be deployed successfully in isolated areas of British Columbia, and that even if this resistance failed, the trees may have outgrown their most susceptible age before a virulent pathotype could build up. The hypertrophic response in western white pine seedlings conditioned by the Cr2 gene for total resistance will be continued in British Columbia; however, the breeding programs will continue to rely on partial resistance mechanisms and tolerances for the major part of the tree breeding effort (King and Hunt 2004).

5.1.5 Strategies, guidelines, and research for WPBR resistance breeding programs

Strategies and guidelines for establishing a breeding program for whitebark pine have been described by Burns *et al.* (2008), Mahalovich and Dickerson (2004), Schoettle and Sniezko (2007) and Schwandt (2006), and likely have similar application for limber pine. A rust resistance breeding program may involve the following steps (Burns *et al.* 2008):

- Seed and scions are collected from putatively resistant trees identified in natural forests;
- Progeny are screened for resistance in the greenhouse or nursery beds;

- Resistant progeny are established in a seed orchard;
- Controlled crosses can be performed and seed can be supplied for reforestation.

Interim resistant seed can likely be obtained from cones collected from plus trees that show above average resistance to blister rust in natural populations. Additional resistance can be obtained through a selective breeding program (Burns *et al.* 2008). These authors caution, however, that even when genetic resistance is found, the possibility exists that resistance could be overcome by more virulent races of the WPBR pathogen, especially when resistant mechanisms are controlled by a single major gene.

Schwandt (2006) provides the following list of conservation and restoration strategies that can be employed for whitebark pine, and may be similarly applied for limber pine restoration:

- **Assess forest health** – previous surveys of WPBR incidence and tree mortality have been conducted and should be continued periodically in the future in established permanent plots.
- **Conserve genetic diversity** – the gene pool may be retained or protected by collecting and archiving seed from isolated populations or from those that may be threatened by extinction.
- **Harness natural resistance** – evidence has been found in nurseries in Oregon and Idaho that natural resistance to WPBR does occur in whitebark pine. Once blister rust resistant trees or seedlings are identified, they can be grown in seed orchards to produce seed for restoration purposes.
- **Reduce competing vegetation** – prescribed burns may be conducted, similarly as in project trials established by Parks Canada and elsewhere.
- **Enhance natural selection** – natural selection for WPBR resistance will be strongest in younger trees that are survivors within stands with a high rate of infection and tree mortality.
- **Prevent bark beetle losses** – protection against MPB attacks may be necessary and is most likely feasible using the antiaggregant pheromone Verbenone, especially for protecting trees identified as blister-rust resistant and maintained for cone collections.

A comprehensive whitebark pine restoration strategy for the Pacific Northwest Region of the U.S.A. has been developed (Aubry *et al.* 2008) and is being implemented. Key elements of the strategy are: restore degraded habitat; protect genetic resources through gene conservation; increase blister rust resistance in whitebark pine populations; evaluate the health and status of whitebark pine stands where information is lacking; and increase understanding of the threats to and develop effective restoration techniques.

All nine species of five-needle pines native to United States and Canada are susceptible to WPBR, and some level of genetic resistance to the rust exists in all of these species (Sniezko 2008; King *et al.* 2010). At the recent Fourth International Workshop on the genetics of host-parasite interactions in forestry, several reviews on WPBR resistance breeding were presented. Kegley *et al.* (2011) reported on major screening efforts for WPBR in Oregon and Washington. They observed that some families of whitebark pine inoculated with WPBR showed high levels of canker-free seedlings. In other studies, Sweeney *et al.* (2011) and Sniezko *et al.* (2011) assessed the genetic resistance to WPBR on western white pine and whitebark pine using hypersensitive reaction criteria (e.g., “needle-spot” phenotype) in inoculated seedlings. Results in whitebark pine after five years post-inoculation, indicated there was geographic variability in resistance and that both western white pine and whitebark pine showed family variation in resistance (Sniezko *et al.* 2011).

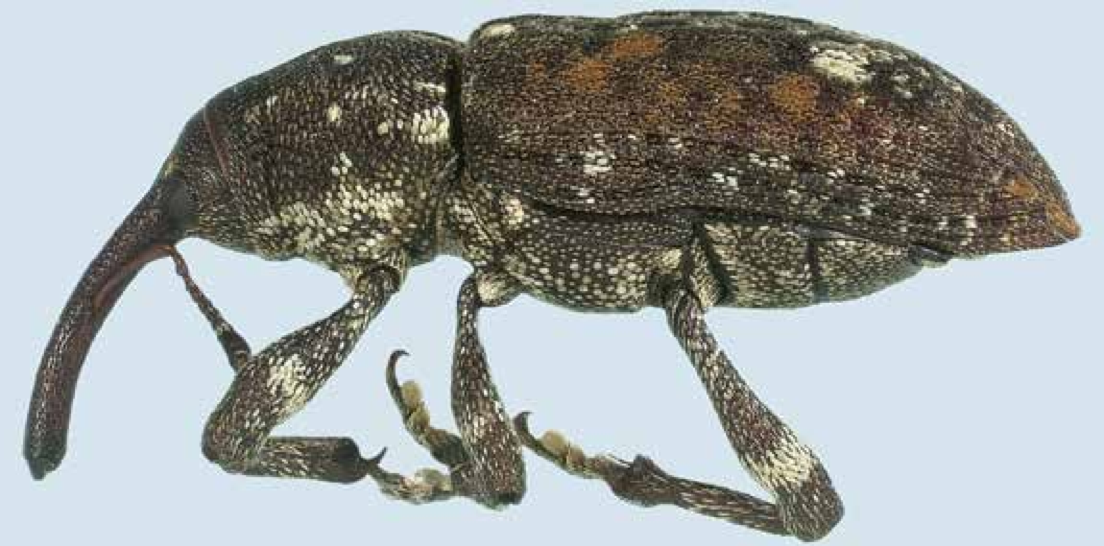
In Alberta, both whitebark and limber pine are now designated as Endangered under the Alberta Wildlife Act. Provincial recovery plans for both species are being prepared (Gould 2011; Jones 2011). Recent surveys of WPBR infection/tree mortality in Alberta and eastern British Columbia indicated 43 per cent of limber pine trees were infected and 35 per cent were dead, whereas for whitebark pine, 41.3 per cent were infected and 21 per cent were dead (Gould 2011). A long-term goal of the recovery strategy for these two species is to ensure viable, self-sustaining populations by identifying putatively resistant trees, collecting seed, screening and propagating genetically resistant seedlings for site restoration plantings (Jones 2011).

A similar genetic conservation strategy for whitebark pine has been prepared for British Columbia, with various initiatives being undertaken by disparate agencies to conserve whitebark pine communities (GCTAC-Forest Genetics Council 2009). For western white pine in British Columbia, a WPBR forest health stand establishment decision aid has been developed that summarizes information collected over several decades and applied in current management regimes to reduce spread and damage effects of WPBR. The information provides a framework for genetic resistance studies applied to whitebark and limber pine.

Genetic management of WPBR has been actively conducted for eastern white, western white and sugar pine, and seed orchards are now able to capture and transmit genetic resistance for these species. Investigations and preliminary screenings have recently been initiated for other white pines including whitebark and limber pine (King *et al.* 2010). Different approaches to breeding for resistance in white pines in North America are reviewed by King *et al.* (2010) and include three broad categories: ontogenetic resistance (host age-related), R-gene resistance (major gene resistance), and partial resistance. Partial resistance implies that the host is able to tolerate or impede disease development without eliminating the pathogen, and is expressed by responses in seedlings and presumed to be multigenic and partially controlled by recessive genes. For sugar pine, the breeding program can combine R-gene resistance with partial resistance to produce seedlings that have both vertical and horizontal resistance, thus combining advantages of both schemes. However, in British Columbia, since the Cr gene is not endemic, it must be incorporated into seed from production orchards by pollen (King *et al.* 2010). This combination of R-gene and partial resistance is therefore only used on sites of greatest hazard in British Columbia and provides protection from WPBR infection for the first 12-14 years after planting, after which ontogenetic resistance becomes effective.

A next phase of research is to relate specific infection response characteristics with selected genotypes. It is suggested that new molecular and genomic techniques could help to facilitate this aspect of research and advance genetic approaches toward more durable resistance in the management of WPBR. Two specialized fields of genomics are suggested: apply functional genomics to investigate gene transcription, translation, and protein-protein interactions, which may lead to a better understanding of the biological system underlying resistance. The other approach is to apply ecological genomics, the techniques of which are currently being developed. Other suggested future approaches in molecular biology, aimed at understanding the complex WPBR pathosystem include *in vitro* screening, microscopic techniques, tissue culture and micropropagation (King *et al.* 2010).

5.2 Case History 2: White Pine Weevil (*Pissodes strobi* [Peck])



The WPW, is native to North America and is the most serious and economically important insect pest of spruce and pine regeneration in Canada. Its distribution extends across Canada and it primarily attacks Sitka, white and Engelmann spruces in British Columbia and white and Engelmann spruces in Alberta (Alfaro, *et al.*1994; King and Alfaro 2009). Other conifer species somewhat less commonly attacked in western Canada, include lodgepole, jack and Scotch pines as well as black, blue and Norway spruces (Alfaro *et al.* 2007). In eastern Canada, the name "white pine weevil" was originally designated in reference to its high level of economic injury in plantations of eastern white pine, while in western Canada, the species was recognized for its stronger attraction and behaviour on spruce hosts and was originally designated as two separate species, the "Sitka spruce weevil" and the "Engelmann spruce weevil". Although these names are now synonymous with *P. strobi* on eastern white pine, there is wide variation in its genetic, morphological and behavioural traits (Laffin *et al.* 2004). Based on a genetic analysis using weevil protein electrophoresis of 41 weevil populations sampled across Canada, four geographic sub-population groups were recognized. These are: Eastern population (Alberta and eastward), Interior B.C. population, South B.C. coast population and North B.C. coast population (Alfaro *et al.* 2007). The results of this study suggested that breeding programs for weevil resistant trees should consider the target weevil population within these broad geographic areas. In Alberta, most weevil populations appear to fall into the Eastern population strain with some Interior B.C. population strain in north western Alberta (Alfaro *et al.* 2007).

The WPW develops through one generation per year. Adults attack host trees in early spring after they have dispersed by crawling or flying, and seek out vigorously growing, unshaded trees mostly 1 to 8 m tall. Feeding, mating and egg laying occur on the previous year's leader, and later as the larvae develop, their feeding in the bark phloem extends downward and results in girdling and killing the leader. Usually the current-year and the previous year's leader growth are killed. This results in height growth reduction, increased susceptibility to decay organisms, forked and multiple stems and stem deformation. Weevil-attacked trees at maturity may have a volume loss of recoverable lumber of up to 20 per cent (Alfaro *et al.* 2008).

Several control options are available for *P. strobi*, but none have proven to be entirely effective. These include hazard rating of stands, applying silvicultural control (e.g., by manipulating stand density and shading, encouraging multi-tree species mixtures, delaying thinning, and pruning off infested leaders), direct control with insecticides and biologicals, and the use of genetic tree resistance (Heppner and Turner 2006; Wilson and Bechinski 2006). The current recommended approach to control WPW in plantations is through integrated management strategies, applying all techniques in conjunction with selected genetic tree resistance. Selecting and breeding trees with WPW resistance currently provides one of the most promising avenues for minimizing losses caused by this insect (Alfaro *et al.* 2008).

Early screening for white pine weevil resistance in Sitka spruce was based on measured leader attack rates in infestations that had developed naturally in provenance trials from three geographic sources in coastal B.C. (Alfaro *et al.* 2008; Ying 1991). Subsequent screening techniques for resistant spruce genotypes have been improved by augmenting natural weevil populations at each test site. The augmentation procedures have increased the efficiency of the screening method and provided a useful tool in weevil resistance research, as well as confirmed resistance selection for different weevil attack rates (Alfaro *et al.* 2008). A second phase of the F1 breeding program of weevil resistant trees was established in 2006 with test plantings located in various sites rated for different weevil hazard levels (King and Ponsford 2006). Some of the new focus is on selection for specific resistant mechanisms such as constitutive characteristics involving sclereid cells, resin cells and inducible traumatic resin cell production. Although the exact mechanisms of resistance are not fully understood for WPW, it is speculated that there is a hierarchy of resistant features that include attractant volatiles, resin flow, toxicity of the resin to weevil life stages, resin canal structure, formation of traumatic resin and resinosis, and tree vigour (Yanchuk 2006a). Although both constitutive and induced resin defences may contribute to the resistance mechanism in Sitka spruce, the terpenoid resin defence pathways are complex and multi-faceted, and are possibly under control by quantitative trait loci (King and Alfaro 2009). These authors have also stated that the greatest effect in the weevil resistance breeding program thus far has been the significant and overwhelming effect of provenance for resistance.

Planting trees from resistant regions has produced seedlings that have significantly less attack rate than those seedlings originating from more susceptible sources. The resistant genotypes of Sitka spruce selected are now being used in planting programs in British Columbia and appear to provide effective and durable resistance to *P. strobi* (Alfaro *et al.* 2008; King and Alfaro 2009). Yanchuk (2006a) considers the resistant breeding program of Sitka spruce in B.C. to be one of the most successful programs for pests in the world.

The first interior spruce (White, Engelmann and hybrids) trial in B.C. was established in 1973 based on 173 wind-pollinated families and was evaluated for WPW resistance 17 years later (Kiss and Yanchuk 1991; Alfaro *et al.* 2004). Weevil resistance rankings based on weevil damage were shown to be heritable, with a family heritability value of 0.7 (Alfaro *et al.* 1996; King *et al.* 1997; Kiss and Yanchuk 1991). The resistant mechanisms against WPW in white/Engelmann spruces are thought to be similar to those in Sitka spruce. The resin canals in the leader bark are believed to be one of the main mechanisms providing a defence against attack, by acting as a physical or chemical barrier to invasion. In spruce species generally, the bark of the leader contains a ring of large resin canals with a second outer ring of smaller canals. This network of canals can provide an effective barrier by oozing resin into adult feeding and oviposition punctures or by drowning eggs and young larvae (Alfaro *et al.* 2004). Trees resistant to weevil attack may have a higher resin canal density than non-resistant trees. Measurement of bark resin canal characteristics may provide a useful tool for indirect screening of interior spruce families for inclusion in breeding programs (Alfaro *et al.* 2004). Data presented by these authors indicated that interior spruce resistance is inherited in F1 progeny from R x R parental crosses and can be incorporated into WPW management strategies. Genetic variation for WPW resistance has also been demonstrated in eastern white pine in eastern Canada (Daoust and Beaulieu 2004).

Geographic variation of white spruce has been extensively studied in Alberta, supported by various provenance trial results (ASRD 2004; Rweyongeza and Yang 2005b; Rweyongeza *et al.* 2007). Large differences were found among provenances and test sites for height and diameter growth traits, which could influence WPW host selection. The level of genetic variation in growth potential among white spruce populations was rated as moderate, and slightly higher than observed elsewhere in North America (Rweyongeza *et al.* 2007). Percentage incidence of WPW attack assessed on trees at several planted sites with representative northern white spruce provenance materials (Breeding Regions D1, E and H) indicated wide variation after 11 and 18 years after seed (e.g., 1.1 per cent to 29.9 per cent and 4 per cent to 28 per cent incidences, respectively).

Significant variation was evident among half-sib families for incidence of WPW attack, and heritability for WPW resistance was rated as low to moderate (ASRD 2004). For Breeding Region D1, the G132 progeny trial series produced family heritabilities for WPW of 0.48 at 10 years and 0.62 at 15 years (Alberta Tree Improvement & Seed Centre [ATISC] unpublished data). For the northern Alberta G133 white spruce provenance-family trial series, heritabilities for the site with the highest infection rate (28 per cent) were 0.45 for family and 0.18 for individual (ASRD 2005).

The WPW incidence of attack levels provide the basis for initial screening of WPW resistant tree selection and provide guidelines for the genetic roguing of weevil-susceptible phenotypes (ASRD 2004; Hansen *et al.* 2005).

5.3 Case History 3: Lodgepole Pine Dwarf Mistletoe (*Arceuthobium americanum* Nutt.)

Dwarf mistletoes are seed-producing plants that are parasitic and grow on conifers. As plants, they have roots, stems, and reproduce by seeds. The aerial shoots of mistletoe plants contain chlorophyll; however, little food is produced to sustain their parasitic habit. Consequently they rob their host plants of water and nutrients, and depend upon the host for support (Allen *et al.* 1996; Parks and Flanagan 2001). The dwarf mistletoe plants also produce chemicals that cause abnormal branches to develop, called “witches’- brooms”. These interactions with the host plant cause a variety of dysfunctions in the host, such as reduction in height and diameter growth and wood quality; reduced seed and cone development; top-killing, large knot size from abnormal branches, and often end in tree mortality (Allen *et al.* 1996; Parks and Flanagan 2001). The infections are known to increase susceptibility of the host to pathogens and insect attacks (Kliejunas *et al.* 2009).

While there are many endemic species of dwarf mistletoe occurring in North America, only one species, the lodgepole pine dwarf mistletoe (*Arceuthobium americanum*), occurs in Alberta and infects lodgepole pine and jack pine as its main

hosts throughout most of their ranges in the province (Brandt *et al.* 1998; Brandt *et al.* 2004a, 2005). It affects trees of all age classes (Baranyay and Safranyik 1970). *Arceuthobium americanum* plants are dioecious, grow separately as male and female plants and are typically 5 to 8 cm long. Estimated annual growth losses for jack pine infected with dwarf mistletoe in the three prairie provinces are 314,000 cubic metres, while annual tree mortality losses are estimated as an additional 1,478,999 cubic metres. Annual growth loss estimates for lodgepole pine in Alberta and Saskatchewan due to mistletoe are 486,000 cubic metres and tree mortality losses are 69,000 cubic metres (Brandt 2006). Lodgepole pine tends to be less severely impacted by dwarf mistletoe infections than is jack pine (Brandt 2006). Hawksworth and Johnson (1989) list whitebark and limber pines as occasional hosts of *A. americanum*, and white and Engelmann spruces and Douglas-fir as rare hosts.

The biology and life cycle development of dwarf mistletoe on lodgepole pine was summarized by Baranyay (1970) and Hawksworth and Johnson (1989), and by Brandt (2006) for jack pine in Alberta. In Alberta, dwarf mistletoe produces flowers during April and May. Pollination and fertilization follow from pollen produced on separate male plants. This results in a fruit or berry, each of which contains a single seed. The berries remain on the plant for about one year before ripening and forcibly discharging the seeds. Ejection of seeds and their dissemination occurs between mid-August and late-September. The seeds possess a mucilaginous substance (viscin) that, upon ejection, enables it to adhere to whatever surface it lands on such as on the needles of its host tree. The viscin absorbs moisture and allows the seed to slide to the bark surface where it remains dormant overwinter until the following spring. Germination of the seed commences in April and is completed by mid-June, provided that specific light, moisture and temperature conditions are met. Some seed germination on jack pine occurs during fall in central Alberta (Brandt *et al.* 2005).

Germination and establishment of dwarf mistletoe on its host typically consists of three stages. During the first stage, the seed radicle elongates after germination. The second stage is characterized by the cessation of radicle elongation and the formation of a holdfast, which firmly attaches the germinating seed to its host surface. During the third stage, one or more wedge-shaped infection pegs develop and penetrate through the phloem, cambium and into xylem tissues, thus beginning the infection process (Brandt *et al.* 2005). Swelling of the host branch at the site of infection develops during the second summer, and first aerial shoots appear during the third year. By the fourth summer, separate male and female plants are recognizable, followed by microsporogenesis. In April of the fifth year, pollination commences, followed by fertilization and megasporogenesis in May. Development and maturing of the berry and seed occurs in the sixth year, with seed dispersal commencing by September. The length of time required to complete the life cycle from one seed ejection to the next seed ejection appears to be 6 or 7 years on lodgepole pine, but is shorter (5 years) on jack pine (Brandt 2006; Hawksworth and Johnson 1989). The incubation period from infection to emergence of aerial shoots is reported to be shorter on jack pine than on lodgepole pine, and this difference may account for its shorter life cycle (Brandt 2006).

Most dwarf mistletoe infections occur on needle-bearing twigs. If the infection occurs on relatively young host tissues, dormant host buds are stimulated to produce a dense mass of branches or witches'-broom (Hawksworth and Johnson 1989). Generally larger brooms form on jack pine than on lodgepole pine, and they tend to survive and enlarge during the life of the host tree. Tree survival is highly variable once infections occur and partly depends upon the number of infections, broom size and their distribution within the crown (Baranyay and Safranyik 1970; Hawksworth and Johnson 1989).

Where control has been necessary, stands infected with dwarf mistletoe have generally been effectively treated by silvicultural means, which have been cost effective and relatively easy to apply (Baranyay 1970; Hawksworth and Johnson 1989; Shamoun and DeWald 2002; Van Sickle and Wegwitz 1978). Considerable study has also been devoted to the use of chemicals for control of mistletoes, especially the selective use of herbicides and growth regulators. However, these compounds have had only limited application such as on high-value trees and in recreational areas (Hawksworth and Johnson 1989; Shamoun and DeWald 2002). Many fungi and insects are pathogenic or feed as herbivores on dwarf mistletoe plants and have value in providing biological control. Some of the species appear promising for development in biological control programs, but little progress has been made in this area (Shamoun and DeWald 2002).

Relatively few cases of tree resistance to dwarf mistletoes have been reported (Scharpf 1984; Scharpf and Roth 1992; Shamoun and DeWald 2002). In spite of the many attempts to limit the impacts of dwarf mistletoe infections through silvicultural methods, severe damages continue to occur. Planting resistant trees in many situations could provide another method of control and help to reduce losses from this parasite. Genetic resistance studies on dwarf mistletoes have generally been ignored; the reason has presumed to be largely because mistletoe control requirements could be met with silvicultural treatment (Roth 1978). In early studies, Roth (1966) reported that little was known about the nature and origin of resistance to mistletoe, and trees exhibiting phenotypic resistance were rarely observed. He had observed some ponderosa pine trees that possessed a drooping needle character, which apparently made infection more difficult than on trees with erect needles and ascribed this to be a form of genetic resistance. In a later publication, Roth (1978) suggested that trees resist damage from dwarf mistletoe in four genetically related

ways: 1) by immunity accompanying co-evolution of the Pinaceae and Arceuthobium during their past evolution; 2) by vertical resistance (possessing a specific resistant gene); 3) by possessing horizontal resistance (aggregate combinations of genes may have developed to create a phenotypic response which suppress infection); and 4) by disease escape based on heritable characters. He suggested that single gene resistance to dwarf mistletoe was probably rare, and noted that a hypersensitive reaction (sudden death of host cells at the site of infection), indicating single gene resistance, had been observed with dwarf mistletoe on ponderosa pine. Horizontal resistance appeared to be more likely to occur because it can develop in the absence of selection pressure and can arise from a wide range of gene combinations (Roth 1978). Grafted ponderosa pines that had been selected and tested for dwarf mistletoe infection remained mostly mistletoe-free during 10 or more years. Older trees tended to be more resistant to dwarf mistletoe than younger trees, and if large trees remained substantially mistletoe-free under conditions of high exposure, they are likely exhibiting horizontal resistance (Roth 1978). Applications of resistant trees could be used to enhance silvicultural treatments such as in under-plantings, establishing immune border strips of trees, and in selecting leave trees during thinnings.

To date, most research on resistance to dwarf mistletoe has been on ponderosa pine and its resistance to western dwarf mistletoe (*A. campylopodum* subsp. *crytopodum*). Evidence of resistance was observed for both ponderosa and Jeffrey pines (Scharpf and Roth 1992; Hawksworth and Wiens 1996; Shamoun and DeWald 2002). The studies did not identify what variables may be contributing to resistance, but suggested that foliar habit, tree size and crown characteristics may be partly involved. Hawksworth and Wiens (1996) noted that earlier studies by Roth (1974) showed that susceptibility to infection on ponderosa pine decreased with increasing tree age up to 150 years. Susceptibility to infection was expressed in Jeffrey pine seedlings up to about the first 10 years (Scharpf and Roth 1992). This suggested that young seedlings might be more susceptible to infection. Field-observed trees that were mistletoe-free, and therefore assumed to be resistant, were identified for ponderosa, Jeffrey and lodgepole pines, and for Douglas-fir and western hemlock, although other conifers have been examined as well (Hawksworth and Wiens 1996; Shamoun and DeWald 2002). However, progeny of these “resistant” trees have not generally been tested for resistance. These observations suggested, however, that variation of genetic resistance exists within host populations. Scharpf and Roth (1992) reported a high correlation between resistant ponderosa pine parents and their scions grafted and out-planted in areas of heavy mistletoe infection. The data appeared to verify that resistance is being controlled genetically rather than environmentally. Other studies have indicated that growth rate was not a reliable indicator of mistletoe resistance (Shamoun and DeWald 2002). Scharpf and Roth (1992) concluded that the resistance of ponderosa pine was not based on simple inheritance, but involved juvenile susceptibility and a range in resistance among parent trees selected. They further suggested that high levels of resistance exist within populations of ponderosa pine in Oregon, that the probability of identifying resistant pines from field observations was good, and that similar resistant traits likely exist in other western conifers as well.

Observations of *A. americanum* resistance in lodgepole and jack pines have received little attention. One unpublished study in Colorado examined the putative resistance of selected lodgepole pine seedlings propagated from apparent resistant trees located in a small fast-growing stand (Shamoun and DeWald 2002). Preliminary inoculation tests on the seedlings from the putatively resistant trees, compared to seedlings from susceptible sources, indicated that initial infection after 2-3 years was lower on seedlings from resistant sources (Hawksworth and Wiens 1996). However, the infection rates 10 years after inoculation for putatively resistant families and susceptible families were essentially the same (Shamoun and DeWald 2002).

5.4. Case History 4: Mountain Pine Beetle (*Dendroctonus ponderosae* Hopkins)

5.4.1 Hosts, distributions, and life history

The MPB is an indigenous bark beetle species native to western North America and is considered the most destructive biotic agent of mature pine forests (Safranyik and Carroll 2006). Populations of this beetle periodically erupt into epidemics when it is capable of causing landscape-scale tree mortality. The natural distribution of MPB extends from northern Mexico to northwestern British Columbia (latitude 56° N), and in recent years, it has invaded western and northwestern Alberta and the Cypress Hills on the Saskatchewan-Alberta border (Safranyik and Carroll 2006). Principal hosts in western Canada include lodgepole, ponderosa and western white pines, but other native and exotic pine species are also readily attacked. These include whitebark, limber, and jack pines (including lodgepole-jack pine hybrids) and the exotic Scotch pine. Safranyik and Carroll (2006) cite evidence that the influence of the different pine host species can cause variation in several life history parameters such as survival, fecundity, body size, rate of development, and phenology.

The life history and behaviour of MPB have been adequately described in Safranyik and Carroll (2006), and are briefly reviewed here. Four life stages occur (egg, larva, pupa and adult), and all except a dispersal phase of mature adults, occurs within the subcortical tissue of their host trees. During initial attack on live trees, adult females burrow into the bark and construct egg galleries upward on the stem where they deposit their eggs. As the eggs hatch, the young larvae extend galleries at right angles away from the main egg gallery. At completion of development, after four growth instar stages, each larva enlarges the end of its gallery to form a small cavity in which it pupates and matures to an adult.

The length of the life cycle varies somewhat throughout its range and is dependent upon ambient temperature. MPB is univoltine in that its life cycle from egg to adult normally occurs in one year. Warmer than normal summers may allow some parent adults to emerge from a brood tree and establish a second brood, although this may be rare in Alberta. However, during cooler summers, and especially at high elevations, some or all of the brood may require two years to complete development. For the normal univoltine population, emergence from the host tree, new host tree selection and colonization, mating, egg gallery construction and oviposition all occur during late July to mid-August. Eggs normally hatch within a week and the larval instar stages that develop before fall freeze-up (especially third and fourth instars) will be the primary over-wintering population. During mild winters, however, a large proportion of parent adult beetles may also survive the winter. The larvae resume feeding in the spring and develop to new adults during late June to mid-July.

5.4.2 Host selection, behaviour, and associated microorganisms

MPB preferentially selects large diameter-size trees within a stand to attack. These trees tend to be the fastest growing and most vigorous. Total initial attacks and brood production are positively related to tree age and diameter at breast height of lodgepole pine (Safranyik and Carroll 2006). The beetles may select large trees, partly because of the positive relationship with thick phloem, since brood production is directly related to phloem thickness. Studies have shown that in trees with thick phloem, MPB lays more eggs/cm of gallery, larvae are less subject to intraspecific competition and develop faster, and ultimately produce larger brood beetles, compared to beetle development in trees with thin phloem. However, stand and site conditions can influence phloem thickness. Young trees with thin bark and small diameter are usually avoided by attacking beetles, except under conditions of high beetle population pressure.

From an MPB population dynamics perspective, lodgepole pine of a diameter less than 25 cm are considered as beetle sinks (i.e., more beetles attack and enter the tree than emerge), whereas attacked trees greater than 25 cm in diameter are beetle sources and usually contribute to expanding populations (Safranyik and Carroll 2006).

During its attack on live pine hosts, MPB utilizes two effective strategies to overcome the natural resistance defences of lodgepole pine. The natural defences of the host tree include constitutive resin in the tree's resin duct system and secondary induced resinosis produced in cells adjacent to wounds that is produced in response to

wounding such as that made by the entry chewing of beetles. The first behaviour strategy results from a large number of female beetles that cooperatively attack a tree stem (referred to as a “mass attack”) in response to aggregation pheromones. As a result of the mass attack, constitutive resin ducts are severed as the beetles bore through the phloem. The flow of constitutive resin impedes the attacking beetles and their associated microorganisms (e.g., blue-stain fungi), and may even expel the beetles (“pitch out”) from the tree. The induced response results in a breakdown of parenchyma cells, the formation of traumatic resin ducts and production of secondary resin that comprises an increased concentration of terpene and phenolic compounds. These compounds are antagonistic to the blue-stain fungi (Safranyik and Carroll 2006). The phloem adjacent to beetle wounds becomes saturated with liquid resin, and resin often exudes to the bark exterior to form “pitch tubes”. If the induced response is rapid and extensive, the beetles and associated microorganisms may be confined and killed in a lesion of dead tissue.

The second behavioural strategy results from the mutualistic relationship between MPB and several species of blue-stain fungi. Spores of three common fungi, *Grosmannia clavigera* (formerly *Ophiostoma clavigerum*), *Ophiostoma montium*, and *Leptographium longiclavatum*, are carried on the exoskeleton of adult beetles and are inoculated into trees as the beetles chew through the bark. These spores germinate and penetrate living cells in the phloem and xylem, causing desiccation and disruption of transpiration and nutrient transport, and thereby terminate resin production by the tree. As the fungi colonize a tree, moisture and resin flow are reduced allowing MPB broods to develop successfully. Successful colonization by MPB depends upon the death of its host tree (Safranyik and Carroll 2006). Successful colonization therefore depends upon sufficient numbers of beetles arriving and attacking at a rate that exceeds the resistance capacity of the particular tree’s defence mechanisms. The attack period in late summer may often coincide with drought periods, which reduce host defences, often in favour of successful MPB colonization. Bentz *et al.* (2010) note that climate stress as a consequence of climate change can directly affect tree death through carbon starvation and cavitation of water columns within the xylem, and that climatic water stress can have profound effects on tree susceptibility to bark beetle attack.

Plants attempt to avoid drought induced hydraulic failure by stomatal closure, which may in turn result in carbon starvation and ultimately limit within-plant allocation of carbohydrates available for growth, defence, tissue repair, and production of constitutive or induced chemical defences. The presence of symbiotic fungi associated with MPB may further amplify water transport interruption, thereby altering the tree defensive capacity and reducing the threshold number of beetles necessary for successful mass attack (Bentz *et al.* 2010). During the current MPB outbreak in British Columbia, drought stress and associated elevated temperature facilitated MPB population progression from an incipient level to an epidemic level (Carroll *et al.* 2006; Bentz *et al.* 2010).

At the stand level, resistance of lodgepole pine to colonization by MPB and its blue-stain fungal associates is affected by the normal stand aging process. Stands between 40 and 60 years of age tend to be most resistant, after which resistance declines rapidly with age. The vigour of trees also declines as they reach maturity (e.g., 80 to 100 years) and begin to compete for resources; they are highly susceptible to the MPB within this age class (Safranyik and Carroll 2006).

The mechanism of host selection by MPB, as reviewed by Safranyik and Carroll (2006) is only partly understood. The most popular theory proposes that pioneer female beetles utilize a combination of visual orientation and random landings on the tree stem, with subsequent direct assessment of host suitability after landing. There is also evidence that dispersing adults orient to lodgepole pine trees suffering from injury or disease, or to odours of host trees in the absence of visual cues. After landing on a potential host tree, the decision to initiate a gallery is made based on gustatory assessment of compounds present in the bark. If a tree is considered acceptable, females begin to construct a gallery, and in the process they instigate a mass attack involving a complex synergism of host-produced (kairomones) and beetle-produced (pheromones) volatile chemicals. While chewing through the bark the female oxidizes the host monoterpene alpha-pinene to produce the aggregation pheromone trans-verbenol. The release of this compound is attractive to both sexes, though preferentially to male beetles, which subsequently arrive, and they in turn release the pheromone exo-brevicomin. This compound at low concentrations attracts mainly female beetles. The kairomones alpha-pinene and myrcene synergize the aggregation pheromones and trigger the characteristic mass attack response, a process that is normally completed in 1-2 days on individual trees. Attack density on the host tree is limited and terminated at or near optimum attack density of about 60 attacks per m^2 of bark surface, by the production of chemical cues. Though the process is not fully understood, attack density is believed to be regulated in part by the production of high concentrations of exo-brevicomin and frontalin and 2-phenylethanol by male beetles, the release of 1-octen-3-ol by female beetles, and by the production of the anti-aggregation pheromone verbenone by intestinal and gallery-inhabiting microbes within both sexes of beetles.

5.4.3 Natural control and management strategies

Within its environment under the bark of trees, temperature and moisture are the two most important abiotic factors affecting brood development and survival. Temperature is important by acting directly to delimit growth and development, setting growth development rates, regulating cold-hardiness, and determining survival (Safranyik and Carroll 2006). Temperature and moisture also act indirectly through effects on host trees by affecting food quality and tree resistance. Within the host tree, cold temperature is often the single most important mortality factor of MPB life stages, with the egg stage being the least cold tolerant, and larvae the most cold tolerant. Over winter survival of brood is attained by the gradual production and accumulation of glycerol in the beetle's hemolymph as temperatures decline in autumn. Large diameter size trees, trees with thick bark and heavy snow cover are factors that help to insulate and increase over winter brood survival. Other important mortality factors include competition for food and space, host quality and host defences, and natural enemies.

MPB does not have a diapause, which could functionally help to synchronize populations with critical phenological events. However, the beetle has developed adaptations that help to insure its properly timed emergence as adults for successful mass attack. Brood are phenologically timed to mature to cold-tolerant life stages in preparation for over wintering. In addition, to insure that populations maintain their phenological timing, MPB has evolved regional differences in its development rate. For example, in cooler environments such as those at higher elevations and near the northern limits of its distribution, heat accumulation is often insufficient to maintain the univoltine life cycle, but the beetle is then able to become semivoltine, completing its life cycle over two years (Safranyik and Carroll 2006). These adaptations are especially important in the beetles' apparent dispersal, spread and successful attack in Alberta on other pine hosts such as the high elevation whitebark pine, limber pine, lodgepole-jack pine hybrids, and more recently on jack pine (Cullingham *et al.* 2011).

A suite of natural biotic enemies affects all life stages of MPB including predators, parasites and diseases. However, their role in the population dynamics of MPB is not well understood (Safranyik and Carroll 2006). Major insect predators include the fly, *Medetera aldrichi*, clerid beetles such as *Thanasimus undulatus* and *Enocleris sphegeus*, and the hymenopterous parasite, *Coeloides dendroctoni*. Woodpecker species are also considered important mortality agents of larvae, pupae and adults.

A large amount of information has been developed on techniques and strategies to detect, predict, survey, monitor, measure, assess and control MPB populations, and the risks and damages this beetle imposes on lodgepole pine forests. This information has been developed for management systems that focus on MPB for reducing tree, stand-level and forest-level susceptibility, and in maintaining low levels of beetle populations (Shore *et al.* 2006). The management systems incorporate knowledge of the biology and epidemiology of MPB in relation to stand dynamics of lodgepole pine and its distribution over the landscape, as well as information on interactions between the beetle, its associated microorganisms, and its tree hosts. Effective management systems require an integration of “direct control” treatments aimed at reducing MPB populations and “indirect controls” or “preventive management” aimed at increasing stand vigour or to reduce the amount and concentration of susceptible pine forests (Shore *et al.* 2006). Direct control treatments may include various cultural, mechanical or chemical treatments, and can incorporate single, multiple-tree and stand level treatments in conjunction with strategic deployment of aggregation and anti-aggregation pheromones (see reviews in chapters 6, 7, and 8 Safranyik and Wilson [eds.] 2006).

Indirect controls or preventive management includes maintaining stand hygiene (i.e., removing damaged or diseased trees) and vigour, managing tree species composition, age class distributions and stand density (Whitehead *et al.* 2006). Through silvicultural practices, stand density management can limit inter-tree competition for moisture and nutrients and result in more vigorous trees with increased growth, and therefore less likely to succumb to attack by endemic levels of MPB populations. A prescription that has shown promise is thinning some mature stands to a uniform inter-tree spacing at less than 600 stems/ha (also referred to as “beetle proofing”). This requires thinning from below to enhance tree vigour, which increases the trees’ ability to produce resins for primary defence against attacks. The uniform spacing creates a stand microclimate of higher temperatures, light and air movement that hinder beetle dispersal, attack behaviour and survival (Amman and Logan 1998). However, as Whitehead *et al.* (2006) point out, beetle proofing is intended to prevent transition between endemic and incipient phases of the outbreak cycle, and should not be expected to save stands during an epidemic.

5.4.4 Genetics and tree resistance

As a consequence of the current widespread MPB–caused tree mortality of its prime host lodgepole pine in British Columbia and Alberta, its advancement into new habitats of whitebark, limber, lodgepole-jack pine hybrids and jack pine in Alberta and a warming climate, new areas of research are being explored (Yanchuk *et al.*2008). Surveys of young lodgepole pine between the ages of 20-55 years in British Columbia were carried out to quantify MPB-caused mortality. Stands as young as 20-25 years sustained high levels of attack in areas of extreme beetle pressure. Percentage attacked trees ranged from 1 per cent to 61 per cent (Maclauchlan 2006). The beetle also attacked lodgepole pine progeny test sites and seed orchards, and this provided the opportunity to examine genetic variation of differential attack and tree resistance.

Yanchuk *et al.* (2008) examined variation of attack in 20-year old open-pollinated family trials originating from several provenances. Trees were assessed for tree resistant attributes, attack, tree survival, MPB gallery formation, and infection by *Ophiostoma* sp. Significant levels of genetic variability were found at two sites but with narrow sense heritabilities of 0.20 to 0.26. Provenance differences were also significant, indicating that some population structure is present for the resistant attributes measured. Family means for blue-stain (i.e., presence of *Ophiostoma* sp.) ranged from 0 to 57 per cent; 11 per cent to 63 per cent for egg galleries present; and 0 to 57 per cent for egg chamber/eggs. Family traits for these resistant attributes were not highly statistically significant.

In Alberta, MPB damage surveys in family tests, seed orchards and clone banks have been carried out since 2007 (ASRD 2011b; ESRD 2012). To date, there have been no reported or detected attacks within progeny trials or clone banks although mature trees in the immediate vicinity of several pine trials have been attacked and killed by MPB. The major beetle over flight from B.C. in 2006 led to attack of approximately 20 trees in a lodgepole pine seed orchard near Grande Prairie. Attacked trees were subsequently removed and sanitized and the orchard has been protected by pesticide application to tree boles during the flight period in subsequent years. Several adult mountain pine beetle were also captured in baited funnel traps in the vicinity of a lodgepole pine seed orchard at Brooks in 2009. However, there was no evidence of current 2009 attack on pine orchard or plantation trees in the vicinity (Cerezke 2009).

In another study, Ott *et al.* (2011) examined the genetic and environmental variation on 45 half-sib families of 20-year old lodgepole pine for chemical defences against MPB and its associated symbiotic fungus, *G. clavigera*. Changes in terpenoid abundance were followed after simulated MPB attack and inoculation of the fungus. Both constitutive and induced terpenoid levels were significantly affected by family, with low to medium heritabilities obtained. The wounding and inoculation with *G. clavigera* resulted in typical necrotic lesions in phloem and xylem tissues (Reid *et al.* 1967; Raffa and Berryman 1982) and significantly affected the abundance and quantity of terpenoids within the necrotic tissue. The quantity of total terpenoids was higher in induced tissue than in constitutive tissue, similarly as reported by Raffa and Berryman (1982) in their examination of differences between mature trees resistant and trees susceptible to MPB attack. The overall trend for 7 most abundant terpenoids was to increase after 7 days following inoculation. The rapid response in abundance of the monoterpenes following induction and the formation of necrotic tissue characterize the hypersensitive reaction defence against the bark beetle attack (Ott *et al.* 2011). The results of this study have indicated that lodgepole pine has significant genetic variation in constitutive bark terpenoids, and that genetic variation is present for chemical changes in response to attack or challenge from *G. clavigera* associated with MPB. The study also demonstrated that monoterpenoid abundances are under significant genetic control. The study provides information on MPB defence, the selection of lodgepole pine families with less risk of attack and mortality, and will be important in future management plans and strategies of MPB in the context of climate change, genetic improvement and other beetle hazard relationships.

5.4.5 Mountain pine beetle and pine host genomics

The genome sciences (genomics), the study of the complete genome of an organism (i.e., all hereditary information encoded in the DNA) is viewed as an important innovation strategy for expanded research to help mitigate some of the major challenges to the forest sector such as those related to climate change, forest productivity, forest health, and new threats of native and introduced pests. Other technologies included in genomics are transcriptome, proteomics, metabolomics and metagenomics (CFHG 2009). At the molecular level, the genome technology and research can be applied to identify specific genes, genetic variation and molecular pathways to better understand biological processes and their interactions with environmental factors.

The application of genomic sciences are stated to provide a new and comprehensive level of understanding of insect pests and diseases, their impacts and interactions on host trees and on forest ecosystems that may potentially enhance management strategies in the areas of risk analyses, decision support systems, pest monitoring and pest resistance breeding programs (CFHG 2009).

Genomic research associated with the current MPB epidemic in British Columbia and Alberta is large-scale and is established and functioning under the umbrella of the “Tria Mountain Pine Beetle Genomics Project” (www.thetriaproject.ca). It encompasses research resources focussed on the three interrelated components: the pine tree host, the bark beetle vector and its associated fungal pathogens. The project is funded under “Genome Canada” with co-funding provided by “Genome British Columbia”, “Genome Alberta” and the University of Alberta. Specific objectives of the Tria Project are to develop new knowledge about MPB, its fungal associates, interactions between these organisms, and how these interactions impact MPB population dynamics, and ultimately to integrate this information to strengthen forest management options, policies and strategies (Cooke and Bohlmann *et al.* 2009). The approach of the Tria Project is multi-disciplinary and collaborative involving many researchers in genomics, population genetics, molecular biology, ecology, systematics and mathematics (Cooke and Bohlmann *et al.* 2009). A listing of relevant publications by members of the Tria Project team can be found on the following

web site: www.thetriaproject.ca/index.php?article=pubsbyauth. The intent of this Case History is not to review all information generated by the Tria Project researchers, but to focus on information especially relevant to the MPB situation in Alberta.

Several studies have investigated MPB genetic variation, species interactions and behaviour over broad geographic landscapes. For example, Mock *et al.* (2007) described the pattern and degree of genetic variation in MPB across its wide range, determined whether there are detectable genetic differences among MPB populations on different host trees, and determined whether there is a molecular signature of demographic expansion range-wide at the northern edge of the current range. Bentz *et al.* (2011) describe geographic patterns of phenotypic plasticity in MPB development time and adult size. They found significant genetic and phenotypic variation among MPB populations and suggested that thermally-regulated traits may be directly linked to rapid numerical change and contribute to MPB outbreaks, particularly in a changing climate. In another study, James *et al.* (2011), compared and contrasted spatial genetic variation in MPB and its fungal symbiont *G. clavigera* and determined whether landscape features help explain observed genetic variation in each species. Their data suggested that MPB genetic variation was associated with geographic location, while that of the fungus was not, and that pine volume and climate explained MPB variation in the northern part of its recent outbreak expansion. In a similar study, Roe *et al.* (2011) examined the spatial variation in MPB-fungal associations as a function of latitude and elevation, representing the leading edge of the outbreak in western Canada. The results suggested that complex processes of competitive exclusion and coexistence help determine fungal community composition and that the consequences of these processes vary spatially. Differences in the constitutive terpene profile in phloem samples from lodgepole pine populations in British Columbia were analysed for differential resistance traits to MPB attack. Northern lodgepole pine populations generally had higher levels of constitutive terpenes and beetle attack than southern populations (Clark *et al.* 2010).

The threat of MPB invading the boreal forest and attacking jack pine has prompted several studies related to MPB's potential success and relationships with this new host. The susceptibility of jack pine to MPB is a major concern, but because lodgepole pine readily hybridizes with jack pine within a large zone in central Alberta, the exact boundary lines of species distributions are unclear. The studies of Cullingham *et al.* (2011) applied microsatellite markers to reliably distinguish lodgepole pine, jack pine and their hybrids and to delineate more clearly Alberta's lodgepole x jack pine hybrid zone. They demonstrated that MPB has undergone host range expansion into a new habitat on jack pine within the boreal forest. Coops *et al.*(2012) modeled lodgepole and jack pine vulnerability to MPB expansion into the boreal forest of western Canada with a changing climate to predict for the future periods 2001-2030 and to 2010-2040. The area of vulnerable lodgepole pine forests was 40,000 km^2 and 45,000 km^2 for the two periods, and for jack pine, the area of vulnerable forest ranged from 4,000 to 8,000 km^2.

Several studies have focussed on pine host reaction to MPB attack and its associated fungi in order to characterize the trees' defence reaction by production of a complex mixture of terpenes in their resin. Phloem resin was sampled on mass-attacked lodgepole pine in British Columbia during two periods for comparison: the first in early July at the beginning of flight period and the second at the end of August at the end of flight period (Clark *et al.* 2012). Trees that did not survive had higher phloem resin monoterpene levels at the end of August compared with levels in July, whereas trees that did survive mainly did not show a significant difference between the two sample dates. In a review paper, Zulak and Bohlmann (2010) describe terpenoid biosynthesis and specialized cells of conifer defence. The diversity of fungi associated with MPB on lodgepole pine in British Columbia was examined in a large sample of isolates: nine species of fungi were identified. The three most frequently isolated species were *G. clavigera*, *Ophiostoma minutum*-like species and *O. montium* (Lee *et al.* 2006a). Applying genomics, Hesse-Orce *et al.* (2010) investigated which genes are important for *G. clavigera's* ability to overcome antifungal pine terpenoids and phenolic compounds. They identified genes expressed in spores prior to germination and genes involved in response to treatment with lodgepole pine phloem extract. Variation in pathogenicity of *G. clavigera* was investigated on young plantation-grown lodgepole pine in British Columbia using five different isolates of this fungus. These were inoculated into trees (Plattner *et al.* 2008). Variability in pathogenicity was assessed based on three pathogenic indicators: phloem lesion length, sapwood occlusion area and sapwood moisture content. Variability in pathogenicity resulted from different isolates as well as with sample time post-inoculation. The pathogenicity of a recently reported fungal associate of MPB was identified as *Leptographium longiclavatum* sp. nov. (Lee *et al.* 2006b). It was suggested that this fungus is pathogenic to lodgepole pine and may contribute to mortality of attacked pines.

DiGuistini *et al.* (2011) applied genomics and transcriptome analyses of *G. clavigera* and report insights into how this fungus tolerates conifer defence chemicals of lodgepole pine, including oleoresin terpenoids during host colonization. The RNA-seq data indicated that terpenoids induce antimicrobial stress on *G. clavigera*, which may detoxify the terpenoids by using them as a carbon source.

The effect of water stress and *G. clavigera* inoculation in seedlings of lodgepole pine and jack pine was assessed to determine the effect on monoterpene content and needle tissue after inoculation, and to compare reaction differences between the two hosts (Lusebrink *et al.* 2011). Their results suggested that monoterpenes in

pine-MPB interactions differ between lodgepole and jack pine, and that they are affected by water availability.

Rice *et al.* (2007) and Rice and Langor (2009) investigated the fungal associates of MPB in lodgepole, jack pine and their hybrids in Alberta. In an inoculation experiment with *G. clavigera*, *O. montium* and *L.longiclavatum*, all three fungi caused lesions on lodgepole, jack and their pine hybrids. Their data suggested that all three fungal species are pathogenic on the pine hosts tested and that they showed comparable virulence (Rice *et al.* 2007). All three fungi were isolated from MPB-attacked lodgepole x jack pine hybrids in northwestern Alberta (Rice and Langor 2009).

In anticipation that MPB will advance into jack pine stands in Saskatchewan where jack pine budworm (*Choristoneura pinus pinus*) and dwarf mistletoe (*Arceuthobium americanum*) may co-inhabit the same trees and stands, some ecological and tree-mediated interactions are anticipated (Colgan and Erbilgin 2010, 2011; Klutsch and Erbilgin 2011). These authors speculated that trees weakened by either jack pine budworm or dwarf mistletoe could make them more susceptible to MPB attacks.

6.0 Reviews and Prioritization of Coniferous Pests for Resistance Breeding and Climate Change Adaptation Work

Table 1 lists twenty important insect and disease species occurring in Alberta and the ratings given in the second and third columns provide an approximate prioritization of the overall economic importance of each pest. However, the ratings may not provide a clear enough definition as to which pest or pests to focus on in an initial tree improvement program for resistance breeding and climate change adaptatation. It may be prudent and economically feasible to focus on only one or two species initially. Tables 2 and 3 are an attempt to help prioritize species importance by considering the status of each pest within each of seven Categories defined in Table 2 and assigning points (allotted somewhat subjectively) for each Category, based on author's familiarity with the pest species and their impacts in Alberta. Some Categories are weighted more heavily than others because of perceived relative importance in relation to economic and/or ecologic impacts. For example, in Category 1, one point is allotted if the species is native, but two points if the species is non-native, since the latter generally presents a higher risk. In Category 2, spread potential takes into consideration several factors such as host tree distribution, environmental factors, habitat suitability, tree age susceptibility, pathogen virulence and epidemiology, etc. Category 3 represents a subjective judgement of potential levels (risks) of pathogen infection or insect infestation in three intensity levels, Low, Medium and High, where a "High" level risk is allotted the most points. Category 4 considers susceptibility for three host tree age classes, where the maximum number of points allotted is three if the organism is known to affect all age classes. In Category 5, an attempt is made to break down all levels of damage impact where stem growth reduction, whole-tree mortality and product degrade are assigned highest values. Point ratings allotted here are accumulated for all impacts affected by each agent. Category 6 attempts to rate the relative importance of tree host species, whether they are of high commercial and/or ecological value, and whether they are currently classed as a species that "May Be At Risk" or "Endangered", with a maximum value of three assigned if the host tree can be considered in all three classes. The last Category 7 considers alternate control strategies other than genetic resistance breeding, whether these are readily available, are economical to apply and are effective in reducing impact. This Category also considers whether the strategies are mandatory to apply for various economic and/or ecologic reasons [e.g., MPB control strategies implemented in Alberta (ASRD 2007a, 2007b)], and whether the application of strategies is considered optional. Higher points are allotted in cases where control strategies appear not to be available, or have been ineffective, such as in the case of white pine blister rust (Burns *et al.* 2008; Geils *et al.* 2010; King *et al.* 2010).

Table 2. Categories and the number of points allotted in each Category for rating important insect and disease pests of conifers in Alberta.

Category	No. of Points Allotted
1. Native pest species:	1
Non-native pest species:	2
2. Spread potential within host range:	
Partial	1
Complete	2
3. Potential levels of infection or infestation:	
Low	1
Moderate	2
High	3
4. Susceptibility of infection/infestation by host age class:	
Seedlings	1
Saplings	1
Mature trees	1
5. Potential tree damage impacts:	
Branch/Leader mortality	1
Bud and needle loss	1
Cone reduction and seed loss	1
Root and stem decay	1
Stem growth reduction	2
Whole-tree mortality	3
Product degrade	2
6. Host tree status classification:	
Important commercial species	1
Important ecological species	1
Species “May Be At Risk”, or “Endangered”	1
7. Economical and effective control strategies:	
Strategies available	1
Strategies not-available, ineffective or non-economical to apply	2
Strategies mandatory	2
Strategies optional	1

Table 3 - presents a summary of the maximum points allotted to each pest species for each of the seven Categories listed in Table 2 - and the last column gives the total number of points, summed over all seven Categories. By this prioritization rating, the top three pest species ranked of highest importance are: **White pine blister rust (25 points), mountain pine beetle (24 points) and Armillaria root disease (20 points)**.

Table 3. Summary of the number of point ratings for each insect and disease species identified in Table 1 and according to the seven categories given in Table 2.

Pest species	1	2	3	4	5	6	7	Total points allotted
Mountain pine beetle	2	2	3	2	9	3	3	24
Spruce budworm	1	1	2	2	7	2	2	17
Spruce beetle	1	1	2	1	8	2	2	17
White pine weevil	1	1	2	1	7	2	2	16
White spotted sawyer beetle	1	1	2	1	2	2	2	11
Yellow headed spruce sawfly	1	1	2	1	6	2	2	15
Western spruce budworm	1	1	2	2	6	2	2	16
Douglas-fir beetle	1	1	2	1	8	2	2	17
Warren rootcollar weevil	1	1	1	2	6	2	2	15
Spruce cone maggot	1	2	2	2	1	2	2	12
Armillaria root disease	1	2	2	2	8	2	3	20
White pine blister rust	2	2	3	3	8	3	4	25
Comandra blister rust	1	1	2	2	6	2	2	16
Western gall rust	1	2	2	2	7	2	2	18
Tomentosus root rot	1	1	1	1	7	2	2	15
Red ring rot	1	1	1	1	7	2	2	15
Dwarf mistletoe	1	1	1	2	9	2	2	18
Pine needle cast	1	1	1	2	5	2	3	15
Atropellis canker	1	1	1	2	7	2	2	16
Stalactiform blister rust	1	1	1	2	6	2	2	15

7.0 Discussion of Important Pests that Need to be Addressed through Genetics and Breeding in Alberta

White pine blister rust, mountain pine beetle and Armillaria root disease are currently identified as the three most economically and ecologically important pests that should be given highest priority to address for forest genetics and breeding (Tables 1 and 3). While MPB is invasive in Alberta and has high economic and environmental impact, there is currently insufficient risk and impact in lodgepole and jack pine plantations and other stands to warrant a major genetics breeding program. While genetic resistance for MPB has been found present, it is at a low frequency (Yanchuk *et al.* 2008; Ott *et al.* 2011). Yanchuk (2006a) suggested that even if future planting stock could be improved for MPB resistance, the genetic gains would be minimal in cases during high population levels that create intense tree attack pressures.

A number of insect and disease pests identified in Tables 1 and 3 that primarily impact young conifer stands may all be considered of equal importance and of a similar feasibility level to consider for resistance screening and a tree breeding program. This list includes white pine weevil, comandra and stalactiform blister rusts, western gall rust, yellow headed spruce sawfly, pine needle cast, Warren rootcollar weevil, dwarf mistletoe, spruce cone maggot and Atropellis canker. It should be noted that some level of resistance screening in Alberta has already been done for several of these pests in plantations and seed orchards, and to some extent, during the process of selecting plus trees. For example, natural mortality has removed comandra blister rust and western gall rust (especially trees with stem galls) infected trees in one or more established seed orchards (Cerezke and Hoberg 1996). Similarly, natural mortality caused by Armillaria root disease and the Warren rootcollar weevil has likely removed trees most susceptible to these biotic agents in some plantations. In addition, roguing of white spruce seed orchards has also reduced tree susceptibility to white pine weevil (ASRD 2004; Hansen *et al.* 2005). Similar screening, based on phenotypic characters and roguing could be carried out on an on-going basis for a number of these pests, but may require annual monitoring to identify and record individual trees and families that may show higher susceptibilities and risks. This level of screening may be all that's necessary or economically feasible to achieve a satisfactory level of pest impact reduction, especially when screening is carried out when trees are young, after which ontogenetic resistance becomes effective for some species (e.g., Armillaria root disease, white pine weevil, yellowheaded spruce sawfly). The extent of genetic screening and breeding considered for each of these pests needs to be weighed against all other forms of pest control strategies.

Some initial screening may be considered for spruce budworm and western spruce budworm. However, the damage impact caused by these pests is most severe in mature stands and screening for resistant trees in situ would require considerable survey effort. Genetic programs for these species, as well as for the spruce beetle and the Douglas-fir beetle may not be economically viable at this time. Similarly, genetics breeding programs for tomentosus root rot, red ring rot, and the white spotted sawyer beetle are not likely to be economically feasible since they may be more efficiently managed through silvicultural and forest management practices.

Long-term provenance and progeny tests established in Alberta since the 1970's for important commercial confer species such as white spruce, lodgepole pine and jack pine now provide valuable information on patterns of growth potential and for developing guidelines for seed transfer that will help optimize growth and yield (Rweyongeza *et al.* 2010, 2011). These programs in both Alberta and British Columbia have demonstrated that the anticipated genetic gain in growth and volume may not always be achievable without alleviating negative impacts of some common insect and disease pests (Hunt and Ying 2005). For example, in white and Engelmann spruce, the white pine weevil is considered a major insect pest attacking young trees (King and Alfaro 2009; Rweyongeza et al, 2011). Studies in British Columbia have indicated that high weevil hazard areas consistently correspond to areas with hot, dry summers where weevils develop through required heat sums and trees may suffer some drought stress. Thus, hazard zones of the weevil are delineated on the basis of summer heat sums and potential vapour pressure deficit (King and Alfaro 2009).

In Alberta, in an 18-year old white spruce progeny trial, white pine weevil attack incidence showed an east-west trend in family variation, increasing from east to west. Attack incidence also appeared higher in provenances from higher elevations compared to lower elevations, and was also higher in provenances with a low growth potential (Rweyongeza *et al.* 2011).

For lodgepole and jack pine in Alberta, studies have shown an east-west cline of lodgepole pine resistance to gall infections caused by western gall rust, with resistance declining from east to west (Rweyongeza *et al.* 2010). In British Columbia, the tree improvement program of lodgepole pine incorporates disease resistance based on trials with different populations, including population introgression with jack pine (Hunt and Ying 2005). These authors reported that provenances from the northern and southern extremes, as well as from less cold hardy coastal provenances, were highly susceptible to infection by pine needle cast disease (*Lophodermella concolor*) and western gall rust. The studies also showed a clear geographic trend for resistance genes maintained in provenances where pests were more prevalent. Hunt and Ying (2005) noted that several of the rust diseases tend to be more common at lower elevations because of a longer growing season, which favours increased inoculum. There are also more frequent episodes of warmth

and moisture at lower elevations, which favours spore germination and successful host infection. They noted that increased rust cankering by stalactiform blister rust, western gall rust and pine needle cast (*L. concolor*) occurred when high elevation provenances of lodgepole pine were moved to lower elevations.

Disease resistance of lodgepole pine has been found to be mainly associated with provenance in British Columbia, and the resistance has tended to be highly consistent in diverse environments (Hunt and Ying 2005). Thus provenances susceptible to *L. concolor* and western gall rust for example, are likely to perform poorly over the range of test sites. In the zone of introgression of lodgepole with jack pine, there was a similar trend for decreased disease resistance consistent for three important needle and stem diseases (*L. concolor, C. coleosporioides* and *E. harknessii*) (Hunt and Ying 2005).

Recent studies of Douglas-fir seedlings from interior British Columbia that were screened for resistance to Armillaria root disease (*A. ostoyae*) indicated there were differences in seedling survival due to *A. ostoyae* infection, most of which could be explained by zone from which the family of seedlings originated (Cruikshank *et al.* 2010). Seedlings that were less susceptible to *A. ostoyae* originated from the drier and warmer zones. A general conclusion of this study was that moderate levels of family variation in resistance and low-moderate heritability suggested that gains in resistance of Douglas-fir to *A. ostoyae* could be achieved through genetic breeding (Cruikshank *et al.* 2010).

These studies of genetic pathogen resistance, the prevalence of family variable resistance traits, and the identification of general geographic areas of higher or lower risks for insect and disease pest species can provide valuable supportive information for seed transfer guidelines in the management of forest health and in strengthening reforestation policies (Mather *et al.* 2010; Woods *et al.* 2010; Kliejunas 2011). However, as pointed out by several authors (Heineman *et al.* 2010; Mather *et al.* 2010; Woods *et al.* 2010; Kliejunas 2011; Sturrock *et al.* 2011), projections are that the risks of damage due to insect and disease pests are likely to increase with climate warming as well as a higher frequency of extreme climatic events, all of which provide a high degree of uncertainty for future forest pest management and whether discovered resistant traits will be durable. As a consequence of projected elevated activities of pest species induced by climate change, it seems appropriate to increase the focus on tree resistance traits as well as on growth potential (Woods *et al.* 2010).

As Yanchuk and Allard (2009) point out, with the prospect of increased insect and disease risks in a changing climate, the “reaction time” for developing options for pest resistance may be strained and limited. They question whether resistance mechanisms currently being used will be able to provide some protection from new or related insects and diseases. They also suggest that funding sources and research capacity could become more restrained in the future, and that a better alignment of forest genetics and forest health programs will be required.

The insect and disease pest species listed in Table 1 on conifer species in Alberta are currently considered of highest priority for their economic impact on provincial forest resources. The list was limited to ten species of each category of insects and diseases largely on the basis of their prioritized status. Other lesser important common pest species could have been selected such as larch sawfly (*Pristiphora erichsonii*), Ips species of bark beetles, other needle diseases (e.g., needle casts, blights and rusts), as well as additional root and stem decay and stain pathogens. For most of these lesser economically important species, however, there is often only limited and sporadic reference to episodes of significant impact. It should be noted too that because of future climate uncertainties, some of the species listed in Table 1, as well as of other lesser important species, could become more prominent as pests in future decades, and similarly some species now classed as major pests could become less prominent. There is also the possibility of new pests developing, either of native species or of introduced species (Kliejunas *et al.* 2009; Woods *et al.* 2010; Sturrock *et al.* 2011).

This report does not include pests of hardwoods, but does make reference to abiotic stress such as drought and its dramatic effect on large-scale aspen dieback. The effects of drought are also impacting conifer species although critical impact data are generally lacking (Hogg *et al.* 2008; Worrall *et al.* 2010; Michaelian *et al.* 2011).

Case studies of resistance breeding programs are reviewed in detail for four important but different pest species. Two of the case studies, white pine blister rust on white pines and white pine weevil on Sitka and white spruce, are among the very few of such programs in forestry that are considered relatively successful, in that they are currently being applied and integrated into pest management strategies (Hunt and Ying 2005; King and Alfaro 2009; Zeglen *et al.* 2009; King *et al.* 2010). The relative success of these programs, however, has only been achieved after decades of research development (Hunt and Ying 2005; Yanchuk and Allard 2009). Woods *et al.* (2010) have suggested that, because of climate change, host-plant interactions are changing rapidly and generally in favour of the pests (Logan *et al.* 2003). Consequently, there is the possibility that the rate of change may exceed the current capacity of breeding programs to keep pace.

The third case study reviews the extent of tree breeding trials for resistance against dwarf mistletoe with application to lodgepole and jack pine. The fourth Case History study reviews MPB with a special focus pertaining to the current outbreak situation in Alberta. At risk are the severe losses of mature lodgepole pine, invasion of the beetle into lodgepole-jack pine hybrids, and the possibility of populations advancing into boreal forest jack pine habitats (Safranyik *et al.* 2010). In addition, MPB has been a contributing factor in the decline and mortality of stands of whitebark and limber pine in the province (Gould 2011). New approaches in the studies of MPB are applying genomics research to help unravel molecular interactions between the host tree, the beetle and its associated fungal microorganisms, as well as to better understand the mechanisms of host tree resistance.

Numerous other pathogen and insect resistance screening trials have been conducted in British Columbia and Alberta but primarily at the phenotypic selection level. These have included such pests as pine stem rusts, pine needle cast, Sequoia pitch moth and white pine weevil (Hunt *et al.* 1987; Ying and Hunt 1987; Wu *et al.* 1996, 1998; Yang *et al.* 1997; Wu and Ying 1997; Yang *et al.* 1998; Dhir *et al.* 2005). While some level of resistance was demonstrated in all cases, the mechanisms of resistance were not identified except for the white pine weevil (King and Alfaro 2009). Other insect and disease pests of conifers in Alberta that could be considered for initial phenotypic resistance screening of parent trees, as well as incorporating these in selection and breeding procedures where progeny or family data on pest incidence may be available, include Warren rootcollar weevil, yellowheaded spruce sawfly, spruce cone maggot, lodgepole terminal weevil (*Pissodes terminalis*), Atropellis canker, Armillaria root disease, and Douglas-fir needle cast (*Rhabdocline pseudotsugae*). It should, however, be noted that genetic improvement that may be realized for increased genetic resistance for these pests may be minimal or not significant without robust screening techniques.

The following Table 4 lists pest species in Tables 1 and 3 and rates them according to a priority level from highest to lowest for considering development of forest genetics and tree breeding programs, including strengthening of existing programs.

Table 4. List of important conifer pest species in Alberta and priority ratings from highest to lowest for considering the development of new or strengthening of existing genetic tree breeding programs.

Insect and pathogen species	Priority rating	Urgency
White pine blister rust	1	High[1]
Armillaria root disease	2	Medium
White pine weevil	3	Medium[1]
Comandra blister rust	3	Low
Stalactiform blister rust	3	Low
Western gall rust	3	Medium[1]
Yellow headed spruce sawfly	3	Low
Pine needle cast	3	Low
Warren root collar weevil	3	Low
Dwarf mistletoe	3	Low
Spruce cone maggot	3	Low
Spruce budworm	4	Nil
Western spruce budworm	4	Nil
Atropellis canker	4	Low
Mountain pine beetle	5	Low[1]
Spruce beetle	5	Nil
Douglas-fir beetle	5	Nil
Tomentosus root rot	6	Nil
Red ring rot	6	Nil
White spotted sawyer beetle	6	Nil

[1] Existing genetic tree breeding programs

8.0 Conclusions

Pest resistance breeding in forestry, compared to agriculture, is considered still in its infancy but is expanding rapidly for both insects and diseases. While few examples of successful resistance breeding programs exist in forestry thus far (e.g. white pine blister rust and white pine weevil), pest resistance breeding can provide an important tool on a wider scale to enhance forest productivity, health, and to help maintain genetic diversity for coniferous species in Alberta. To date, there has been limited focus in Alberta forest genetics and tree improvement programs for pest resistance breeding and only a few pests have been addressed in genetic screening and seed orchard genetic rouging. These include white pine weevil and western gall rust. A program for white pine blister rust resistance breeding is being considered as part of the whitebark pine and limber pine endangered species recovery plans. There is abundant evidence that genetic resistance is a function of co-evolution between host and pathogen or insect pest (Bower and Aitken 2011; Wagner 2002) and the fact that geographic trends in resistance genes are maintained where pests are more prevalent (Hunt and Ying 2005), means there is a need to incorporate this information into seed transfer guidelines and reforestation policy.

This report identifies the most common and economically important insect and disease species attacking conifer species in Alberta. Included among the insects is the mountain pine beetle as an example of a recent invasive pest that may now be well established in Alberta. Its colonization and devastating tree killing of mountain and foothills lodgepole, limber and whitebark pine forests are unprecedented in the history of this province. The beetle is now threatening to extend its range eastward into the boreal jack pine forests. Climate warming of winter and summer temperatures have provided, in large part, the triggering mechanism for the mountain pine beetle to expand its range northward and to higher elevations in British Columbia, and eastward into Alberta (Carroll *et al.* 2004). Similar devastating events of severe spruce mortality have occurred in the Yukon and Alaska as a result of a spruce bark beetle epidemic triggered by severe and prolonged drought (Berg *et al.* 2006; Garbutt *et al.* 2006). As reviewed in this document, climate warming is predicted to affect forest health, insect and pathogen biology, directly affect host trees, and the interaction between the pathogen, insect pest, host and climate (Kliejunas *et al.* 2009; Sturrock *et al.* 2011). Woods *et al.* (2010) emphasized an urgent need to better understand how climate change will affect biotic and abiotic disturbances and how forests will respond to them. They and others (Dukes *et al.* 2009; Kliejunas 2011; Sturrock *et al.* 2011) stress the need for improved and more comprehensive monitoring programs (e.g., monitoring, forecasting, modeling and risk assessments) to develop this understanding. As an example, Heineman *et al.* (2010)

surveyed a large number of 15- to 30-year old lodgepole pine stands in interior British Columbia and quantified the presence of important biotic agents and their damage risks to trees. They found evidence that increased risk of damage by several insect and pathogen pests was associated with climate warming and increasingly dry conditions. They predicted that the impact of disease and insect pests and abiotic disturbance events related to climate change will increase in future decades, and will influence silvicultural planning and timber supply prediction. There are also concerns that the predicted increased damages will impact the free-to-grow status of young stands since 27 per cent of young lodgepole pine stands surveyed were no longer free-growing after having been declared free-to-grow (Mather *et al.* 2010).

The review of science pertaining to breeding for pest resistance applications and the detailed case history studies of four important pest species provide background information to help guide the future work program of insect and disease selection procedure and prioritization. Adding additional traits to the selection and breeding scheme, such as insect and pathogen resistance traits, require regular revision of breeding plans, genetic testing and field-monitored test sites. The future challenges of insect and disease pests, disturbance-induced changes in Alberta’s forests and uncertainties associated with climate changes will all require projects to be reviewed and resistance breeding programs and objectives to be implemented and strengthened. Considerable additional resources, long term program commitments (20 years or more) and cooperation between ESRD, industry, Canadian Forest Service, Parks Canada and University of Alberta scientists will be required for addressing these needs. A good start in this regard has already been made with MPB program special funding to ATISC and endangered species recovery plans under development by ESRD.

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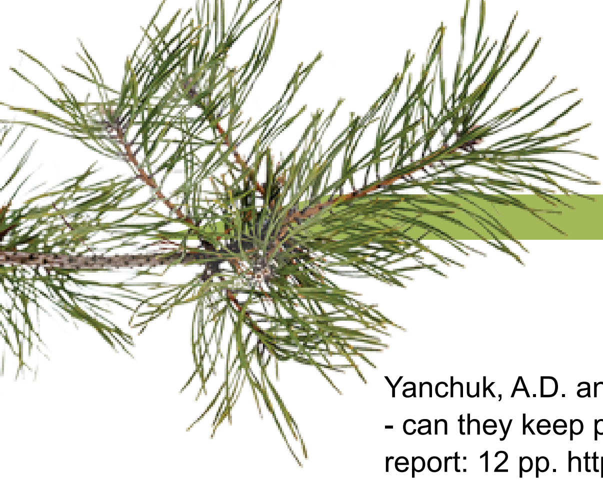

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