COSEWIC
Assessment and Status Report

on the

Limber Pine
Pinus flexilis

in Canada

ENDANGERED
2014

COSEWIC
Committee on the Status
of Endangered Wildlife
in Canada

COSEPAC
Comité sur la situation
des espèces en péril
au Canada

COSEWIC status reports are working documents used in assigning the status of wildlife species suspected of being at risk. This report may be cited as follows:

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Limber Pine — Photo: C. Smith.

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COSEWIC
Assessment Summary

Assessment Summary – November 2014

Common name
Limber Pine

Scientific name
Pinus flexilis

Status
Endangered

Reason for designation
This tree species is imminently and severely threatened throughout its Canadian range by White Pine Blister Rust (an introduced pathogen), Mountain Pine Beetle, and climate change. Surveys at a number of sites in 2009 document an average of 43% and 35% of infected or dead trees, respectively. Repeated survey information leads to an estimated decline in the Canadian population of about 1% per year. At that rate, close to 2/3 of mature individuals are expected to be lost over the next 100 years, and local subpopulations could become extirpated.

Occurrence
British Columbia, Alberta

Status history
Designated Endangered in November 2014.

COSEWIC
Executive Summary

Limber Pine
Pinus flexilis

Wildlife Species Description and Significance

Limber Pine is a five-needled pine, typically 3-15 m tall, with a much-branched, rounded crown. The seed cones are egg-shaped (7-15 cm long by 4-6 cm wide) and light-brown to greenish-brown. The cones open to release the seeds and then fall to the ground. Its large seeds are brown, 10-15 mm long and usually wingless.

Limber Pine growth rings can provide information on climate and river flows back 500-1000 years, much further than historical records, which are generally 100 years at most. This information is important for understanding and projecting scenarios of climate change, including drought and river flows. Limber Pine is also a "keystone" species, the seeds providing important food for bears, small mammals and birds, and the trees sheltering other species.

Distribution

Limber Pine naturally occurs only in western North America, extending from southeastern British Columbia and southwestern Alberta south to northern Arizona and New Mexico, and southern California. In Canada, it extends in southeastern British Columbia, from near Field, south along the eastern side of the Rocky Mountain Trench nearly to the Canada-United States of America (U.S.) border and, in southwestern Alberta, from near Kootenay Plains south in the Rocky Mountains and Foothills to the Canada-U.S. border.

Habitat

In Canada, Limber Pine occurs typically on warm, dry sites in the lower portions of the mountains and foothills at elevations of ca. 850 m to 1900 m. Some occurrences are as high as around 2000 m and may form mixed stands with Whitebark Pine. Limber Pine can occur at both lower and upper treeline sites. Aspects are usually southerly or westerly and slopes vary from gentle to steep. In British Columbia, most stands are on steep, exposed cliffs and ridges, while in Alberta, some stands are in more gently rolling terrain as well as rocky ridges and outcrops. Limber Pine sites are often exposed to strong winds, which in conjunction with shallow, well to rapidly drained soils and warm aspects, create droughty conditions.

Biology

Limber Pine is a long-lived species, frequently reaching several hundred years and trees over 1000 years old are known. Cones are typically produced at about 50 years of age, although this may be delayed, and the largest cone crops are produced decades later. Cone production is irregular with some years of very low seed production. Seeds are primarily dispersed by birds but also by small mammals. However, most seedlings germinate from seeds dispersed by birds, so dispersal by small mammals likely contributes little to recruitment. Both seedlings and trees are physiologically adapted to tolerate harsh environmental conditions, especially drought.

Limber Pine is dependent on mycorrhizal fungi, which enable the roots to take up nutrients and also aid in protecting the roots from pathogens. Other fungi can damage seeds, needles, stems and roots. Limber Pine needles are the sole food of a small ermine moth, which is rare in Canada.

Population Sizes and Trends

The number of mature Limber Pine trees in Canada is estimated to be 44.4 million. The Canadian population is declining at an average annual rate of about 1%, which over 100 years is a 66% decline. Rescue from populations in the U.S. is not a realistic possibility because the same threats are affecting those populations, many of which are declining as well.

Threats and Limiting Factors

Limber Pine is imminently and severely threatened throughout its Canadian range by White Pine Blister Rust (an introduced species), Mountain Pine Beetle, and climate change. While each taken singly poses a significant threat, they interact to further increase the severity of the impacts. With climate change, the frequency, intensity and duration of drought is projected to increase, and fire is projected to be more frequent and severe. Stressed trees are likely to be more susceptible to pathogens and insects.

Protection, Status, and Ranks

Limber Pine is listed as Endangered in Alberta under the *Wildlife Act*, although no provisions exist under that act to provide broad legal protection for either individuals or habitat. A provincial recovery plan is being prepared. In British Columbia, Limber Pine has no legal protection, although it is a Blue-Listed (special concern) species. Some protection is provided in both provinces for small subpopulations in provincial protected areas. Limber Pine also occurs in national parks in Alberta and British Columbia, where both individuals and habitat are protected.

Limber Pine has a NatureServe conservation rank of Imperilled (S2) in Alberta and Vulnerable (S3) in British Columbia.

TECHNICAL SUMMARY

Genus species: Pinus flexilis

Limber Pine Pin flexible

Range of occurrence in Canada: Alberta, British Columbia.

Demographic Information

Generation time (1/mortality rate of mature individuals + age at first reproduction) – see section Life Cycle and Reproduction	150-250 yrs
Is there an [observed, inferred, or projected] continuing decline in number of mature individuals?	Yes, observed and projected
Estimated percent of continuing decline in total number of mature individuals within [5 years or 2 generations]	51-76% (mean = 66%), observed and estimated over 100 yrs
[Observed, estimated, inferred, or suspected] percent [reduction or increase] in total number of mature individuals over the last [10 years, or 3 generations].	Unknown
Projected percent reduction in total number of mature individuals over the next 100 years.	51-76% (mean = 66%)
[Observed, estimated, inferred, or suspected] percent [reduction or increase] in total number of mature individuals over any [10 years, or 3 generations] period, over a time period including both the past and the future.	51-76% (mean = 66%), observed and estimated over 100 yrs
Are the causes of the decline clearly reversible and understood and ceased? Some causes (White Pine Blister Rust, Mountain Pine Beetle) are understood to some extent, but not ceased, and, while some impacts may be mitigated, essentially not reversible.	No
Are there extreme fluctuations in number of mature individuals?	No

Extent and Occupancy Information

Estimated extent of occurrence	44,460 km²
Index of area of occupancy (IAO) (2 km x 2 km grid value, Biological AO much smaller)	1480 km²
Is the total population severely fragmented?	no
Number of locations* (threats of Mountain Pine Beetle and White Pine Blister Rust)	1
Is there a projected continuing decline in extent of occurrence? Climate change will affect EO but details are unclear as suitable habitat shifts.	unknown but likely
Is there a projected continuing decline in index of area of occupancy? Local subpopulation extirpations likely by rust, beetle and climate change.	yes

* See Definitions and Abbreviations on COSEWIC website and IUCN 2010 for more information on this term.

Is there an [observed, inferred, or projected] continuing decline in number of subpopulations?	yes
Is there an [observed, inferred, or projected] continuing decline in number of locations*?	no
Is there a projected continuing decline in area, extent and/or quality of habitat? Habitat quality will continue to decline but area and extent unclear as climate change shifts suitable habitat.	yes
Are there extreme fluctuations in number of subpopulations?	no
Are there extreme fluctuations in number of locations*?	no
Are there extreme fluctuations in extent of occurrence?	no
Are there extreme fluctuations in index of area of occupancy?	no

Number of Mature Individuals (in each subpopulation)

Subpopulation	**N Mature Individuals**
Insufficient information to delineate	–
Total Estimated from IAO of 1480 sq km and mean density of 300 individuals/ha in monitoring plots	44.4 million

Quantitative Analysis

Probability of extinction in the wild is at least [20% within 20 years or 5 generations, or 10% within 100 years].	not done

Threats (actual or imminent, to subpopulations or habitats)

White Pine Blister Rust, Mountain Pine Beetle, climate change.

Rescue Effect (immigration from outside Canada)

Status of outside population(s)? Populations in U.S. have same threats as in Canada and are declining.	
Is immigration known or possible?	possible
Would immigrants be adapted to survive in Canada? Adapted to current climate but no better adapted to blister rust or pine beetle.	possibly
Is there sufficient habitat for immigrants in Canada?	unlikely

* See Definitions and Abbreviations on COSEWIC website and IUCN 2010 for more information on this term.

Is rescue from outside populations likely?	no

Status History

COSEWIC: Designated Endangered in November 2014.

Status and Reasons for Designation

Status: Endangered	**Alpha-numeric code:** A3e+4ae
Reasons for designation: This tree species is imminently and severely threatened throughout its Canadian range by White Pine Blister Rust (an introduced pathogen), Mountain Pine Beetle, and climate change. Surveys at a number of sites in 2009 document an average of 43% and 35% of infected or dead trees, respectively. Repeated survey information leads to an estimated decline in the Canadian population of about 1% per year. At that rate, close to 2/3 of mature individuals are expected to be lost over the next 100 years, and local subpopulations could become extirpated.	

Applicability of Criteria

Criterion A (Decline in Total Number of Mature Individuals): Meets A3e for Endangered, with a decline of 66% projected over the next 100 years, based on (e) the effects of an introduced pathogen. Meets A4ae for Endangered, with a decline of 66% from the past (1996) to 100 years into the future, based on the same indicator as above, plus direct observation of mortality and infection rates by White Pine Blister Rust in sample plots.
Criterion B (Small Distribution Range and Decline or Fluctuation): Meets B2ab(ii,iii,v) for Threatened, with IAO < 2,000 km², fewer than 10 locations, and continuing decline in (ii) area of occupancy (local extirpation), (iii) quality of habitat (due to climate change), and (v) number of mature individuals (high infection and mortality rates).
Criterion C (Small and Declining Number of Mature Individuals): Does not apply as the number of mature individuals exceeds thresholds.
Criterion D (Very Small or Restricted Total Population): Meets D2 for Threatened, with less than 5 locations, and capable of becoming Endangered in a very short time period because of the projected population decline.
Criterion E (Quantitative Analysis): Not done.

COSEWIC HISTORY

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) was created in 1977 as a result of a recommendation at the Federal-Provincial Wildlife Conference held in 1976. It arose from the need for a single, official, scientifically sound, national listing of wildlife species at risk. In 1978, COSEWIC designated its first species and produced its first list of Canadian species at risk. Species designated at meetings of the full committee are added to the list. On June 5, 2003, the *Species at Risk Act* (SARA) was proclaimed. SARA establishes COSEWIC as an advisory body ensuring that species will continue to be assessed under a rigorous and independent scientific process.

COSEWIC MANDATE

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assesses the national status of wild species, subspecies, varieties, or other designatable units that are considered to be at risk in Canada. Designations are made on native species for the following taxonomic groups: mammals, birds, reptiles, amphibians, fishes, arthropods, molluscs, vascular plants, mosses, and lichens.

COSEWIC MEMBERSHIP

COSEWIC comprises members from each provincial and territorial government wildlife agency, four federal entities (Canadian Wildlife Service, Parks Canada Agency, Department of Fisheries and Oceans, and the Federal Biodiversity Information Partnership, chaired by the Canadian Museum of Nature), three non-government science members and the co-chairs of the species specialist subcommittees and the Aboriginal Traditional Knowledge subcommittee. The Committee meets to consider status reports on candidate species.

DEFINITIONS
(2014)

Wildlife Species	A species, subspecies, variety, or geographically or genetically distinct population of animal, plant or other organism, other than a bacterium or virus, that is wild by nature and is either native to Canada or has extended its range into Canada without human intervention and has been present in Canada for at least 50 years.
Extinct (X)	A wildlife species that no longer exists.
Extirpated (XT)	A wildlife species no longer existing in the wild in Canada, but occurring elsewhere.
Endangered (E)	A wildlife species facing imminent extirpation or extinction.
Threatened (T)	A wildlife species likely to become endangered if limiting factors are not reversed.
Special Concern (SC)*	A wildlife species that may become a threatened or an endangered species because of a combination of biological characteristics and identified threats.
Not at Risk (NAR)**	A wildlife species that has been evaluated and found to be not at risk of extinction given the current circumstances.
Data Deficient (DD)***	A category that applies when the available information is insufficient (a) to resolve a species' eligibility for assessment or (b) to permit an assessment of the species' risk of extinction.

* Formerly described as "Vulnerable" from 1990 to 1999, or "Rare" prior to 1990.

** Formerly described as "Not In Any Category", or "No Designation Required."

*** Formerly described as "Indeterminate" from 1994 to 1999 or "ISIBD" (insufficient scientific information on which to base a designation) prior to 1994. Definition of the (DD) category revised in 2006.

Environment Canada — Environnement Canada
Canadian Wildlife Service — Service canadien de la faune

Canada

The Canadian Wildlife Service, Environment Canada, provides full administrative and financial support to the COSEWIC Secretariat.

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WILDLIFE SPECIES DESCRIPTION AND SIGNIFICANCE

Name and Classification

Scientific name: *Pinus flexilis* E. James

Synonyms: *Apinus flexilis* (E. James) Rydberg

Common names: Limber Pine, Pin Flexible

Family: Pinaceae (Pine Family)

Major plant group: Gymnosperms (conifers)

Following recent phylogenetic, DNA-based studies (e.g., Liston *et al.* 1999, 2007; Gernandt *et al.* 2005; Syring *et al.* 2005, 2007; Eckert and Hall 2006), Limber Pine is placed in the subgenus *Strobus,* section *Quinquefolia*, subsection *Strobus,* which includes 22 species of pine worldwide.

Limber Pine is most closely related to Southwestern White Pine (*P. strobiformis*) and Mexican White Pine (*P. ayacahuite*) (Earle 2010) and appears to hybridize with Southwestern White Pine where the two species overlap in the southwestern U.S. (Andresen and Steinhoff 1971). This morphologically intermediate form has been described as *P. flexilis* var. *reflexa* and is confined to the southwestern U.S. While there is ongoing controversy about the relationships and taxonomy of Limber Pine, Southwestern White Pine, and Mexican White Pine, these do not involve the Canadian populations of Limber Pine. Of the three, only Limber Pine is found in Canada.

Morphological Description

In Canada, mature trees are typically 3-15 m tall, with a much-branched, rounded crown (Figure 1). On exposed sites, the trees may be stunted and sculpted by the wind. In sheltered, mesic sites, the trees are usually taller (up to 20 m), with a straight trunk and conical crown (Douglas *et al.* 1998). The bark is grey and nearly smooth on young trees, becoming dark brown to blackish and checked into scaly plates in age (Kral 1993; Douglas *et al.* 1998).

The needles are in bundles of five and are 3-7 cm long and 1-1.5 mm thick (Kral 1993). The seed cones are ovoid, 7-15 cm long by 4-6 cm wide, and light-brown to greenish-brown. The cones open to release the seeds and then fall to the ground. The seeds are obovoid, brown, 10-15 mm long and usually wingless. The pollen cones are ca. 15 mm long and yellowish (Kral 1993).

Figure 1. Mature Limber Pine tree. Photo: C. Smith.

Limber Pine can be confused with Whitebark Pine (*P. albicaulis*) where the ranges of the two species overlap in southwestern Alberta and southeastern British Columbia. Both species have five needles, often grow on rocky exposed sites, and can have a similar canopy shape. Seed cones of Limber Pine are typically longer at 7-15 cm vs. 5-8 cm for Whitebark Pine, are tan coloured in Limber Pine vs. purple in Whitebark Pine, and, in Limber Pine, open to release the seeds, which then drop from the tree vs. Whitebark Pine in which the cones remain closed and on the tree unless removed by animals (Kral 1993). The presence of cones on the ground beneath a tree is often the clearest evidence for separating Limber and Whitebark pines. The pollen cones of Limber Pine are typically yellowish vs. scarlet for Whitebark Pine.

Western White Pine (*Pinus monticola*) is the only other five-needled pine that occurs within the range of Limber Pine in Canada. It usually grows in more mesic habitats than Limber Pine and co-occurrence of the two species in a stand is rare. Western White Pine can be distinguished by its larger cones (10-25 cm) and longer, more slender needles (4-10 cm x 0.7-1 mm vs. 3-7 cm x 1-1.5 mm in Limber Pine and Whitebark Pine).

Population Spatial Structure and Variability

Genetic structure in Limber Pine has been assessed with allozyme and DNA analysis (Schuster *et al.* 1989; Latta and Mitton 1997; Mitton *et al.* 2000; Schuster and Mitton 2000; Jorgensen *et al.* 2002; Bower *et al.* 2011). These studies include some Canadian populations and the similarity of Canadian populations to those in the Northern Rockies of the U.S. suggest that results from studies of U.S. populations can be inferred to Canadian populations.

The overall pattern is one in which most of the genetic diversity is within local populations rather than being due to differences among populations. Both this pattern and the amount of diversity are similar to other bird-dispersed species of pine in western North America (Jorgensen *et al.* 2002; Bower *et al.* 2011). However, the diversity is typically about one-third that of wind-dispersed pines (Bower *et al.* 2011). This pattern also reflects the origin of contemporary Limber Pine populations from multiple Pleistocene refugia, followed by contemporary gene flow among populations (Mitton *et al.* 2000; Jorgensen *et al.* 2002). Gene flow appears to be both by pollen transfer and seed dispersal (Schuster *et al.* 1989; Schuster and Mitton 2000), such that isolated, marginal populations have nearly as high genetic diversity as large, central populations (Mitton *et al.* 2000). Despite the naturally fragmented population distribution, this gene flow, mainly by pollen, is estimated to be sufficient to overcome genetic drift (Schuster *et al.* 1989; Jorgensen *et al.* 2002; Richardson *et al.* 2010).

Limber Pine is the most widespread white pine in North America but only weak trends, mostly north-south, are apparent in quantitative traits, e.g., cone size, seed weight, seedling growth (Steinhoff and Andresen 1971).

Designatable Units

There are no taxonomic subspecies or varieties currently recognized for this species and there is no evidence of significant genetic structure or barriers to gene flow among the Canadian populations. Thus, only one designatable unit, the species as a whole, is recognized.

Special Significance

In much of its range, Limber Pine grows near or forms a lower elevational treeline adjacent to dry, upland grasslands. These trees are subject to drought stress and their annual growth rings provide a record of precipitation and other hydrologic variables extending back 500-1000 years, whereas historical and instrumental records go back only about 100 years (Case and MacDonald 1995; 2003; MacDonald and Case 2005; Perez-Valdivia *et al.* 2010; Vanstone *et al.* 2010). This information has important economic and social implications for understanding the frequency and severity of droughts. For example, the 1918-1922 drought in southern Alberta, which caused much economic and social disruption, was neither atypical nor the most severe in the past 500 years (Case and MacDonald 1995). Also, the information currently used to apportion river flows among the prairie provinces is from a time period that was atypically stable and moist (Sauchyn *et al.* 2002; Case and MacDonald 2003).This information is also significant to understanding broad scale climatic phenomena (e.g., El Niño-Southern Oscillation, Pacific Decadal Oscillation) and in testing models of future climate change (St. Jacques *et al.* 2011).

Limber Pine is often the only tree species that can occupy steep, windswept headwater habitats and plays a key role in snow capture, mediating snow melt, and controlling erosion (Schoettle 2004). On more mesic sites, as an early seral species, it facilitates the establishment of other conifer species and succession (Rebertus *et al.* 1991; Donnegan and Rebertus 1999).

With its northern range boundary in Canada, Limber Pine is important for studies of genetic and evolutionary processes in response to climate change and the effects of introduced species, such as White Pine Blister Rust, *Cronartium ribicola* (Franks *et al.* 2014). Understanding these processes will be crucial to modelling and adapting to future climate change.

Limber Pine is also a “keystone mutualist” species (Mills *et al.* 1993), which is a species “so closely involved with other organisms that if it becomes extinct or even seriously depleted, the effects will ramify throughout the ecosystem” (Lanner 1996) – see **Interspecific Interactions** section. Whitebark Pine has a similar ecological role. However, it is an Endangered species in Canada (COSEWIC 2010) as it is declining due to many of the same factors affecting Limber Pine, and there is little overlap in geographic or habitat range between the two species. Therefore, Whitebark Pine is unlikely to replace the ecological role of Limber Pine.

Several cultivars of Limber Pine have been developed from various sources across its range and are available from some nurseries. Its drought tolerance makes it attractive for shelter belts and other landscape uses. It has been successfully grown outside its native range (NDSU 2013).

DISTRIBUTION

Global Range

Limber Pine occurs only in western North America (Figure 2) extending along the Rocky Mountains from Alberta and British Columbia to southern Montana, from where the range extends south along the Rocky Mountains to New Mexico and southwest across the Great Basin to southern California (Kral 1993; Tomback and Achuff 2010). Eastern outliers occur in western North Dakota, western South Dakota (Black Hills), and western Nebraska, with a western outlier in northeastern Oregon (Wallowa Mountains). While fossil evidence indicates a broader range during the Pleistocene, extending further south and east into the Great Basin of the U.S., northern Mexico, central Nebraska, Kansas, and Texas (Wells 1983; Wells and Stewart 1987; Betancourt 1990; Rhode and Madsen 1998), reports of Limber Pine occurring in Mexico currently appear to be based on a different taxonomic treatment than used here (e.g., Earle 2010; IUCN 2010b).

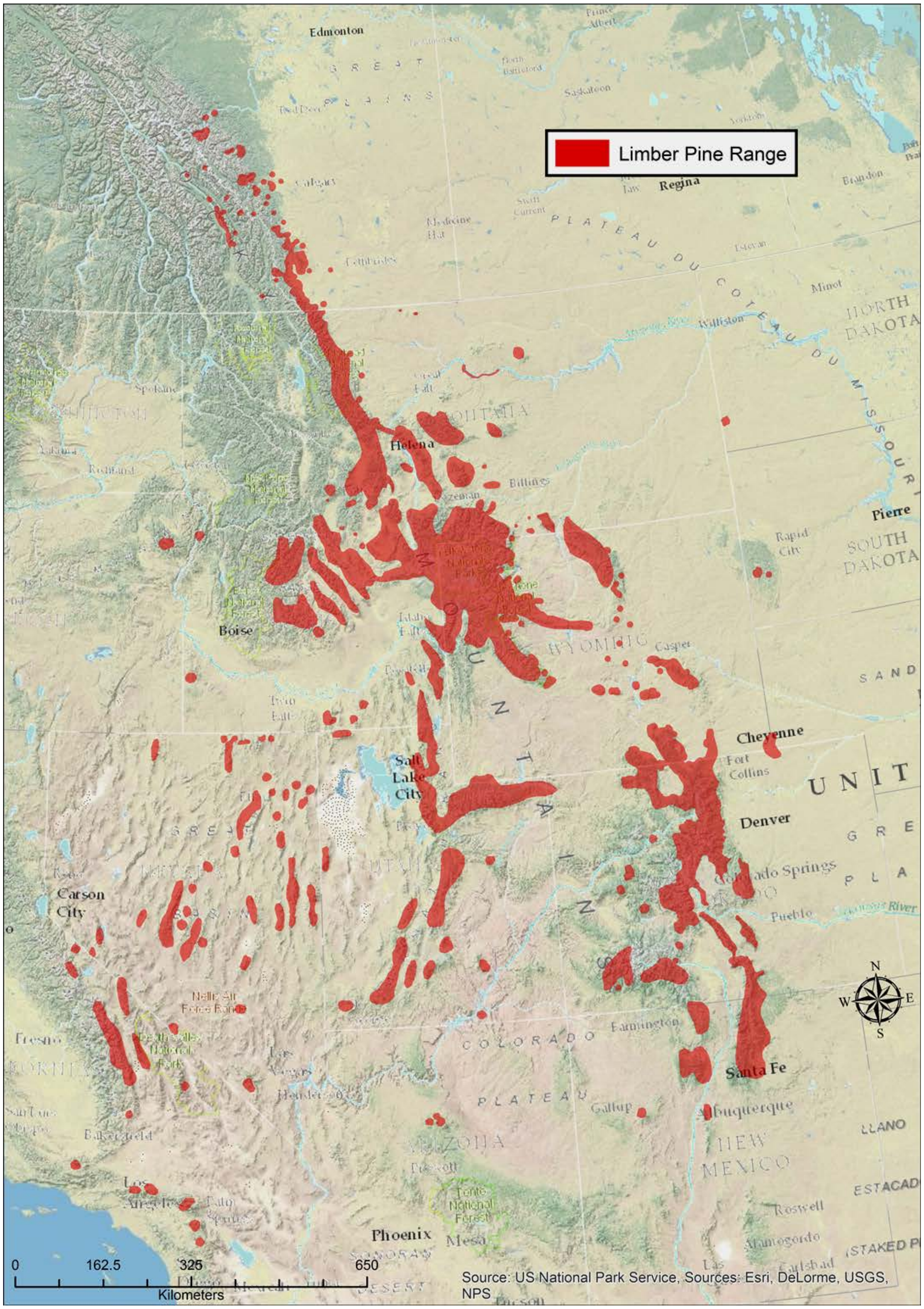

Figure 2. Global range of Limber Pine.

Canadian Range

The Canadian range of Limber Pine (Figure 3) extends from southeastern British Columbia (near Field, ca. 51° 26'N) south along the eastern side of the Rocky Mountain Trench nearly to the Canada-U.S. border, and from southwestern Alberta (near Kootenay Plains, ca. 52° 16'N) to the Canada-U.S. border in the Rocky Mountains and Foothills. This range includes portions of the Montane, Subalpine, Foothills Parkland, and Foothills Fescue Natural Subregions of Alberta (Downing and Pettapiece 2006) and the Interior Douglas-fir, Montane Spruce, and Engelmann Spruce-Subalpine Fir biogeoclimatic zones in British Columbia (Meidinger and Pojar 1991).

Approximately 10% of the global range occurs in Canada. The distribution is generally fragmented, with small populations being disjunct, particularly near the northern boundaries.

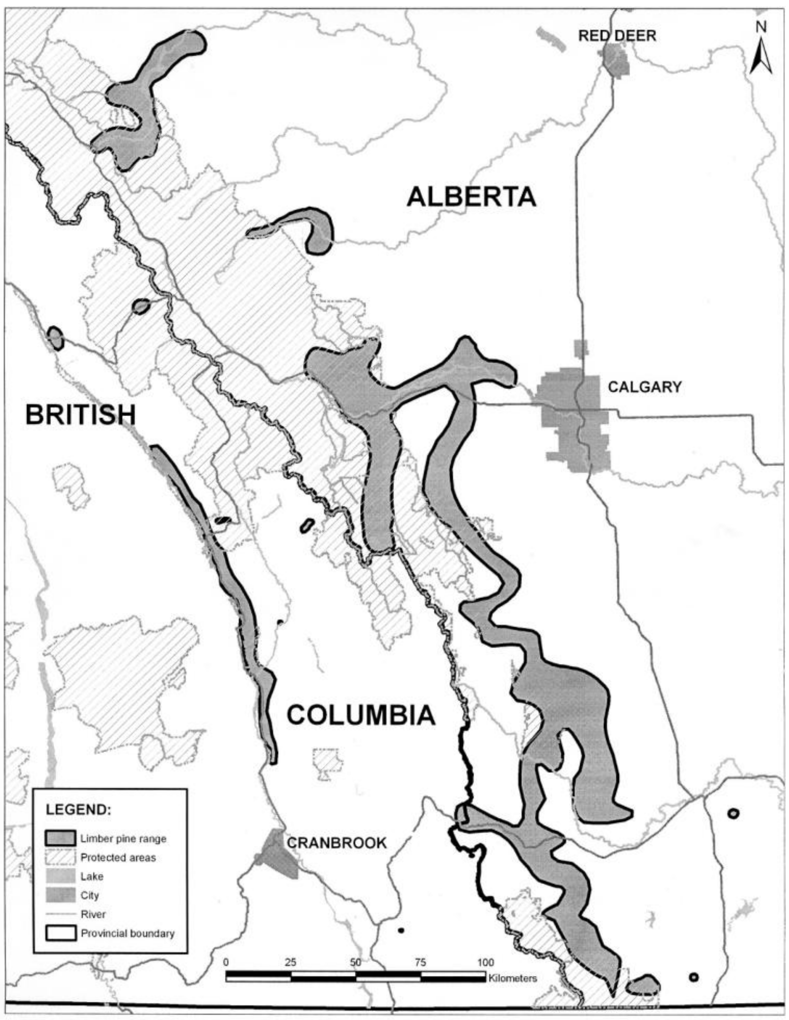

Figure 3. Canadian range of Limber Pine (currently occupied).

Extent of Occurrence and Area of Occupancy

The extent of occurrence (EO) in Canada is estimated as 44,460 sq km with about 80% in Alberta and 20% in British Columbia.

The index of area of occupancy (IAO), estimated with a 2 km x 2 km grid and element occurrence data (ACIMS 2011; BC-CDC 2011; Moody, pers. comm. 2011; Achuff, pers. obs.), is 1480 km^2 with 1420 km^2 in Alberta and 60 km^2 in British Columbia. The element occurrence data likely do not contain all local populations, which leads to an underestimate of IAO. However, because many Limber Pine populations occupy areas of <1 km^2, using the 2 km x 2 km grid overestimates the biological area of occupancy.

Search Effort

Most of the information on the range of Limber Pine in Canada is derived from natural resource inventories and operational monitoring in both Alberta (e.g., Holland and Coen 1982; Achuff *et al.* 2002; ACIMS 2011; ESIS 2011; FIAS 2011; WLIS 2011) and in British Columbia (e.g., Achuff *et al.* 1984; Lea 1984; Achuff *et al.* 1993; BC-CDC 2011; BEC 2011; E-flora BC 2011). Information from the provincial conservation data centres includes specimens deposited in university and government agency herbaria, as well as from university research projects. This amounts to hundreds, if not thousands, of person-days of search effort distributed across the entire range of Limber Pine in Canada.

In addition, targeted searches have been done recently in southeastern British Columbia comprising about 35 person-days. As well, the scientific literature has been searched for information on the occurrence of Limber Pine in Canada.

With this search effort, the range (EO) of Limber Pine in Canada is known with a high degree of confidence. However, more detailed information on the locality of local subpopulations (used to determine IAO) is less well known. Thus, it has not been possible to delineate the number of subpopulations.

HABITAT

Habitat Requirements

In its Canadian range, Limber Pine occurs typically on warm, dry sites in the Montane and lower portion of the Subalpine natural sub-regions in Alberta (Downing and Pettapiece 2006) and the Interior Douglas-fir, Montane Spruce, and lower portion of the Engelmann Spruce-Subalpine Fir biogeoclimatic zones in British Columbia (Meidinger and Pojar 1991). Elevations occupied generally are from ca. 850 m to 1900 m. Some occurrences are in the Upper Subalpine, as high as around 2000 m, and may form mixed stands with Whitebark Pine. High elevation occurrences, to 3800 m (Steele 1990; Millar *et al.* 2007), are more common in the U.S. portion of its range. Limber Pine can thus occur at both lower and some upper treeline sites. Aspects are usually southerly or westerly and slope angle varies from gentle to steep (20-80%). In British Columbia, most stands are on steep, exposed cliffs and ridges, while in Alberta, some stands are in more gently rolling terrain as well as rocky ridges and outcrops. Limber Pine sites are often exposed to strong winds, which in conjunction with shallow, well to rapidly drained soils and warm aspects, help create significant moisture deficits and affect tree growth.

Limber Pine occurs on a variety of bedrock materials, including limestone and sandstone, as well as morainal and stream gravel materials. Soils are typically well to rapidly drained, Regosolics or Brunisolics (Timoney 1999; Achuff *et al.* 2002).

Limber Pine typically grows as an open forest or as scattered trees with a grassy or shrubby understory. Species that frequently occur with it in Canada include: Douglas-fir (*Pseudotsuga menziesii*), Lodgepole Pine (*Pinus contorta*), Rocky Mountain Juniper (*Juniperus scopulorum*), Common Juniper (*J. communis*), Creeping Juniper (*J. horizontalis*), Shrubby Cinquefoil (*Dasiphora fruticosa*), Buffaloberry (*Shepherdia canadensis*), Foothills Rough Fescue (*Festuca campestris*), and Junegrass (*Koeleria macrantha*) (Timoney 1999; Achuff *et al.* 2002; ACIMS 2011).

Limber Pine is a major component of six ecological communities of conservation concern (tracked) in Alberta (Allen 2010), most of which are ranked as Imperilled (S2). In British Columbia, Limber Pine communities have been described but not ranked (Utzig *et al.* 1977; BC-CDC 2011).

Limber Pine is considered to be shade-intolerant and studies of stand dynamics at both high and low elevations indicate that it is an early colonizer of fire-disturbed sites (Rebertus *et al.* 1991; Webster and Johnson 2000). Following establishment, Limber Pine often facilitates the establishment of other plants, including trees that successionally may replace it (Rebertus *et al.* 1991; Baumeister and Callaway 2006). In mesic, mixed species stands, it may be replaced by other conifers, such as Douglas-fir, Engelmann Spruce (*Picea engelmannii*), Subalpine Fir (*Abies lasiocarpa*), and Lodgepole Pine (Steele 1990; Rebertus *et al.* 1991; Donnegan and Rebertus 1999; Coop and Schoettle 2009). Its persistence in such habitats, where it is subjected to intense competition from other conifers, appears dependent on periodic, high-intensity wildfire (Coop and Schoettle 2009).

Fire-return intervals in Limber Pine communities vary greatly, ranging from 2-30 years in low elevation sites (Wright and Bailey 1982) to several hundred years in some upper elevation stands (Veblen 1986; Rebertus *et al.* 1991; Coop and Schoettle 2009; Coop *et al.* 2010). Metapopulation dynamics are apparent in some stands, which were extirpated by fire and then re-established by seed dispersal from adjacent subpopulations (Webster and Johnson 2000; Coop and Schoettle 2009). Other stands in the same area experienced periodic fire but were not extirpated, while yet others showed no fire history over centuries (Webster and Johnson 2000; Sherriff *et al.* 2001). In stands with fires, episodes of increased recruitment were apparent after fires (Donnegan and Rebertus 1999; Webster and Johnson 2000; Coop and Schoettle 2009). In some Limber Pine stands at the edge of its range with grasslands, frequent fire seems to have restricted its regeneration. Recent fire exclusion has allowed it to expand into adjacent grasslands or for stands to become denser (Keane *et al.* 2002; Brown and Schoettle 2008).

Some Limber Pine stands, often in more extreme, droughty sites, form stable, long-persisting communities (Webster and Johnson 2000; Tomback *et al.* 2005), probably due to its greater physiological tolerance compared to other tree species.

Habitat Trends

There likely has been no significant loss of habitat area for Limber Pine over the past century in Canada. However, fire exclusion (prevention and suppression) may have reduced habitat quality through greater competition, more rapid successional replacement and increased fire severity. Future habitat quality is expected to decline due to climate change as discussed below. The area and extent of habitat is expected to change with climate change. However, the rates and amounts of change are uncertain. Similar trends in quality and amount of suitable habitat are expected in the U.S.

BIOLOGY

Life Cycle and Reproduction

Limber Pine is a long-lived species, frequently reaching several hundred years (McCune 1988) and trees older than 1000 years are known (Schuster *et al.* 1995; Keeley and Zedler 1998). Maximum age generally increases with elevation in response to decreasing fire frequency (Schuster *et al.* 1995). Reproduction is solely by seeds (Steele 1990). Cones are generally first produced no younger than about 50 years of age and may be delayed until 200 years (Schoettle 2004). Cone production may continue over several hundred years.

The reproductive cycle is similar to other pines, comprising a two-year period from cone initiation to seed maturity. Pollen is wind-dispersed mainly in June and July (Steele 1990), mostly locally although some long-distance dispersal of >100 km does occur (Schuster *et al.* 1989; Schuster and Mitton 2000). Fertilization occurs the following spring or early summer, about 13 months after pollination, with cones maturing typically in August and September (Schmidt and Lotan 1980). Seeds are large (10-15 mm) and generally wingless, although some have a vestigial wing which is essentially non-functional for wind dispersal (Lanner 1985; Kral 1993). Mast seeding occurs every 4-5 years, although there is much variability both spatially and temporally (Steele 1990; Keane and Schoettle 2011).

As the seed cone opens in late summer, the seeds are removed, dispersed and cached, primarily by Clark's Nutcracker and Red Squirrels (Benkman *et al.* 1984; Tomback and Linhart 1990; Tomback *et al.* 2005). Following dispersal, seeds not retrieved by birds or eaten by rodents generally germinate within two years (Webster and Johnson 2000). Seedling survival appears to be related primarily to moisture stress (Keuppers 2010) and is better when seedlings are sheltered by "nurse objects" which create favourable microtopography (Coop and Schoettle 2009). Limber Pine seedlings do not compete well with other plant species and their life history strategy is weighted toward persistence through tolerance of conditions not suitable for other species rather than competitive ability (Schoettle and Rochelle 2000; Schoettle 2004).

Generation time is difficult to estimate for a long-lived tree species for which there are few demographic data available. Assuming that current average annual mortality rate of mature individuals (1%) is about twice the "normal" rate, and that age at first reproduction is about 50 yrs, the formula "1/mortality + age at first reproduction" yields an estimate of 250 yrs (1/0.005 + 50 yrs = 250 yrs; IUCN 2013 – eq. 2). This is consistent with the values Field *et al.* (2012) estimated for healthy mature trees of Limber Pine: a mean survival rate of 0.9950 (0.9840 – 1.000). Using current mortality rate yields an estimate of 150 yrs (1/0.01 + 50 = 150).

Physiology and Adaptability

Physiological studies of Limber Pine have highlighted its ability to deal with moisture stress and optimize photosynthesis (Schoettle and Rochelle 2000; Letts *et al.* 2009). In addition to the structural and physiological traits in conifers generally that are associated with resistance to drought stress (Gao *et al.* 2002), Limber Pine exhibits traits that enable it to maintain a positive net annual photosynthetic balance: high needle longevity (4.4-9.6 years (Barrick and Schoettle 1996), low specific leaf area (Letts *et al.* 2009), and low stomatal density (Schoettle and Rochelle 2000). Plants with a low stomatal density tend to have higher photosynthetic water use efficiency (Letts *et al.* 2009).

Net photosynthetic rates are highest in the spring and early fall when moisture stress is lower than July and August (Letts *et al.* 2009), indicating a sensitivity to high atmospheric moisture demand. The growth response of Limber Pine to temperature is mixed with some studies finding it not particularly responsive to air temperature (Schoettle and Rochelle 2000) while others found a complex response to the interaction of temperature and precipitation (Millar *et al.* 2007). Seedling establishment and growth seems more affected by water availability than temperature (Kueppers 2010; Moyes *et al.* 2013).

Mature Limber Pine are quite resistant to drought stress as indicated by long-lived trees (>1000 years; Case and MacDonald 2003) that have survived many severe droughts. Growth is highly correlated with total annual precipitation and older trees are less sensitive to climatic variables (Case and MacDonald 1995; Millar *et al.* 2007).

Overall, Limber Pine appears to exhibit a wide physiological tolerance or plasticity (Schoettle and Rochelle 2000) and to be limited at its lower elevational extent by moisture stress. While some studies suggest that these constraints do not limit its potential upward movement (Schoettle and Rochelle 2000; Letts *et al.* 2009; Reinhardt *et al.* 2011), another (Moyes *et al.* 2013) suggests that moisture stress limits seedling establishment at treeline as well.

Limber Pine has been successfully grown from seed and transplanted to natural habitats (Asebrook *et al.* 2011; Casper *et al.* 2011; Smith *et al.* 2011b) and seed transfer guidelines have been developed based on genetic diversity patterns (Mahalovich 2006).

The response of Limber Pine to fire depends largely on fire intensity and fire-return interval. Limber Pine does not have a thick, fire-resistant bark and can be easily killed by more severe fires. However, in the dry, open sites often occupied by Limber Pine, fuels may be sparse and discontinuous, which may result in a patchy, low-intensity fire that kills only a portion of the Limber Pine subpopulation (Webster and Johnson 2000; Brown and Schoettle 2008). Following more severe, stand-replacing fires, Limber Pine can be extirpated in an area but then can be dispersed rapidly from adjacent populations into the burned area by Clark's Nutcrackers and re-establish a local subpopulation (Rebertus *et al.* 1991; Donnegan and Rebertus 1999; Webster and Johnson 2000; Brown and Schoettle 2008; Coop and Schoettle 2009). The drought-resistant physiology of Limber Pine enables it to establish on dry sites that may be unfavourable for other conifer species (Coop and Schoettle 2009).

Dispersal and Migration

Limber Pine is largely dependent on Clark's Nutcracker for seed dispersal and successful regeneration (Tomback and Kramer 1980; Lanner 1988; Tomback and Linhart 1990; Tomback *et al.* 2005). Clark's Nutcrackers remove seeds from the cone on the tree and disperse them into caches of 1-5 seeds for distances typically of a few metres to several kilometres, but up to 22 km (Vander Wall and Balda 1977; Carsey and Tomback 1994; Tomback *et al.* 2005). They can carry up to 125 seeds at a time in a sublingual pouch and have been estimated to cache more than 30,000 seeds per hectare in one year (Lanner and Vander Wall 1980). Steller's Jays (*Cyanocitta stelleri*) also will harvest seeds from open cones and cache them in the ground or other sites (Tomback *et al.* 2011) but they do not occur in most of the range of Limber Pine in Alberta (FAN 2007) and their role appears to be much less important than that of Clark's Nutcracker.

As seed cones open, some seeds are retained in the resinous cones (Tomback and Kramer 1980) while others fall to the ground where they may be gathered and dispersed short distances to caches by small rodents. These seeds do not appear to be of much importance in regeneration (Schoettle and Rochelle 2000; Tomback *et al.* 2005, 2011).

Gene flow among populations occurs both by wind-dispersed pollen and movement of seeds, primarily by Clark's Nutcrackers. Despite the naturally fragmented population distribution, this gene flow is estimated to be sufficient to overcome genetic drift (Schuster *et al.* 1989; Schuster and Mitton 2000; Jorgensen *et al.* 2002) and Limber Pine is not considered to be *severely fragmented* in Canada.

Potential migration in response to climate change is discussed below in the **Climate Change** section.

Interspecific Interactions

The crucial dependency of Limber Pine on Clark's Nutcracker for dispersal and reproduction is described above in the **Dispersal and Migration** section. Interactions with White Pine Blister Rust and Mountain Pine Beetle (*Dendroctonus ponderosae*) are described below in the **Limiting Factors and Threats** section.

Limber Pine is linked to other species mostly by its seeds, which are an important food source for many animals including Red Squirrels (*Tamiasciurus hudsonicus*) and other small mammals, both Black Bears (*Ursus americanus*) and Grizzly Bears (*U. arctos*), and a number of birds, most particularly, Clark's Nutcracker (*Nucifraga columbiana*) (Smith and Balda 1979; Kendall 1983; Benkman *et al.* 1984; Tomback and Linhart 1990; Benkman 1995; McCutchen 1996; Tomback 2001; Peters 2011; Tomback *et al.* 2011).

Squirrels can harvest a large portion of the cones before seed release. This predation appears to have exerted a selection pressure to reallocate energy and resources from seed production to a greater defensive cone morphology (Smith 1970; Benkman 1995; Siepielski and Benkman 2007, 2008).

Limber Pine often interacts with other plant species, including trees, to facilitate their establishment, particularly in harsh sites where Limber Pine provides shelter to create protected microsites (Rebertus *et al.* 1991; Baumeister and Callaway 2006). Later in successional development, these species may create competitive conditions unfavourable for Limber Pine persistence (e.g., Douglas-fir) or, as with currants and gooseberries (*Ribes* spp.), increase the incidence and severity of White Pine Blister Rust.

Interactions with fungi may be either positive or negative. As in all pines, Limber Pine is dependent on mycorrhizal fungi for normal growth and survival, mainly through nutrient uptake but also through protection from pathogens, soil grazers, heavy metals and drought (Smith and Read 1997). More than 26 species of mycorrhizal fungi have been found in association with Limber Pine and further investigations are currently underway (Cripps and Antibus 2011). Some mycorrhizal species are limited to five-needled pines and there is increasing evidence of specificity for tree host species and age, and local habitat conditions (Tedersoo *et al.* 2009). These interactions could be crucial in establishing seedlings in depleted stands or in new sites reached by assisted or natural migration (Desprez-Loustau *et al.* 2007).

However, non-mycorrhizal fungi may also cause seed mortality and a variety of other fungi can cause damage to needles, stems and roots (Burns and Honkala 1990). Perhaps most significant is a needle blight (*Dothistroma septosporum*) (Jackson and Lockman 2003; Woods *et al.* 2005), which has caused significant recent mortality in Montana (Schwandt *et al.* 2010) and appears to be extending its range (Watt *et al.* 2009; Sturrock *et al.* 2011). Another fungus, Comandra Blister Rust (*Cronartium comandrae*), naturally hybridizes with White Pine Blister Rust and has recently been discovered to occur on Limber Pine (Joly *et al.* 2006). The implications of this for Limber Pine are currently unknown.

Limber Pine is also affected by other parasites including Limber Pine Dwarf Mistletoe (*Arceuthobium cyanocarpum*), which is not known yet to occur in Canada but is affecting Limber Pine in portions of Montana and is considered to be second only to White Pine Blister Rust in importance in the western U.S. (Taylor and Mathiasen 1999). With climate change, this parasitic plant may extend its range into Canada.

Also of potential significance is the relationship with Small Ermine Moth (*Argyresthia flexilis*), the larvae of which feed exclusively on Limber Pine needles (Freeman 1972). This moth is apparently rare in Canada and is on the candidate list for assessment of the COSEWIC Arthropods SSC (COSEWIC 2013). Declining Limber Pine populations could affect this insect, including loss of local populations resulting in coextirpation of these two species (Colwell *et al.* 2012). Because this interaction is not symmetrical, i.e., the moth is dependent on Limber Pine but not vice-versa, the risk is potentially greater for the moth. Similarly, the bark beetle (*Ips woodi*) may be completely or largely restricted to Limber Pine in Canada, although it has also been found associated with Whitebark Pine in British Columbia (one record from Valemount (Bright 1976)) and Washington State (Furniss and Johnson 1995)

POPULATION SIZES AND TRENDS

Sampling Effort and Methods

Information on population trend is derived from monitoring studies involving Parks Canada, Canadian Forest Service, U.S. National Parks Service, Alberta Environment and Sustainable Development, and Alberta Parks. Monitoring plots have been established across the range of Limber Pine in both Alberta and British Columbia (Smith *et al.* 2011a). In 2003 and 2004, 12 plots surveyed in 1996 were re-surveyed and 73 new plots were established across the Canadian Rockies; all 85 plots were then re-surveyed in 2009 (Smith *et al.* 2011a, 2013). Each time, trees were classified as live or dead.

Abundance

The number of mature Limber Pine trees was estimated using the index of area of occupancy and the mean density (number of mature trees/ha), where a mature tree has a diameter at breast height (dbh) >10 cm. Using data from plot measurements in both Alberta and British Columbia (Smith *et al.* 2013), the mean density is 300 mature trees/ha. Total abundance of mature Limber Pine in Canada is estimated at 44.4 million trees (300 mature trees/ha X 148,000 ha). There is some uncertainty in this estimate because trees with stem cankers may not be "mature individuals" (i.e., capable of reproduction) because the stem canker may kill portions of the tree canopy where cones are produced, thus leading to an overestimate of mature trees. On the other hand, in some habitats, individuals with a stunted, krummholz growth form can be less than breast height/<10 cm dbh and still produce cones, i.e., are mature individuals. There are no reliable estimates of the amount of canopy killed by stem cankers or of mature krummholz individuals.

Fluctuations and Trends

Limber Pine populations in Canada are declining currently and are expected to continue to decline due to the combined effects of White Pine Blister Rust, Mountain Pine Beetle, and climate change. Limber Pine populations do not undergo rapid or extreme (i.e., more than one order of magnitude) fluctuations in population numbers.

White Pine Blister Rust is currently the main cause of population decline (Smith *et al.* 2011a, 2013). From 2003-2004 to 2009 in Canada, the blister rust infection rate increased from 33% to 43% (Smith *et al.* 2011a, 2013). Mountain Pine Beetle populations are currently low in Limber Pine habitat in Canada and are not currently killing many Limber Pine. Only 4% of the trees that died between 2003-2004 and 2009 were killed by Mountain Pine Beetle (Smith *et al.* 2013). The effect of climate change on mortality cannot be estimated at this time, although it is expected to first manifest itself in greater effects of both White Pine Blister Rust and Mountain Pine Beetle. Thus, the population trend below is essentially due solely to the effects of White Pine Blister Rust.

For the purpose of this assessment, mean annual mortality rates were estimated for each of the 85 sampling sites of Smith *et al.* (2011a), using two formulas depending on whether sampling sites had been surveyed two or three times (Table 1; Appendix 1). For sites surveyed two times, the annual mortality rate was estimated as the % of dead trees in 2009 minus the % of dead trees in 2003-2004; the difference was then divided by 5.5 yrs, i.e., the average time interval between 2003-2004 and 2009. For sites surveyed three times, the annual mortality rate was estimated as the slope of a linear regression of % dead trees through time.

Table 1. Limber Pine mortality in the Canadian Rockies (from Smith *et al.* 2011a)

Zone and location	Mean % mortality			% annual mortality[1]
All years	**1996**	**2003-04**	**2009**	**All**
Northern				
Bow Valley to Kootenay Plains	-	12	13	0.18
Central				
Hwy 3 to Bow Valley	-	32	37	0.91
Whaleback	15	43	32	1.45
Southern				
Hwy 3 to Waterton Lakes National Park	-	45	52	1.27
Waterton Lakes National Park	40	56	52	0.99
Mean ± Standard Deviation				0.96 ± 0.44
From full dataset (n = 85 plots)[2]				
Mean	32.04	28.85	33.02	1.06
Standard Deviation	15.87	19.40	21.76	1.61
95% Confidence Interval	9.00	4.12	4.63	0.34

Estimated that way, the annual mortality rates varied among regions between 0.18% and 1.45%, with a general mean of 1.06% and a 95% confidence interval of 0.34% (Table 1). Projecting the mean annual mortality rate over 100 years into the future gives an estimated decline of 66% for Limber Pine in Canada [$1 - (1 - 0.0106)^{100} = 0.66$; (Table 3)][3]. Using the lowest and highest values of the annual mortality rate set as its mean ± 95% confidence interval, projections give rates of decline over 100 yrs in the range of 51% - 76% (Table 3).

Table 2. Threat assessment for Limber Pine (IUCN and CMP 2006).

Threat/Level	Scope	Severity	Timing	Impact
White Pine Blister Rust (8.1 Invasive non-native species)	Pervasive	Extreme	High	Very High
Mountain Pine Beetle (8.2 Problematic native species)	Pervasive	Extreme	High	Very High
Climate change (11. Climate change)	Pervasive	Extreme	High	Very High

[1] See **Fluctuations and Trends** section for details on how those values were computed.

[2] See Appendix 1.

[3] Current annual population growth rate (lambda) = 1 – 0.0106 = 0.9904. Population growth rate over next 100 yrs = $(0.9894)^{100}$ = 0.3445, which is a decline of 1 - 0.3445 = 0.6555 (or 66%).

Table 3. Estimated Limber Pine population decline in Canada over 100 years, with a range of probable mortality rates.

Year	Annual mortality rate[1]:					
	1.06%		1.40%		0.72%	
	No. mature trees	Decline	No. mature trees	Decline	No. mature trees	Decline
0	44,400,000	0%	44,400,000	0%	44,400,000	0%
10	39,911,866	10%	38,561,340	13%	41,304,812	7%
20	35,877,411	19%	33,490,472	25%	38,425,395	13%
30	32,250,775	27%	29,086,430	34%	35,746,706	19%
40	28,990,734	35%	25,261,525	43%	33,254,752	25%
50	26,060,232	41%	21,939,601	51%	30,936,515	30%
60	23,425,956	47%	19,054,514	57%	28,779,887	35%
70	21,057,965	53%	16,548,819	63%	26,773,600	40%
80	18,929,339	57%	14,372,627	68%	24,907,174	44%
90	17,015,884	62%	12,482,607	72%	23,170,859	48%
100	15,295,848	66%	10,841,128	76%	21,555,585	51%

1 – The values here are the mean and the upper and lower bound of the 95% confidence interval (0.34%).

The 100 yrs projections remain uncertain, as are all population projections, for various reasons. In this case, sources of uncertainty include the small number of years (5 to 13) for which data are available relative to the temporal extent of the projection, the geographical, temporal, and size-dependent variation in both infection and mortality rates, the unknown future contribution of recruitment to population growth, and the potential for natural resistance to develop over the 100 year time period.

The annual mortality and fertility rates are likely to change in the short term. The high number of trees with active stem cankers and branch cankers within 15 cm of the stem, which are likely to grow into the stem and be lethal within a decade (Kearnes *et al.* 2009) suggests that the number of topkilled trees will increase soon (Smith *et al.* 2013). Note that Limber Pine does not exhibit the “functionally dead” phenomenon as strongly as Whitebark Pine, in which blister rust kills the upper, reproductive portion of the canopy. Instead, Limber Pine can produce cones on the lower portion of the canopy, but cone production is still decreased in trees with canopy kill.

Current population growth is considered to be determined solely by mortality of mature trees because recruitment of mature trees from seedlings appears to be very low, likely negligible (Smith pers. comm. 2013). Little information is available on recruitment rate. Seedlings die within 1-3 years of being infected (Schoettle and Sniezko 2007) and seedlings decompose quickly, thus making detection of seedling mortality difficult (Field *et* *al.* 2012). Smith *et al.* (2013) found a slight increase in the number of plots with seedlings from 76% to 85% and a decrease in rust-infected seedlings from 8% to 4% over a 5-6 year period. However, there were higher rates of infection on taller, older seedlings in both measurement periods suggesting that infection may increase episodically over time, most probably during “wave years” when environmental conditions are favourable for spread of blister rust. The declining proportion of seedlings in the larger size class suggests that fewer seedlings are likely to be recruited into mature trees. Greenhouse studies indicate that Limber Pine seedlings have three times the infection level of Whitebark Pine seedlings (Hoff and McDonald 1993). Given that estimates for Whitebark Pine indicate that, due solely to rust-caused mortality, only about 3% of seedlings reach an age of 100 years (calculated using age class survival rates in Ettl and Cotone 2004 and Keane *et al.* 1990), the amount of recruitment from Limber Pine seedlings is likely to be very small.

Additional factors reducing recruitment include the trend of decreasing seed dispersal due to animals consuming an increasing proportion of a decreased seed crop (Peters 2012), and, given the fragmented distribution of Limber Pine stands, interstand seed dispersal becoming less likely. Consequently, the recruitment of mature trees from seedlings is considered to be essentially negligible.

The projection of mortality rate into the future assumes that the rust infection level will remain constant over the next 100 years. It is not unrealistic to expect rust levels to be at current or even greater levels given the North American history of increasing infection and mortality (Schwandt *et al.* 2010; Burns *et al.* 2011; Smith *et al.* 2011a). Also, during this 100-year period, Mountain Pine Beetle epidemics can be expected as have occurred at least twice in Canada in the 20th century (AFLW 1986; Wood and Unger 1996; Langor 2007; CFS 2008; Raffa *et al.* 2008). Because mortality rates result from a combination of interacting factors, projected population declines based solely on the White Pine Blister Rust mortality (the major current threat) likely underestimates future decline.

Rescue Effect

There are populations of Limber Pine in the U.S. that are close to or essentially contiguous with Canadian populations in Alberta. Seed dispersal by Clark’s Nutcrackers to areas of suitable habitat in Canada is theoretically possible. However, U.S. populations of Limber Pine also have suffered declines due to the same factors (Kearnes and Jacobi 2007; Asebrook *et al.* 2011; Burns *et al.* 2011; Klutsch *et al.* 2011). The effects of this decline on Clark’s Nutcracker are not clear but its numbers can be expected to decrease given its relationship with Limber Pine and Whitebark Pine, which is also declining, thus decreasing seed dispersal. Nor are the predicted effects of climate change any less in the U.S. (Warwell *et al.* 2007) than in Canada. Consequently, the probability of successful rescue from U.S. populations of an extirpation or population decline in Canada is extremely low.

Also, while it is possible that genes for WPBR resistance be naturally transferred from U.S. to Canada’s populations through pollen dispersal, this remains undocumented. No rescue seems possible at this time.

THREATS AND LIMITING FACTORS

White Pine Blister Rust

White Pine Blister Rust (blister rust) originated in Eurasia and was introduced accidentally to North America (McDonald and Hoff 2001; Geils *et al.* 2010). Its spread into the range of Limber Pine was from Vancouver Island, where it was initially discovered in 1921 (Geils *et al.* 2010). By 1952, it had reached Limber Pine in Alberta (Gautreau 1963), and has subsequently spread throughout nearly the entire North American range (Tomback and Achuff 2010). Limber Pine has been affected severely; throughout the species' range only a few stands show no infection (Schwandt *et al.* 2010), and in many stands in Canada there is greater than 60% infection and over 50% mortality due to the rust (Smith *et al.* 2011a). Overall in Canada, both blister rust infection and mortality rates are increasing (Smith *et al.* 2011a). Infection and mortality are greatest in southwestern Alberta, decreasing to the north but blister rust is present throughout the Canadian range.

The extent of blister rust infection depends not only on the distribution of Limber Pine, but also on that of its alternate host, primarily native currant and gooseberry shrubs, which are widespread in western North America (Zambino 2010). Recent evidence indicates that native species of Paintbrush (*Castilleja miniata*) and Bracted and Sickle-top Lousewort (*Pedicularis bracteosa, P. racemosa*) may also serve as alternate hosts (McDonald *et al.* 2006; Zambino *et al.* 2007).

The pine host is infected by wind-borne basidiospores from the alternate host that attack the needles, usually in late summer (McDonald and Hoff 2001). After the initial infection of the needles, hyphae grow down the vascular bundle and enter the phloem in the branch or stem. As the rust spreads through the phloem, the nutrient supply can be cut off to branches and portions of the upper stem. Two to four years following infection, cankers form and rupture the bark surface. Seedlings and saplings are particularly susceptible, often being killed within 1-3 years following infection (Schoettle and Sniezko 2007). The low seedling infection rate observed in some stands is not due to a low infection probability. Rather, due to a combination of negative effects of the fungal infection, natural mortality, and brief residence time, infected seedlings are not reliably sampled (Field *et al.* 2012). Although a canker may become large enough to girdle the affected stem, infection may not be the direct cause of death. Concentrations of nutrients in cankers attract rodents, which chew the canker, thus removing vascular tissue and often, girdling the stem. The loss of vascular tissue and invasion by secondary pathogens into the wound are the main causes of mortality in all age classes.

Besides direct mortality, blister rust infection also can greatly reduce recruitment through various mechanisms. It can reduce or prevent seed production by killing the outermost portions of the branches, which is where the cones are produced. It can reduce cone production, survival to the seed dispersal stage, and likelihood that seed will be dispersed by Clark's Nutcrackers (see section **Rescue Effect** above). Such reduced fertility and dispersal could result in a virtual complete loss of regeneration over large portions of the range of Limber Pine.

Blister rust also interacts with Mountain Pine Beetle in that Limber Pines infected with blister rust likely are more susceptible to beetle infestation (Schwandt *et al.* 2010).

Limber Pine trees that are phenotypically blister rust-resistant are known in natural forests, albeit at low frequencies (Hoff *et al.*1980). This resistance may be genetically based as in other pines (e.g., Western White Pine, Whitebark Pine) (King *et al.* 2010). Genetic resistance and resistance mechanisms have been studied (Burns *et al.* 2008; ASRD 2009; Schoettle *et al.* 2011), and one major resistance gene (named *Cr4*) was recently identified in healthy and recently invaded populations in the Southern Rocky Mountains (Schoettle *et al.* 2014). Investigations to identify other types of resistance to WPBR in Limber Pine are underway.

Following identification of resistant genes, a blister rust-resistance breeding program might be undertaken to develop blister rust-resistant trees for planting. However, this process will likely take several decades at best (Hoff *et al.* 2001) and genetic variation in virulence of the blister rust may overcome the tree resistance (McDonald and Hoff 2001).

Mountain Pine Beetle

Although Mountain Pine Beetle is a native species that has co-existed with Limber Pine for more than 8500 years (Brunelle *et al.* 2008) and occurs throughout the range of Limber Pine in Canada, epidemic population levels have spread to portions of the range in Alberta and British Columbia (CFS 2008). Human-caused factors (i.e., fire exclusion and climatic warming from greenhouse gas emissions) have been shown to be significant in this spread (Carroll *et al.* 2003; Taylor *et al.* 2006; Logan and Powell 2008; Raffa *et al.* 2008).

Climatic warming results in less severe winter temperatures, warmer summer temperatures, and a longer growing season, all of which contribute to increased Mountain Pine Beetle survival, growth, and reproduction (Carroll *et al.* 2003; Taylor *et al.* 2006; Logan and Powell 2008). In the past, beetles frequently took 2-3 years to complete their life cycle (Amman *et al.* 1997). With warmer conditions, 1-year life cycles are more common (Logan *et al.* 2010) and some populations now have two broods per season (Mitton and Ferrenberg 2012). These shorter life cycles permit faster population growth and reduce the probabilities of mortality from low winter temperatures, bird predation, and fungal disease (Bentz *et al.* 2011). Continued climatic warming is expected to further increase favourable conditions for beetle epidemics (Logan and Powell 2008).

Fire exclusion has increased the amount of landscape occupied by susceptible age-class pine trees, including Lodgepole Pine and Ponderosa Pine (*P. ponderosa*). This has allowed the buildup of epidemic Mountain Pine Beetle conditions in large portions of the landscape, with subsequent spread to Limber Pine stands (AFLW 1986; Raffa *et al.* 2008).

A Mountain Pine Beetle epidemic in southwestern Alberta in the 1980s affected large areas of Limber Pine. Control measures resulted in the loss of nearly 40,000 trees (AFLW 1986) and additional thousands were killed directly by the beetle (Langor 2007).

Additionally, Limber Pine is quite susceptible to Mountain Pine Beetle attack and produces proportionally more brood of the beetle than most other pines (Amman 1982; Langor 1989; Langor *et al.* 1990). The interaction of Mountain Pine Beetle and White Pine Blister Rust is also of grave concern. Not only are trees weakened by blister rust infection more susceptible to beetle infestation (Schwandt *et al.* 2010) but beetles may kill the remaining mature Limber Pine trees in a stand that have not been killed or rendered non-reproductive by blister rust.

Mountain Pine Beetle is not currently in an epidemic phase in Limber Pine populations in Canada. Monitoring indicates few trees (4% of those dying between 2003-2004 and 2009) being killed by Mountain Pine Beetle (Smith *et al.* 2013). However, Mountain Pine Beetle is still present in the landscape around Limber Pine in Canada and can be expected to again develop epidemic populations as has occurred in western Canada as early as the 1890s, as well as in the late 1930s to early 1940s, in the mid-1980s, and most recently in the late 1990s to early 2000s (AFLW 1986; Alfaro *et al.* 2007; Safranyik *et al.* 2010). The 1980s epidemic caused widespread Limber Pine mortality in southwestern Alberta (AFLW 1986; Langor *et al.* 1990; Langor 2007).

Climate Change

Climate change is projected to affect Limber Pine in both the Alberta and British Columbia portions of its range, although there is considerable uncertainty about these effects and how Limber Pine will respond to them. In these areas, models predict that by the 2080s there will be increases of mean annual temperature of 2-6^{o} C with the greatest increases in winter and spring. In Alberta, small increases in mean annual precipitation are predicted with greatest increases in winter and spring (Barrow and Yue 2005; Sauchyn and Kulshreshtha 2008). In southeastern British Columbia, a decrease in mean annual precipitation is expected with increases in winter and spring offset by a decrease in summer precipitation (Spittlehouse 2008; Walker and Sydneysmith 2008; Utzig 2012). The net effect across the Canadian range is increased evapotranspiration and a decrease in soil moisture levels of 20-30% during the growing season (Rweyongeza *et al.* 2010; Schindler and Donahue 2012).

The effects of these changes will be most significant along the ecotone between foothills forests and adjacent grasslands (MacDonald 1989; Henderson *et al.* 2002; Sauchyn and Kulshreshtha 2008), which is mostly where Limber Pine currently occurs. The frequency, intensity and duration of drought is projected to increase (Gillett *et al.* 2004; Sauchyn and Kulshreshtha 2008; Utzig 2012), fire will be more frequent and severe (de Groot *et al.* 2002; Flannigan *et al.* 2005; Utzig *et al.* 2012), and stressed trees are likely to be more susceptible to pathogens (Saporta *et al.* 1998; Logan and Powell 2008).

These factors likely will result in reduced tree growth, regeneration failure in dry years, mortality due to drought and pathogens, and a gradual reduction in tree population size. Because of the long generation time of Limber Pine and its tolerance to stresses, mature trees may resist climate-driven change for decades (Roberts and Hamman 2011). However, the rate of population decline may increase due to the possibility of a non-linear response caused by "ecological inertia," which involves the ability of mature individuals to cope with increased stress for some time before a threshold is crossed, followed by a rapid die-off and population decline (Saporta *et al.* 1998; Burkett *et al.* 2005).

In situ adaptation to climate change by Limber Pine is expected to be affected by significant adaptational lag due to its relatively small, fragmented populations with low fecundity and late age of seed production (Dullinger *et al.* 2004; Savolainen *et al.* 2007; Aitken *et al.* 2008). Studies of other Northern Hemisphere pine species with more favourable life history characteristics suggest that one generation of selection is insufficient to adapt to climate change and that adaptation may require 10 generations or >1000 years (Rehfeldt *et al.* 1999, 2001, 2002) and that there are likely genetic limitations (Jump and Penuelas 2005).

Climate change over the next 75-100 years is predicted to make much of the current range of Limber Pine in Canada unsuitable (Henderson *et al.* 2002; Hamman and Wang 2006), although mature, healthy trees may be able to persist for some time in conditions where regeneration is no longer possible. Based on "climatic envelope" models, which predict changes in species' range based on suitable habitat inferred from climatic variables, the range of Limber Pine is expected to expand upslope and northward in both Alberta and British Columbia (Hamann and Wang 2006; Rweyongeza *et al.* 2010). However, the climate envelop model for Limber Pine in BC has a relatively low predictive power and "lost habitat statistics are not meaningful" (Hamann and Wang 2006).

While specific areal predictions for Limber Pine in Alberta are not available, similar trends in loss of currently suitable habitat are expected (Henderson *et al.* 2002; Rweyongeza *et al.* 2010) while the amount of new suitable habitat is unclear, especially given the differing physiographic composition of Alberta and British Columbia.

Modelling of the change in global range of Limber Pine by 2100 (McKenney *et al.* 2007) concluded that, with the ability to occupy all new suitable habitat, Limber Pine range would increase by about 8%. Without the ability to occupy new habitat, the range would shrink by about 56%. However, this study overestimates the current range of Limber Pine and thus likely overestimates future range expansion. Given that climatic envelope models likely overestimate the ability of species to occupy new habitat, as discussed below, it is unclear whether Limber Pine will be able to successfully occupy new suitable habitat.

While migration to suitable habitat has been the usual response of plants to climate change in the past (MacDonald 1989; Bradshaw and McNeilly 1991; Huntley 1991; Jackson and Overpeck 2000), given currently predicted rates of change (IPCC 2007; Barrow and Yu 2005; Sauchyn and Kulshreshtha 2008; Walker and Sydneysmith 2008; Schneider *et al.* 2009), it is unlikely that Limber Pine will be able to migrate to suitable habitat throughout much of its range. The latitudinal migration rate of Limber Pine is estimated to be on the order of 100 m/year, based on previous movements, while the rate required to track suitable habitat under a 2X CO_2 scenario is about 1 km/year (Malcolm *et al.* 2002; Aitken *et al.* 2008; Van der Putten 2012). Upward altitudinal migration is likely to be easier than latitudinal migration (Bertrand *et al.* 2011) because of the shorter distance involved but likely still will be constrained in many areas by lack of suitable soil or local terrain that extends upward into favourable areas (Romme and Turner 1991; Bartlein *et al.* 1997; Hamman and Wang 2006; Lenoir *et al.* 2008). Successful migration is likely to be further complicated by, for example, the need for mycorrhizal fungi specific to Limber Pine (Cripps and Antibus 2011), the effects of habitat fragmentation and the limitations of bird dispersal (Van der Putten 2012).

Predicting Limber Pine response to climate change involves considerable uncertainty. While the processes involving climatic variables are relatively well understood, predicting biological responses is much more complicated. Climatic envelope models use a simplified approach to predict suitable habitat/future range based on climatic variables while not including biological variables, for example, dispersal characteristics, life history characteristics, disturbance regimes or biotic interactions (Hamman and Wang 2006; Rehfeldt *et al.* 2006; Aitken *et al.* 2008; Leniham *et al.* 2008; Litell *et al.* 2010; Buckley and Kingsolver 2012). Biotic factors are particularly important for Limber Pine in which the interactions with mycorrhizal fungi, White Pine Blister Rust, and Mountain Pine Beetle are crucial. While long-distance dispersal may move a plant beyond some of its pathogens (Van Grunsven *et al.* 2007), analysis of multi-species historical patterns suggests this advantage is unusual or short-lived (Moorcroft *et al.* 2006). The likely net effect is that future ranges predicted by climatic envelope models are overestimated because most of the biological variables will act to reduce migration rates and successful establishment.

Interaction of Threats

While each of the three human-influenced threats (White Pine Blister Rust, Mountain Pine Beetle, climate change), pose a significant threat to Limber Pine, these threats interact to increase further the severity of the impacts. Climate change will increase stress on Limber Pine trees, making them more susceptible to both White Pine Blister Rust and Mountain Pine Beetle. Climate change also likely will increase the probability and severity of Mountain Pine Beetle attacks, which can kill the remaining trees in a stand already reduced by White Pine Blister Rust. Both White Pine Blister Rust and Mountain Pine Beetle are expected to disperse as fast as Limber Pine and so escape from these two threats by migration appears impossible.

Adequate, timely mitigation of these threats, while potentially possible, appears very problematic (Keane and Schoettle 2011). Development of rust-resistant trees and establishing long-term, sustainable populations for such a wide-ranging species likely will take decades and require significant amounts of resources. Abatement or adaptation to climate change will also require decades of sustained effort and is a major uncertainty in public policy currently. It may be difficult to find resources for a non-commercial species such as Limber Pine. Thus, these threats are expected to be ongoing, continuing for decades at least, and mitigation efforts may be weak.

The level of threats also was assessed using an international system (IUCN and CMP 2006) that considers the scope, severity, timing, and impact of present and future threats. The major threats to Limber Pine (White Pine Blister Rust, Mountain Pine Beetle, climate change) are each rated as having a Very High impact (Table 2). The system does not explicitly deal with threat interactions but, as discussed above, these threats interact to increase the severity of the impacts.

Locations

Determining the number of *locations* (COSEWIC 2012) depends on identifying the “most serious plausible threat” that can cause a single event to “rapidly affect all individuals of the taxon present.” A location may include “part of one or many populations.” It has not been possible to delineate populations of Limber Pine in Canada due to limited information on local stand occurrences, so the entire Canadian population is considered as one entity. Also, the entire population is susceptible to the most serious plausible threat.

Mountain Pine Beetle is the threat that could affect all Limber Pine populations most rapidly. It has occurred in or adjacent to all portions of Limber Pine range within Canada and has resulted in the death of tens of thousands of trees in southwestern Alberta in the 1980s (AFLW 1986; Langor 2007). The scope and speed of the recent Mountain Pine Beetle epidemic in central British Columbia illustrates the ability of this insect to reduce pine populations rapidly over an extensive area. As noted above, Mountain Pine Beetle is not currently affecting all Limber Pine populations in Canada but has the potential to do so, particularly with current trends in beetle spread and climate change. This leads to the conclusion that, in the face of Mountain Pine Beetle threat, Limber Pine populations in Canada constitute one location.

White Pine Blister Rust is perhaps acting more slowly than Mountain Pine Beetle but has been inexorable in its spread and killing of Limber Pine individuals of all ages across the range in Canada over the past 60 years. This non-native species likely has killed more Limber Pine than Mountain Pine Beetle has and is present in all parts of the Canadian range of Limber Pine. Although White Pine Blister Rust is at comparatively low levels in some portions of the range, it can be expected to increase in severity in coming decades. Given the multi-century lifespan of Limber Pine and the impacts of the rust of the past 60 years, the effect of White Pine Blister Rust can be considered to be “rapid” and certainly capable of affecting all individuals of the species. Thus, Limber Pine also comprises one location when the threat of White Pine Blister Rust is considered.

Both Mountain Pine Beetle and White Pine Blister Rust are serious plausible threats that can affect the entire Canadian range of Limber Pine. Which of these is most plausible is difficult to judge. However, given their interaction, in which White Pine Blister Rust kills individuals of many ages and reduces seed production and regeneration, while Mountain Pine Beetle can kill the remaining (perhaps rust-resistant) mature trees in a stand, it is more realistic to regard the combined effects as “a single threatening event.”

PROTECTION, STATUS, AND RANKS

Legal Protection and Status

Limber Pine has no legal protection in Canada (but see below).

Non-Legal Status and Ranks

In Alberta, Limber Pine is listed as Endangered under the *Wildlife Act* (Government of Alberta 2010). However, currently no provisions exist under the Act to provide legal protection for plant species in Alberta. A provincial recovery team was formed in December 2008 and is preparing a recovery plan. In the interim, provincial land management agencies are using existing mechanisms to protect Limber Pine and its habitat.

In British Columbia, Limber Pine has no legal protection, although it is a Blue List species (BC-CDC 2011). Blue-listed species are considered Identified Wildlife under the *Forest Practices Code* but no Accounts and Measures document, which outlines specific habitat management guidelines, has been prepared for this species.

At the international level, Limber Pine was assessed in 1998 as Least Concern on the IUCN Red List (IUCN 2010b). However, the assessment is noted as needing updating. Much new information on Limber Pine has accumulated since 1998.

Limber Pine has a global conservation rank of G4 (apparently secure) (NatureServe 2011). However, the rank reasons say “a multifactor combination of climate stress, dwarf mistletoe, White Pine Blister Rust, and bark beetles have created complex stress situations in Limber Pine forests which has caused high mortality in populations in many areas.” Also cited are “changing fire regimes combined with the poor competitiveness with other species and poor regeneration due to blister rust [which] also cause concern.”

NatureServe (2011) ranks Limber Pine as N3 (vulnerable) in Canada and as N4 (apparently secure) in the U.S. In Alberta, Limber Pine is currently ranked S2 (imperilled) (ACIMS 2011). In British Columbia, it is ranked S3 (vulnerable) (BC-CDC 2011).

In the U.S. (NatureServe 2011), Limber Pine is ranked S1 (critically imperilled) in four states (ND, NE, NM, SD), S4 (apparently secure) in Oregon, S5 (secure) in two states (MT, WY), and SNR (not ranked, usually due to lack of information) in six states (AZ, CA, CO, ID, NV, UT). This range of ranks likely reflects differing ranking dates and completeness of information more than the current situation.

Habitat Protection and Ownership

Limber Pine occurs on both federal and provincial Crown lands as well as private lands in both Alberta and British Columbia. The relative amounts on private and public lands are not known.

The federal Crown lands include Banff and Waterton Lakes national parks in Alberta, and Kootenay and Yoho national parks in British Columbia. Habitat is protected in national parks by the *Canada National Parks Act*, and by management plans and processes pursuant to maintaining or restoring ecological integrity. National park managers in Alberta and British Columbia are aware of the need and have taken measures to protect Limber Pine habitat in park management activities.

Limber Pine also occurs on the Blood, Peigan, Eden Valley, and Stoney Indian reserves in Alberta.

In Alberta, Limber Pine occurs in a variety of protected areas administered by Alberta Parks, including provincial parks, wildland provincial parks, and ecological reserves. Alberta Parks is currently assessing the health and status of Limber Pine in protected areas and considering its conservation in management planning (Gould, pers. comm. 2008). Limber Pine also occurs on Alberta Crown land administered by Alberta Environment and Sustainable Resource Development. Alberta ESRD has taken measures to manage Limber Pine habitat in planning for forest harvesting, fire management, Mountain Pine Beetle management, and petroleum development (Dhir *et al.* 2003; AESRD 2013). As well, Limber Pine occurs on the Black Creek Heritage Rangeland, which is administered by several government agencies. A provincial recovery strategy for Limber Pine is currently being prepared and includes consideration of habitat protection (Jones, pers. comm. 2012).

In British Columbia, Limber Pine occurs on provincial Crown land in provincial forests and in the Columbia Lake and Mt. Sabine ecological reserves.

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INFORMATION SOURCES

Achuff, P.L., W.D. Holland, G.M. Coen, and K. Van Tighem. 1984. Ecological land classification of Kootenay National Park, British Columbia. Volume I: Integrated resource description. Alberta Institute of Pedology Publication M-84-10: 373 pp.

Achuff, P.L., W.S. Taylor, and L.J. Knapik. 1993. Ecological land classification of Yoho National Park, British Columbia. Yoho National Park, Field, British Columbia. 283 pp.

Achuff, P.L., R.L. McNeill, M.L. Coleman, C. Wallis, and C. Wershler. 2002. Ecological land classification of Waterton Lakes National Park, Alberta. Volume I: Integrated resource description. Parks Canada, Waterton Park, Alberta. 226 pp.

ACIMS (Alberta Conservation Information Management System). 2011. Element occurrence file: *Pinus flexilis*. Alberta Tourism, Parks and Recreation, Alberta Parks, Edmonton, Alberta.

AESRD (Alberta Environment and Sustainable Resource Development). 2013. Enhanced Approvals Process. Web site: http://srd.alberta.ca/FormsOnlineServices/EnhancedApprovalsProcess/Default.aspx [accessed 27 November 2013].

AFLW (Alberta Forestry, Lands and Wildlife). 1986. Mountain pine beetle control program 1980-1986. Alberta Forestry, Lands and Wildlife, Forest Service, Edmonton, Alberta, Publication I/43: 14 pp.

Aitken, S.N., S. Yeaman, J.A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1:95-111.

Alfaro, R., B. Hawkes and J. Axelson. 2007. Stand dynamics in even-aged lodgepole pine stands following mountain pine beetle outbreaks. Presentation at 15th Alberta-British Columbia Intermountain Forest Health Workshop, Hinton, Alberta.

Allen, L. 2010. Alberta Natural Heritage Information Centre Preliminary Ecological Community Tracking List. Alberta Tourism, Parks and Recreation, Alberta Parks, Edmonton, Alberta.

Amman, G.D. 1982. Characteristics of mountain pine beetles reared on four different pine hosts. Environmental Entomology 11: 590-593.

Amman, G.D., M.D. McGregor, and R.E. Dolph. 1997. Mountain pine beetle. Forest Insect & Disease Leaflet 2. USDA Forest Service. Web site: http://www.na.fs.fed.us/spfo/pubs/fidls/mt_pine_beetle/mt_pine.htm [accessed February 2003].

Andresen, J.W., and R.J. Steinhoff. 1971. The taxonomy of *Pinus flexilis* and *P. strobiformis*. Phytologia 22:57-70.

Asebrook, J.M., J. Lapp, and T. Carolin. 2011. Whitebark and limber pine restoration and monitoring in Glacier National Park. pp. 335-337, in R.E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith (eds.), The future of high-elevation, five-needle white pines in western North America. USDA Forest Service, Proceedings RMRS-P-63.

ASRD (Alberta Sustainable Resource Development). 2009. Gene conservation plan for native trees in Alberta. Technical Publication T-1141: 108 pp.

Barrack, K.A., and A.W. Schoettle. 1996. A comparison of the foliar nutrient status of elfinwood and symmetrically formed tall trees, Colorado Front Range, USA. Canadian Journal of Botany 74: 1461-1475.

Barrow, E., and G. Yu. 2005. Climate scenarios for Alberta: report prepared for the Prairie Adaptation Research Collaborative, Regina, Saskatchewan in cooperation with Alberta Environment. 73 pp.

Bartlein, P.J., C. Whitlock, and S.L. Shafer. 1997. Future climate in the

Yellowstone National Park region and its potential impact on vegetation. Conservation Biology 11: 782-792.

Baumeister, D., and R.M. Callaway. 2006. Facilitation by *Pinus flexilis* during succession: a hierarchy of mechanisms benefits other plant species. Ecology 87: 1816-1830.

BC-CDC (British Columbia Conservation Data Centre). 2011. Conservation status report: *Pinus flexilis*. BC Species and Ecosystems Explorer. British Columbia Ministry of Environment, Victoria, British Columbia. http://a100.gov.bc.ca/pub/eswp/ [accessed 18 April 2011].

BEC (Biogeoclimatic Ecosystem Classification). 2011. Plot database. Web site: http://www.for.gov.bc.ca/hre/becweb [accessed 24 Feb 2011].

Benkman, C.W. 1995. The impact of tree squirrels (*Tamiasciurus*) on limber pine seed dispersal adaptations. Evolution 49: 585-591.

Benkman, C.W., R.P. Balda, and C.C. Smith. 1984. Adaptations for seed dispersal and the compromises due to seed predation in limber pine. Ecology 65: 632-642.

Bentz, B., E. Campbell, K. Gibson, S. Kegley, J. Logan, and D. Six. 2011. Mountain pine beetle in high-elevation five-needle white pine ecosystems. pp. 78-84, in R.E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith (eds.), The future of high-elevation, five-needle white pines in western North America. USDA Forest Service, Proceedings RMRS-P-63.

Bertrand, R., L. Lenoir, C. Piedallu, G. Riofrio-Dillon, and P. de Ruffray. 2011. Changes in plant community composition lag behind climate warming in lowland forests. Nature 479:517-520.

Betancourt, J.L. 1990. Late Quaternary biogeography of the Colorado Plateau. pp. 259-292, in J.L. Betancourt, T.R. Van Devender, and P.S. Martin (eds.), Packrat middens: the last 40,000 years of biotic change. University of Arizona Press, Tucson, Arizona.

Bower, A.D., S.C. McLane, A. Eckert, S. Jorgensen, A. Schoettle, and S. Aitken. 2011. Conservation genetics of high-elevation five-needle white pines. pp. 98-117 in R.E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith (eds.), The future of high-elevation, five-needle white pines in western North America. USDA Forest Service, Proceedings RMRS-P-63.

Bradshaw, A.D., and T. McNeilly. 1991. Evolutionary response to global climatic change. Annals of Botany 67:5-14.

Bright, D.E. 1976. The insects and arachnids of Canada and Alaska. Part 2. The Bark Beetles of Canada and Alaska: Coleoptera, Scolytidae. Canada Department of Agriculture, Ottawa. 241 pp.

Brown, P.M., and A.W. Schoettle. 2008. Fire and stand history in two limber pine (*Pinus flexilis*) and Rocky Mountain bristlecone pine (*Pinus aristata*) stands in Colorado. International Journal of Wildland Fire 17:339-347.

Brunelle, A., G.E. Rehfeldt, B. Bentz, and A.S. Munson. 2008. Holocene records of *Dendroctonus* bark beetles in high elevation pine forests of Idaho and Montana, USA. Forest Ecology and Management 255:836-846.

Buckley, L.B., and J.G. Kingsolver. 2012. Functional and phylogenetic approaches to forecasting species' response to climate change. Annual Review of Ecology and Systematics 43:205-226.

Burkett, V.R., D.A. Wilcox, R. Stottlemyer, W. Barrow, D. Fagre, J. Baron, J. Price, J.L. Neilson, C.D. Allen, D.L. Peterson, G. Ruggerone, and T. Doyle. 2005. Nonlinear dynamics in ecosystem response to climatic change: case studies and policy implications. Ecological Complexity 2: 357-394.

Burns, K.S., A.W. Schoettle, W.R. Jacobi, and M.F. Mahalovich. 2008. Options for the management of white pine blister rust in the Rocky Mountain Region. USDA Forest Service General Technical Report RMRS-GTR-206: 26 pp.

Burns, K.S., J. Blodgett, M. Jackson, B. Howell, W. Jacobi, A. Schoettle, A.M. Casper, and J. Klutsch. 2011. Monitoring limber pine health in the Rocky Mountains and North Dakota. pp. 47-50, in R.E. Keane, D.F. Tomback, M.P. Murray and C.M. Smith (eds.), The future of high-elevation, five-needle white pines in western North America. USDA Forest Service, Proceedings RMRS-P-63.

Burns, R.M., and B.H. Honkala. 1990. *Pinus flexilis.* pp. 348-354 in Silvics of North America, volume 1, Conifers. USDA Forest Service, Agriculture Handbook 654.

Carroll, A.L., S.W. Taylor, J. Regnière, and L. Safranyik. 2003. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. pp. 223-232, in T.L. Shore, J.E. Brooks, and J.E. Stone (eds.), Mountain pine beetle symposium: challenges and solutions. Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399.

Carsey, K.S. and D.F. Tomback. 1994. Growth form distribution and genetic relationships of tree clusters of *Pinus flexilis,* a bird-dispersed pine. Oecologia 98: 402-411.

Case, R.A., and G.M. MacDonald. 1995. A dendroclimatic reconstruction of annual precipitation on the western Canadian prairies since A.D. 1505 from *Pinus flexilis* James. Quaternary Research 44: 267-275.

Case, R.A., and G.M. MacDonald. 2003. Tree ring reconstructions of streamflow for three Canadian prairie rivers. Journal of the American Water Resources Association 39: 703-716.

Casper, A.M., W.R. Jacobi, A.W. Schoettle, and K.S. Burns. 2011, Restoration planting options for limber pines in the southern Rocky Mountains. p. 375, in R.E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith (eds.), The future of high-elevation, five-needle white pines in western North America. USDA Forest Service, Proceedings RMRS-P-63.

CFS (Canadian Forest Service). 2008. Meet the mountain pine beetle. Canadian Forest Service, Natural Resources Canada. Web site: http://mpb.cfs.nrcan.gc.ca/biology/introduction_e.html [accessed 19 December 2008].

Colwell, R.K., R.R. Dunn, and N.C. Harris. 2012. Coextinction and persistence of dependent species in a changing world. Annual Review of Ecology and Systematics 43: 183-203.

Coop, J.D., and A.W. Schoettle. 2009. Regeneration of Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) three decades after stand-replacing fires. Forest Ecology and Management 257: 893-903.

Coop, J.D., R.T. Massati, and A.W. Schoettle. 2010. Subalpine vegetation pattern three decades after stand-replacing fire: effects of landscape context and topography on plant community composition, tree regeneration, and diversity. Journal of Vegetation Science 21: 1-16.

COSEWIC (Canada. Committee on the Status of Endangered Wildlife in Canada). 2010. COSEWIC assessment and status report on the Whitebark Pine *Pinus albicaulis* in Canada. Ottawa. x + 44 pp. (www.sararegistry.gc.ca/status/status_e.cfm).

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2012. COSEWIC Operations and Procedures Manual, Appendix C: Definitions and Abbreviations (November 2011). Web site: http://www.cosewic.gc.ca/538n1sc001/plants/index.cfm [accessed October 2012].

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2013. The Species Specialist Subcommittees' Candidate Lists: Arthropods. Web site: http://www.cosewic.gc.ca/eng/sct3/index_e.cfm#8 [accessed 8 January 2013].

Cripps, C.L. and, R.K. Antibus. 2011. Native ectomycorrhizal fungi of limber and whitebark pine: necessity for forest sustainability? pp. 37-44, in R.E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith (eds.), The future of high-elevation, five-needle white pines in western North America. USDA Forest Service, Proceedings RMRS-P-63.

de Groot, W., P. Bothwell, D. Carlsson, K. Logan, R. Wein, and C. Li. 2002. Forest fire management adaptation to climate change in the Prairies. Canadian Forest Service, University of Alberta, and Prairie Adaptation Research Collaborative, Regina, SK. 97 pp.

Desprez-Loustau, M-L., C. Robin, M. Buee, R. Courtecuisse, J. Garbaye, F. Suffert, I. Sache, and D.M. Rizzo. 2007. The fungal dimension of biological invasions. TRENDS in Ecology and Evolution 22: 472-480.

Dhir, N., L. Allan, and K. Vujnovic. 2003. Limber pine and whitebark pine management in Alberta. pp. 10-11, in Parks Canada (ed.). Whitebark and limber pine workshop proceedings, 28-29 February 2003, Calgary, Alberta. Web site: http://www.whitebarkfound.org/PDF_files/WBPProceedings.pdf [accessed 2006].

Donnegan, J.A., and A.J. Rebertus. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. Ecology 80: 1370-1384.

Douglas, G.D., G.B. Straley, D. Meidinger, and J. Polar. 1998. *Pinus*. pp. 20-23, in Illustrated flora of British Columbia, volume 1: Gymnosperms and Dicotyledons (Aceraceae through Asteraceae). Ministry of Forests. Victoria, British Columbia, Canada.

Downing, D.J., and W.W. Pettapiece (comps.). 2006. Natural regions and subregions of Alberta. Natural Regions Committee, Alberta Government Publication T/852: 254 pp.

Dullinger, S., T. Dirnbock and G. Grabherr. 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. Journal of Ecology 92: 241-252.

Earle, C.J. 2010. *Pinus flexilis*. The Gymnosperm Database. Web site: http://www.conifers.org/pi/pin/flexilis.htm [accessed 21 April 2011].

Eckert, A.J., and B.D. Hall. 2006. Phylogeny, historical biogeography, and patterns of diversification for *Pinus* (Pinaceae): phylogenetic tests of fossil-based hypotheses. Molecular Phylogenetics and Evolution 40: 166-182.

E-flora BC. 2011. Electronic atlas of the flora of British Columbia. Web site: http://www.geog.ubc.ca/atlas/atlas.aspx?sciname=Pinus%20flexilis [accessed 3 Mar 2011].

ESIS. 2011. Alberta Ecological Site Information System. Web site: http://www.srd.gov.ab.ca/lands/geographicinformation/resourcedataproductcatalogue/esis.aspx. [accessed 9 January 2011].

Ettl, G.J. and N. Cottone. 2004. Whitebark pine (*Pinus albicaulis*) in Mt Rainier National Park, Washington, USA. pp. 36-47, in H.R. Akçakaya, M. Burgman, O. Kindvall, C.C. Wood, P. Sjögren-Gulve, J.S. Hatfield, and M.A. McCarthy (eds.). Species Conservation and Management: Case Studies. Oxford University Press. Oxford, United Kingdom.

FAN (Federation of Alberta Naturalists). 2007. The atlas of breeding birds of Alberta: a second look. Federation of Alberta Naturalists, Edmonton, Alberta. 626 pp.

FIAS (Forest Invasive Alien Species). 2011. Canadian Forest Alien Species database: *Pinus flexilis* records 1921-2010. Web site: https://afc-fr.cfsnet.nfis.org/fiaslib/index.jsp?query=pinus+flexilis [accessed 2 May 11].

Field, S.G., A.W. Schoettle, J.G. Klutsch, S.J. Tavener, and M.F. Antolin. 2012. Demographic projection of high-elevation white pines infected with white pine blister rust: a nonlinear disease model. Ecological Applications 22: 166-183.

Flannigan, M.D., K.A. Logan, B.D. Amiro, W.R. Skinner, and B.J. Stocks. 2005. Future area burned in Canada. Climate Change 72: 1-16.

Franks, S.J., J.J. Weber, and S.N. Aitken. 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. Evolutionary Applications 7: 123–139.

Freeman, T.N. 1972. The coniferous feeding species of *Argyresthia* in Canada (Lepidoptera: Yponomeutidae). Canadian Entomologist 104: 687-697.

Furniss, M.M., and J. B. Johnson. 1995. New records of Scolytidae from Washington State. Great Basin Naturalist 55: 335-341.

Gao, Q., P. Zhao, X. Zheng, X. Cai, and W. Shen. 2002. A model of stomatal conductance to quantify the relationship between leaf transpiration, microclimate and soil water stress. Plant, Cell and Environment 25: 1373-1381.

Gautreau, E. 1963. Effects of white pine blister rust in limber pine stands in Alberta. 1963. Canada Department of Forestry, Forest Entomology and Pathology Branch, Ottawa, Ontario. Bi-Monthly Progress Report 19 (4): 3.

Geils, B.W., K.L. Hummer, and R.S. Hunt. 2010. White pines, *Ribes* and blister rust: a review and synthesis. Forest Pathology 40: 147-185.

Gernandt, D.S., G.G. Geada Lopez, S. Ortiz Garcia, and A. Liston. 2005. Phylogeny and classification of *Pinus*. Taxon 54: 29-42.

Gillett, N.P., A.J. Weaver, F.W. Zweirs, and M.D. Flannigan. 2004. Detecting the effect of climate change on Canadian forest fires. Geophysical Research Letters 31: L18211.

Gould, J. pers. comm. 2008. *Verbal report at Whitebark and Limber Pine Team meeting*, 15 December 2008, Edmonton, Alberta. Science Coordinator, Parks Division, Alberta Tourism, Parks and Recreation, Edmonton, Alberta.

Government of Alberta. 2010. Species assessed by Alberta's Endangered Species Conservation Committee: short list. Web site: http://www.srd.ab.ca/FishWildlife/SpeciesAtRisk/SpeciesSummaries/SpeciesAtRiskFactSheets.aspx [accessed 9 January 2013].

Hamman, A., and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87:2772-2786.

Henderson, N, T. Hogg, E. Barrow, and B. Dolter. 2002. Climate change impacts on the island forests of the Great Plains and the implications for conservation policy. Prairie Adaptation Research Collaborative, Regina, Saskatchewan. 116 pp.

Hoff, R.J. and G.I. McDonald. 1993. Variation of virulence of white pine blister rust. European Journal of Forest Pathology 23: 103-109.

Hoff, R.J., D.F. Ferguson, G.I. McDonald, and R.E. Keane. 2001. Strategies for managing whitebark pine in the presence of white pine blister rust. pp. 346-366, in D.F. Tomback, S.F. Arno, and R.E. Keane (eds.). Whitebark pine communities: ecology and restoration. Island Press. Washington, District of Columbia, USA.

Hoff, R.J., R. Bingham, and G. MacDonald. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology 10: 307-316.

Holland, W.D., and G.M. Coen (eds.). 1982. Ecological (biophysical) land classification of Banff and Jasper national parks. Volume 2: soil and vegetation resources. SS-82-44. Alberta Institute of Pedology, University of Alberta, Edmonton, Alberta. 540 pp.

Huntley, B. 1991. How plants respond to climate change: migration rates, individualism and the consequences for plant communities. Annals of Botany 67: 15-22.

IPCC (Intergovernmental Panel on Climate Change). 2007. Climate Change 2007: contributions of Working Groups I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland. 104 pp.

IUCN (International Union for Conservation of Nature). 2010a. Guidelines for using IUCN Red List categories and criteria. IUCN Standards and Petitions Subcommittee, March 2010. 85 pp. Web site: http://intranet.iucn.org/webfiles/doc/SSC/Redlist/RedListGuidelines.pdf [accessed November 2010].

IUCN (International Union for Conservation of Nature). 2010b. *Pinus flexilis*. 2010 IUCN Red List of Threatened Species. Web site: http://www.redlist.org/ [accessed 18 Apr 2011].

IUCN and CMP (International Union for Conservation of Nature and Conservation Measures Partnership). 2006. IUCN-CMP unified classification of direct threats, ver. 1.0 – June 2006. Gland, Switzerland. 17 pp.

Jackson, M., and B. Lockman. 2003. Update on limber pine decline and mortality on the Lewis and Clark National Forest, Montana. USDA Forest Service, Forest Health Protection Report 03-4: 8 pp.

Jackson, S.T., and J.T. Overpeck. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. Paleobiology 26 (Supplement No. 4): 194-220.

Joly, D.L., D.W. Langor, and R.C. Hamelin. 2006. Interspecific hybridization between *Cronartium ribicola* and *C. comandrae* on *Pinus flexilis* in southwestern Alberta. Plant Disease 90: 1552.

Jones, B. pers. comm. 2012. *Conversation September 2012*. Co-chair, Alberta Whitebark and Limber Pine Recovery Team. Alberta Environment and Sustainable Resource Development, Calgary, Alberta.

Jorgensen, S., J.L. Hamrick, and P.V. Wells. 2002. Regional patterns of genetic diversity in *Pinus flexilis* (Pinaceae) reveal complex species history. American Journal of Botany 89: 792-800.

Jump, A.S. and J. Penuelas. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecological Letters 8: 1010-1020.

Keane, R.E., S.F. Arno, J.K. Brown, and D.F. Tomback. 1990. Stand dynamics in whitebark pine (*Pinus albicaulis*) forests. Ecological Modelling 51: 73-96.

Keane, R.E., K.C. Ryan, T.T. Veblen, C.D. Allen, J. Logan, and B. Hawkes. 2002. Cascading effects of fire exclusion in Rocky Mountain ecosystems: a literature review. USDA Forest Service, General Technical Report RMRS-GR-91: 24 pp.

Keane, R.E., and A.W Schoettle. 2011. Strategies, tools, and challenges for sustaining and restoring high-elevation five-needle white pine forests in western North America. pp. 276-294, in R.E. Keane, D.F. Tomback, M.P. Murray and C.M. Smith (eds.), The future of high-elevation, five-needle white pines in western North America. USDA Forest Service, Proceedings RMRS-P-63.

Kearnes, H.S.J., and W.R. Jacobi. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Canadian Journal of Forest Research 37: 462-472.

Kearnes, H.S.J., W.R. Jacobi, and B.W. Geils. 2009. A method for estimating white pine blister rust canker age on limber pine in the central Rocky Mountains. Forest Pathology 39: 177-191.

Keeley, J.E., and P.H. Zedler. 1998. Evolution of life histories in *Pinus*. pp. 219-250 in D.M. Richardson (ed.), Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge, UK.

Kendall, K.C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. International Conference on Bear Research and Management 5: 166-173.

King, J.N., A. David, D. Noshad, and J. Smith. 2010. A review of genetic approaches to the management of blister rust in white pines. Forest Pathology 40: 292-313.

Klutsch, J.G., B.A. Goodrich, and A.W. Schoettle. 2011. Limber pine forests on the leading edge of white pine blister rust distribution in northern Colorado. pp. 222-225, in R.E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith (eds.), The future of high-elevation, five-needle white pines in western North America. USDA Forest Service, Proceedings RMRS-P-63.

Kral, R. 1993. *Pinus*. pp. 373-398, in Flora of North America Editorial Committee (eds.), Flora of North America, volume 2. Pteridophytes and Gymnosperms. Oxford University Press, New York, New York, USA.

Kueppers, L.M. 2010. Sensitivity of subalpine tree seedlings and alpine plants to natural and manipulated climate variation: initial results from an Alpine Treeline Warming Experiment. Abstract GC53A-04 presented at American Geophysical Union, Fall Meeting 2010, San Francisco, California, 13-17 December.

Langor, D.W. 1989. Host effects on the phenology, development, and mortality of field populations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Canadian Entomologist 121: 149-157.

Langor, D.W. 2007. Status of limber pine (*Pinus flexilis*) in Alberta. Alberta Sustainable Resource Development, Wildlife Status Report No. 62: 17 pp.

Langor, D.W., J.R. Spence, and G.R. Pohl. 1990. Host effects on fertility and reproductive success of *Dendroctonus ponderosae* Hopkins) (Coleoptera: Scolytidae). Evolution 44: 609-618.

Lanner, R.M. 1985. Effectiveness of the seed wing of *Pinus flexilis* in wind dispersal. Great Basin Naturalist 45: 318-320.

Lanner, R.M. 1996. Made for each other: a symbiosis of birds and pines. Oxford University Press, New York, New York, USA. 160 pp.

Lanner, R.M. 1998. Seed dispersal in *Pinus*. pp. 281-295, in D.M. Richardson (ed.), Ecology and biogeography of *Pinus.* Cambridge University Press, Cambridge, United Kingdom.

Lanner, R.M., and S.B. Vander Wall. 1980. Dispersal of limber pine seed by Clark's nutcracker. Journal of Forestry 78: 637-639.

Latta, R.G., and J.B. Mitton. 1997. A comparison of population differentiation across four classes of gene markers in limber pine (*Pinus flexilis* James). Genetics 146: 1153-1163.

Lea, E.C. 1984. Biophysical resources of the East Kootenay area: Volume 1 – Vegetation. British Columbia Ministry of Environment, Victoria, British Columbia, Technical Report 5: 75 pp.

Lenihan, J.M., D. Bachelet, R.P. Neilson, and R.J. Drapek. 2008. Simulated response of conterminous United States ecosystems to climate change at different levels of fire suppression, CO_2 emission rate and growth response to CO_2. Global Planet Change 64: 16-25.

Lenoir, J., J.V. Gegout, P.A. Marquet, P. de Ruffray, and H. Brisse. 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320: 1768-1771.

Letts, M.G., K.N. Nakonechny, K.E. Van Gaalen, and C.M. Smith. 2009. Physiological acclimation of *Pinus flexilis* to drought stress on contrasting slope aspects in Waterton Lakes National Park, Alberta, Canada. Canadian Journal of Forest Research 39: 629-641.

Liston, A., W.A. Robinson, D. Pinero, and E.R. Alvarez-Buylla. 1999. Phylogenetics of *Pinus* (Pinaceae) based on nuclear ribosomal DNA internal transcribed spacer sequences. Molecular Phylogenetics and Evolution 11: 95-109.

Liston, A., M. Parker-Defeniks, J.V. Syring, A. Willyard, and R. Cronn. 2007. Interspecific phylogenetic analysis enhances intraspecific phylogeographical inference: a case study in *Pinus lambertiana*. Molecular Ecology 16: 3926-3937.

Litell, J.S., E.E. Oneill, D. McKenzie, J.A. Hicke, J.A. Lutz, R.A. Norheim, and M.M. Eisner. 2010. Forest ecosystems, disturbance and climatic change in Washington State, USA. Climatic Change 102: 129-158.

Logan, J.A., and J.A. Powell. 2008. Ecological consequences of climatic change – altered forest insect disturbance regimes. 33 pp., in F.H. Wagner (ed.). Climate Change in western North America: evidence and environmental effects. Allen Press (in review). Web site: http://www.usu.edu/beetle/publications_bark_beetle.htm [accessed 18 December 2008].

Logan, J.A., W.W. McFarlane, and L. Willcox. 2010. Whitebark pine vulnerability in climate-driven mountain pine beetle disturbance in the Greater Yellowstone ecosystem. Ecological Applications 20: 895-902.

MacDonald, G.M. 1989. Postglacial palaeoecology of the subalpine forest-grassland ecotone of southwestern Alberta: new insights on vegetation and climate change in the Canadian Rocky Mountains and adjacent foothills. Palaeogeography, Palaeoclimatology and Palaeoecology 73: 156-173.

MacDonald, G.M., and R.A. Case. 2005. Variations in the Pacific Decadal Oscillation over the past millennium. Geophysical Research Letters 32: L08703, 4 pp.

Mahalovich, M.F. 2006. Limber pine seed transfer guidelines. USDA Forest Service, Regions1-4, internal report. 4 pp.

Malcolm, J.R., A. Markham, R.P. Neilson, and M. Garaci. 2002. Estimated migration rates under scenarios of global climate change. Journal of Biogeography 29: 835-849.

McCune, B. 1988. Ecological diversity in North American pines. American Journal of Botany 75: 353-368.

McCutchen, H.E. 1996. Limber pines and black bears. Great Basin Naturalist 56: 90-92.

McDonald, G.I., and R.J. Hoff. 2001. Blister rust: an introduced plague. pp. 193-220, in D.F. Tomback, S.F. Arno, and R.E. Keane (eds.). Whitebark pine communities: ecology and restoration. Island Press. Washington, DC, USA.

McDonald, G.I., B.A. Richardson, P.J. Zambino, N.B. Klopfenstein, and M.S. Kim. 2006. *Pedicularis* and *Castilleja* are natural hosts of *Cronartium ribicola* in North America: a first report. Forest Pathology 36: 73-82.

McKenney, D.W., J.H. Pedlar, K. Lawrence, K. Campbell, and M.F. Hutchinson. 2007. Potential impacts of climate change on the distribution of North American trees. BioScience 57: 939-948.

McKinney, S.T., C.E. Fiedler, and D.F. Tomback. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecological Applications 19: 597-607.

Meidinger, D., and J. Pojar (eds.). 1991. Ecosystems of British Columbia. British Columbia Ministry of Forests, Victoria British Columbia, Special Report Series 6: 330 pp.

Millar, C.I., R.D. Westfall, and D.L. Delany. 2007. Response of high-elevation limber pine (*Pinus flexilis*) to multiyear droughts and 20th –century warming, Sierra Nevada, California, USA. Canadian Journal of Forest Research 37: 2508-2520.

Mills, L.S., M.E. Soule, and D.F. Doak. 1993. The keystone-species concept in ecology and conservation. Bioscience 43: 219-224.

Mitton, J.B., B.R. Kreiser, and R.G. Latta. 2000. Glacial refugia of limber pine (*Pinus flexilis* James) inferred from the population structure of mitochondrial DNA. Molecular Ecology 9: 91-97.

Mitton, J.B., and S.M. Ferenberg. 2012. Mountain pine beetle develops an unprecedented summer generation in response to climate warming. American Naturalist 179: E163-E171.

Moody, R. pers. comm. 2011. *Email to P. Achuff, September 2011*. Ecologist, Keefer Ecological Services, Cranbrook, British Columbia.

Moorcroft, P.R., S.W. Pacala, and M.A. Lewis. 2006. Potential role of natural enemies during tree range expansions following climate change. Journal of Theoretical Biology 241: 601-616.

Moyes, A.B., C. Castanha, M.J. Germino, and L.M. Kueppers. 2013. Warming and the dependence of limber pine (*Pinus flexilis*) establishment on summer moisture within and above its current range. Oecologia 171: 271-282.

NatureServe. 2011. *Pinus flexilis*. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia. Web site: http://www.natureserve.org/explorer [accessed: 18 Apr 2011].

NDSU (North Dakota State University). 2013. Limber Pine (*Pinus flexilis*). Web site: http://www.ag.ndsu.edu/trees/handbook/th-3-163.pdf [accesssed 12 July 2013].

Perez-Valdivia, C. J.R. Vanstone, and D. Sauchyn. 2010. Tree-ring reconstruction of 700 years flow at the Oldman River, southwestern Alberta, Canada. Poster presented at American Geophysical Union, 2010 Fall Meeting, San Francisco, California, 13-17 December.

Peters, V.S. 2011. Pre-dispersal seed predation dynamics at the northern limit of limber pine. p. 74 in R.E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith (eds.), The future of high-elevation, five-needle white pines in western North America. USDA Forest Service, Proceedings RMRS-P-63.

Peters, V. 2012. Limber pine seed mutualisms: between the devil and the deep blue sea. Nutcracker Notes 22: 11-13.

Raffa, K.F., B.H. Aukema, B.J. Bentz, A.L. Carroll, J.A. Hicke, M.G. Turner, and W.H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience 58: 501-517.

Rebertus, A.J., B.R. Burns, and T.T. Veblen. 1991. Stand dynamics *of Pinus flexilis*-dominated subalpine forests in the Colorado Front Range. Journal of Vegetation Science 2: 445-458.

Rehfeldt, G.E., C.C. Ying, D.L Spittlehouse, and D.A. Hamilton. 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. Ecological Monographs 69: 375-407.

Rehfeldt, G.E., R.A. Wykoff, and C.C. Ying. 2001. Physiologic plasticity, evolution, and impacts of a changing climate on *Pinus contorta*. Climate Change 50: 355-376.

Rehfeldt, G.E., N.M. Tchebakova, Y.I. Parfenova, R.A. Wykoff. N.A. Kuzmina, and L.I. Milyutin. 2002. Intraspecific responses to climate in *Pinus sylvestris*. Global Change Biology 8: 912-929.

Rehfeldt, G.E., N.L. Crookston, M.V. Warwell, and J.S. Evans. 2006. Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Science 167: 1123-1150.

Reinhardt, K., C. Castanha, M.J. Germino, and L.M. Kueppers. 2011. Leapfrogging of tree species provenances: interaction of microclimates and genetics on upward shifts in tree species' range limits. Abstract B13D-0601 presented at American Geophysical Union, Fall Meeting 2011, San Francisco, California, 5-9 December.

Rhode, D., and D.B. Madsen. 1998. Pine nut use in the Early Holocene and beyond: the Danger Cave archaeobotanical record. Journal of Archaeological Science 25: 1199-1210.

Richardson, B.A., A.K.M. Ekramoddoulah, J.J. Liu, M.S. Kim, and N.B. Klopfenstein. 2010. Current and future molecular approaches to investigate the white pine blister rust pathosystem. Forest Pathology 40: 314-331.

Roberts, D.R., and A. Hamman. 2011. Predicting potential climate change impacts with bioclimate envelope models: a palaeoecological perspective. Global Ecology and Biogeography 21: 121-133.

Romme, W.H., and M.G. Turner. 1991. Implications of global change for biogeographic patterns in the Greater Yellowstone Ecosystem. Conservation Biology 5: 373-396.

Rweyongeza, D., L. Barnhardt, and C. Hansen. 2010. Climate change adaptation by Alberta Sustainable Resource Development. Web site: http://www.afex.ca/afex-events/22-forest-tree-provenance-application-to-reforestation-reclamation-and-adaptation-to-climate-change [accessed 2 April 2012].

Safranyik, L., A.L. Carroll, J. Regnière, D.W. Langor, W.G. Riel, T.L. Shore, B. Peter, B.J. Cooke, V.G. Nealis, and S.W. Taylor. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. Canadian Entomologist 142: 415-422.

Saporta, R., J. Malcolm, and D. Martell. 1998. The impact of climate change on Canadian forests. Chapter 6, in G. Koshida, and A. Avis (eds.), The Canada Country Study: climate impact and adaptation. Volume 7, National Sectoral Volume. Environment Canada, Ottawa, Ontario.

Sauchyn, D. J., E. Barrow, R.F. Hopkinson, and P. Leavitt. 2002. Aridity on the Canadian plains. Geographie physique et Quaternaire 56: 247-259.

Sauchyn, D., and S. Kulshreshtha. 2008. Prairies. pp. 275-328, in D.S. Lemmon, F.J. Warren, J. Lacroix, and E. Bush (eds.), From impacts to adaptation: Canada in a changing climate. Government of Canada, Ottawa, Ontario.

Savolainen, O., T. Pyhajarvi, and T. Knurr. 2007. Gene flow and adaptation in trees. Annual Review of Ecology and Systematics 38: 595-619.

Schindler, D., and B. Donahue. 2012. The impacts of climate change on water in Alberta. Environmental Research and Studies Centre, University of Alberta, Edmonton. Web site: http://www.ualberta.ca/~ersc/water/climate.htm. [accessed: 26 March 2012].

Schmidt, W.C., and J.E. Lotan. 1980. Phenology of common forest flora of the northern Rockies – 1928-1937. USDA Forest Service, Research Paper INT-259.

Schneider, R.R., A. Hamman, D. Farr, X. Wang, and S. Boutin. 2009. Potential effects of climate change on ecosystem distribution in Alberta. Canadian Journal of Forest Research 39: 1001-1010.

Schoettle, A.W. 2004. Ecological roles of five-needle pines in Colorado: potential consequences of their loss, pp. 124-135, in R.A. Sniezko, S. Samman, S.E. Schlarbaum, and B.E. Howard (eds.), Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance. USDA Forest Service Proceedings RMRS-P-32.

Schoettle, A.W., and S.G. Rochelle. 2000. Morphological variation of *Pinus flexilis* (Pinaceae), a bird-dispersed pine, across a range of elevation. American Journal of Botany 87: 1797-1806.

Schoettle, A.W., and R.A. Sniezko. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research 12: 327-336.

Schoettle, A.W., R.A. Sniezko, A. Kegley, and K.S. Burns. 2011. Preliminary overview of the first extensive rust resistance screening tests of *Pinus flexilis* and *Pinus aristata.* pp. 265-269, in R.E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith (eds.), The future of high-elevation, five-needle white pines in western North America. USDA Forest Service, Proceedings RMRS-P-63.

Schoettle, A.W., R.A. Sniezko, A. Kegley, and K.S. Burns. 2014. White Pine Blister Rust Resistance in Limber Pine: Evidence for a major gene. Phytopathology 104:163-173.

Schuster, W.S., D.L. Alles, and J.B. Mitton. 1989. Gene flow in limber pine: evidence from pollination phenology and genetic differentiation along an elevational transect. American Journal of Botany 76: 1395-1403.

Schuster, W.S., and J.B. Mitton. 2000. Paternity and gene dispersal in limber pine (*Pinus flexilis* James). Heredity 84: 348-361.

Schuster, W.S., J.B. Mitton, D.K. Yamaguchi, and C.A. Woodhouse. 1995. A comparison of limber pine (*Pinus flexilis*) ages at lower and upper treeline sites of the Continental Divide in Colorado. American Midland Naturalist 133: 101-111.

Schwandt, J.W., I.B. Lockman, J.T. Kliejunas, and J.A. Muir. 2010. Current health issues and management strategies for white pines in the western United States and Canada. Forest Pathology 40: 226-250.

Sherriff, R.L., T.T. Veblen, and J.S. Sibold. 2001. Fire history in high elevation subalpine forests in the Colorado Front Range. Ecoscience 8: 369-380.

Siepielski, A.M., and C.W. Benkman. 2007. Selection by a predispersal seed predator constrains the evolution of avian seed dispersal in pines. Functional Ecology 21: 611-618.

Siepielski, A.M., and C.W. Benkman. 2008. Seed predation and selection exerted by a seed predator influence subalpine tree densities. Ecology 89: 2960-2966.

Smith, C.C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs 40: 349-371.

Smith, C.C., and R.P. Balda. 1979. Competition among insects, birds and mammals for conifer seeds. American Zoologist 19: 1065-1083.

Smith, C.M. pers. comm. 2013. Scientist Emeritus, Waterton Lakes National Park, Waterton Park, Alberta.

Smith, C.M., D. Langor, C. Myrholm, J. Weber, C. Gillies, and J. Stuart-Smith. 2011a. Limber Pine health in the Canadian Rockies. pp. 63-65, in R.E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith (eds.), The future of high-elevation, five-needle white pines in western North America. USDA Forest Service, Proceedings RMRS-P-63.

Smith, C.M., G. Poll, C. Gillies, C. Praymak, E. Miranda, and J. Hill. 2011b. Limber pine seed and seedling planting experiment in Waterton Lakes National Park, Canada. pp. 365-374, in R.E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith (eds.), The future of high-elevation, five-needle white pines in western North America. USDA Forest Service, Proceedings RMRS-P-63.

Smith, C.M., D. Langor, C. Myrholm, J. Weber, C. Gillies, and J. Stuart-Smith. 2013. Changes in blister rust infection and mortality in limber pine over time. Canadian Journal of Forest Research: 43: 919–928

Smith, S.E., and D.J. Read. 1997. Mycorrhizal symbiosis. Academic Press, San Diego, California, USA.

Spittlehouse, D.L. 2008. Climate Change, impacts, and adaptation scenarios: climate change and forest and range management in British Columbia. B.C. Min. For. Range, Res. Br., Victoria, B.C. Tech. Rep. 045. http://www.for.gov.bc.ca/hfd/pubs/Docs/Tr/Tr045.htm

St. Jacques, J-M., A.Y. Huang, Y. Zhao, S.L. Lapp, and D.J. Sauchyn. 2011. Understanding hydrologic change: analyses of regional streamflow records. Abstract H42H-08 presented at American Geophysical Union, Fall Meeting 2011, San Francisco, CA, 5-9 December.

Steele, R. 1990. *Pinus flexilis* James – Limber Pine. pp. 348-354, in R.M. Burns, and B.H. Honkala (tech. coords.), Silvics of North America: 1. Conifers. Agriculture Handbook 654, USDA Forest Service, Washington, District of Columbia. 675 pp.

Steinhoff, R.J., and J.W. Andresen. 1971. Geographic variation in *Pinus flexilis* and *Pinus strobiformis* and its bearing on their taxonomic status. Silvae Genetica 20: 159-167.

Sturrock, R.N., S.J. Frankel, A.V. Brown, P.E. Hennon, J.T. Kliejunas, K.J. Lewis, J.J. Worrall, and A.J. Woods. 2011. Climate change and forest disease. Plant Pathology 60: 133-149.

Syring, J., A. Willyard, R. Cronn, and A. Liston. 2005. Evolutionary relationships among *Pinus* (Pinaceae) subsections inferred from multiple low-copy nuclear loci. American Journal of Botany 92: 2086-2100.

Syring, J. K. Farrell, R. Businsky, R. Cronn, and A. Liston. 2007. Widespread genealogical nonmonophyly in species of *Pinus* subgenus *Strobus*. Systematic Botany 56: 163-181.

Taylor, S.W., A.L. Carroll, R.I. Alfaro, and L. Safranyik. 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. pp. 67-94, in L. Safranyik, and W.R. Wilson (eds.), The Mountain Pine Beetle: a synthesis of biology, management, and impacts on lodgepole pine. Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia.

Taylor, J.E., and R.L. Mathiason. 1999. Limber pine dwarf mistletoe (FIDL). USDA Forest Service, Northern Region, Forest Health Protection, Forest Insect and Disease Leaflet 171.

Tedersoo, L., T.W. May, and M.E. Smith. 2009. Ectomycorrhizal lifestyle in fungi: global diversity, distribution and evolution of phylogenetic lineages. Mycorrhiza 20: 217-263.

Timoney, K. 1999. Limber pine, whitebark pine, alpine heath and terricolous alpine lichen vegetation alliances in Alberta. Alberta Environmental Protection, Edmonton, Alberta. 196 pp.

Tomback, D.F. 2001. Clark's nutcracker: agent of regeneration. pp. 89-104, in D.F. Tomback, S.F. Arno and R.E. Keane (eds.). Whitebark pine communities: ecology and restoration. Island Press. Washington, District of Columbia, USA.

Tomback, D.F., and P.L. Achuff. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology 40: 186-225.

Tomback, D.F., and K.A. Kramer. 1980. Limber pine seed harvest by Clark's nutcracker in the Sierra Nevada: timing and foraging behavior. Condor 82: 467-468.

Tomback, D.F., and Y.B. Linhart. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology 4: 185-219.

Tomback, D.F., A.W Schoettle, K.E. Chevalier, and C.A. Jones. 2005. Life on the edge for limber pine: seed dispersal within a peripheral population. Ecoscience 12: 519-529.

Tomback, D.F., P.L. Achuff, A.W. Schoettle, J.W. Schwandt, and R.J. Mastrogiuseppe. 2011. The magnificent high-elevation five-needle white pines: ecological roles and future outlook. pp. 2-28, in R.E. Keane, D.F. Tomback, M.P. Murray, and C.M. Smith (eds.), The future of high-elevation, five-needle white pines in western North America. USDA Forest Service, Proceedings RMRS-P-63.

Utzig, G. 2012. Ecosystem and tree species bioclimate envelope modeling for the West Kootenays. West Kootenay Climate Vulnerability and Resilience Project, Report 5: 44 pp. Website: www.kootenayresilience.org [accessed 15 April 2012].

Utzig, G., J. Boulanger, and R.F. Holt. 2012. Climate change and area burned: projections for the West Kootenays. West Kootenay Climate Vulnerability and Resilience Project, Report 4. Website: www.kootenayresilience.org [accessed 15 April 2012].

Utzig, G., D. Macdonald, D. Ailman & J. Pojar. 1977 Kicking Horse River Limber Pines ecological reserve proposal #295.

Van der Putten, W.H. 2012. Climate change, aboveground-belowground interactions and species' range shifts. Annual Review of Ecology and Systematics 43: 365-383.

Vander Wall, S.B., and R.P. Balda. 1977. Coadaptations of the Clark's nutcracker and the pinon pine for efficient seed harvest and dispersal. Ecological Monographs 47: 89-111.

Van Grunsven, R.H.A., W.H. Van der Putten, T.M. Bezemer, W.L.M. Tamis, F. Berendse, and E.M. Veenendaal. 2007. Reduced plant-soil feedback of plant species expanding their range as compared to natives. Journal of Ecology 95: 1050-1057.

Vanstone, J.R., C.A. Perez-Valdivia, and D. Sauchyn. 2010. Tree ring reconstruction of streamflow using early and latewood chronologies as proxies in the North Saskatchewan River Basin, Alberta, Canada. Poster presented at American Geophysical Union, 2010 Fall Meeting, San Francisco, California, 13-17 December.

Veblen, T.T. 1986. Age and size structure of subalpine forests in the Colorado Front Range. Bulletin of the Torrey Botanical Club 113: 225-240.

Walker, I.J., and R. Sydneysmith. 2008. British Columbia. pp. 329-386, in D.S. Lemmon, F.J. Warren, J. Lacroix, and E. Bush (eds.), From impacts to adaptation: Canada in a changing climate. Government of Canada, Ottawa, Ontario.

Warwell, M.V., G.E. Rehfeldt, and N.L. Crookston. 2007. Modelling contemporary climate profiles of whitebark pine (*Pinus albicaulis*) and predicting responses to global warming. pp. 139-142, in E. Goheen (ed.). Proceedings of a conference – Whitebark Pine: a Pacific Coast perspective. USDA Forest Service R6-NR-FHP-2007-01.

Watt, M.S., D.J. Kriticos, A. Alcaraz, A.V. Brown, and A. Leriche. 2009. The hosts and potential geographic range of *Dothistroma* needle blight. Forest Ecology and Management 257: 1505-1519.

Webster, K.L., and E.A. Johnson. 2000. The importance of regional dynamics in local populations of limber pine (*Pinus flexilis*). Ecoscience 7: 175-182.

Wells, P.V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecological Monographs 53: 341-382.

Wells, P.V., and J.D. Stewart. 1987. Cordilleran-boreal taiga and fauna on the central Great Plains of North America, 14,000-18,000 years ago. American Midland Naturalist 118: 94-106.

WLIS. 2011. Whitebark and Limber Pine Information System. USDA Forest Service, Northern and Intermountain Regions, Missoula, MT. Web site: http://www.fs.fed.us/r1-r4/spf/fhp/prog/program2.html [accessed: 8 Feb 2011].

Wood, C.S. and L. Unger. 1996. Mountain pine beetle - a history of outbreaks in pine forests in British Columbia, 1910 to 1995. Pacific Forestry Centre, Victoria, British Columbia.

Woods, A., K.D. Coates, and A. Hamman. 2005. Is an unprecedented *Dothistroma* needle blight epidemic related to climate change? BioScience 55: 761-769.

Wright, H.A., and A.W. Bailey. 1982. Fire ecology. John Wiley and Sons, New York, New York, USA. 501 pp.

Zambino, P.J. 2010. Biology and pathology of *Ribes* and their implications for management of white pine blister rust. Forest Pathology 40: 264-291.

Zambino, P.J., B.A. Richardson, and G.I. McDonald. 2007. First report of the white pine blister rust fungus, *Cronartium ribicola*, on *Pedicularis bracteosa*. Plant Disease 91: 467.

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COLLECTIONS EXAMINED

No collections were examined for this report.

Appendix 1. Percent of dead trees in sampling plots of Limber Pine in the Canadian Rockies, at three points in time. The raw data were provided by C. Smith.

Transect ID	1996[1]	2003 - 2004	2009	% annual mortality rate[2]
L1001		44.44	61.11	3.03
L1002		42.00	57.14	2.75
L1003		23.53	33.33	1.78
L1004		38.00	57.14	3.48
L1005		46.55	65.52	3.45
L1006		38.00	52.00	2.55
L1007		40.00	44.00	0.73
L1008		44.44	53.70	1.68
L1009		37.25	43.14	1.07
L1010		38.00	50.00	2.18
L1011		55.22	68.66	2.44
L1012		45.61	50.88	0.96
L1013		35.85	49.06	2.40
L1014		1.82	3.64	0.33
L1015		30.00	38.00	1.45
L1016		0.00	0.00	0.00
L1017		6.00	9.62	0.66
L1018		8.00	10.00	0.36
L1019		6.00	12.00	1.09
L1020		10.00	22.00	2.18
L1021		12.00	14.29	0.42
L1022		11.11	22.22	2.02
L1023		42.00	48.98	1.27
L1024		10.00	10.00	0.00
L1025		4.00	4.00	0.00
L1026		4.00	3.70	-0.05
L1027		8.00	7.41	-0.11
L1028		0.00	0.00	0.00

[1] Blank cells indicate that the sampling plot was established in 2003 or 2004.
[2] See **Fluctuations and Trends** section for details on how those values were computed.

Transect ID	1996[1]	2003 - 2004	2009	% annual mortality rate[2]
L1029		8.00	8.00	0.00
L1030		22.00	22.00	0.00
L1031		16.00	16.00	0.00
L1032		6.25	6.25	0.00
L1033		5.77	7.69	0.35
L1034		12.00	12.00	0.00
L2001	34.38	60.47	66.15	2.51
L2002	22.39	38.71	44.36	1.72
L2003	40.91	53.57	58.20	1.35
L2004	46.03	59.21	46.36	0.13
L2005	40.91	62.16	59.55	1.52
L2006	50.00	41.18	56.67	0.41
L2007	56.52	86.54	63.64	0.75
L2008	34.04	42.17	23.81	-0.68
L2009		33.87	40.00	1.11
L2010		30.91	46.27	2.79
L2011		25.00	41.86	3.07
L2012		22.00	28.00	1.09
L2013		58.57	60.00	0.26
L2014		60.29	59.42	-0.16
L2015		44.90	50.98	1.11
L2016		45.90	49.18	0.60
L2017		19.23	34.62	2.80
L2018		32.81	37.50	0.85
L2019		40.00	46.30	1.14
L2020		19.23	21.57	0.43
L2021		44.74	46.75	0.37
L2022	19.23	42.31	30.23	0.98
L2023	11.11	40.70	27.54	1.42
L2024		14.58	16.67	0.38
L2025	23.91	50.00	37.74	1.21
L2026	5.10	37.38	33.67	2.32
L2027		26.00	39.71	2.49

Transect ID	1996[1]	2003 - 2004	2009	% annual mortality rate[2]
L2028		51.02	48.15	-0.52
L2029		45.90	60.66	2.68
L2030		25.00	32.69	1.40
L2031		58.18	73.21	2.73
L2032		22.45	38.78	2.97
L2033		39.13	79.59	7.36
L2034		28.00	60.98	6.00
L2035		13.73	23.53	1.78
L2036		18.92	21.05	0.39
L2037		18.75	30.61	2.16
L2038		0.00	0.00	0.00
L2039		8.11	11.36	0.59
L2040		26.47	26.47	0.00
L2041		37.50	45.83	1.52
L2042		29.79	8.33	-3.90
L2043		15.63	15.15	-0.09
L2044		10.42	12.00	0.29
L2045		7.89	7.69	-0.04
L2046		12.70	14.29	0.29
L2047		0.00	0.00	0.00
L2048		2.33	0.00	-0.42
L2049		0.00	0.00	0.00
L2050		66.67	62.22	-0.81
L2051		29.41	4.00	-4.62
Mean	32.00	28.85	33.02	1.06
Standard deviation	15.87	19.40	21.76	1.61