Whitebark Pine Conservation for the Canadian Rocky Mountain National Parks

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Executive Summary:

Whitebark pine (*Pinus albicaulis*) is an essential part of subalpine ecosystems in the Canadian Mountain National Parks. This high elevation keystone species' seeds provide an important food source for a number of animals including squirrels, bears, and in particular, the bird species Clark's nutcracker (*Nucifraga columbiana*). Whitebark pine is the only North American stone pine – a subsection of the pines whose cones remain closed at maturity and seeds are wingless. Clark's nutcracker is thought to have co-evolved with the pine as its only effective seed disperser. Furthermore, whitebark pine plays an important role in watershed protection by aiding soil stability and facilitating a more rapid return to forested landscapes following disturbances on southern exposures where harsh conditions may otherwise limit seed germination.

Whitebark pine is threatened by a number of anthropogenic factors. These include an introduced blister rust species (*Cronartium ribicola*), fire suppression and associated seral replacement by more shade tolerant tree species, and by rapid global climate change. However, the most serious of these problems is the threat of widespread mortality due to blister rust infection. This is more pronounced in the southern regions of the Canadian Rockies, but has serious ramifications for all of the Mountain National Parks.

In 1998, the Lake Louise, Yoho and Kootenay National Parks Field Unit (LLYK) initiated a prescribed burn and monitoring program to aid in the restoration of whitebark ecosystems. In 1999, Waterton Lakes National Park joined in the developing program. This report introduces the background information on the conservation problem and outlines a number of options for developing a broader, more effective approach to the conservation of the ecosystem including:

1. Initiating a detailed inventory of the species throughout the federally administered land base

2. Continuing the prescribed burn restoration efforts

3. Seed collection

4. Studying the geographic distribution of adaptive traits

5. Forming partnerships with other interested agencies and organisations

6. Exploring existing data resources to generate hypotheses about relationships between the pine, its environment, and its stressors

7. Examining potential provincial and federal species at risk listing for whitebark pine

Most importantly, however, is the need for a holistic approach that encompasses all of these aspects into an interagency strategy for the conservation of whitebark pine ecosystems.

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1.0 Whitebark Pine Conservation: Outline and Background

1.1 Plan outline

The National Parks Act sets out the first priority in the management of National Parks as the maintenance or restoration of ecological integrity (Canadian Heritage 2000). Whitebark pine is an essential component of subalpine ecosystems in the Rocky Mountain National Parks, but this role is threatened. In 1998, the Lake Louise, Yoho and Kootenay Field Unit initiated a project to return fire to whitebark pine ecosystems in an effort to aid in restoring and maintaining these systems. Since then the project has been expanded to include Waterton Lakes National Park. The primary objective of this plan is to define the goals of a Parks Canada whitebark pine restoration project and set out clear and effective steps to obtain those goals.

1.2 Whitebark pine: a life history

Whitebark pine (*Pinus albicaulis*) (Figure 1) is found in high elevation forests in the mountainous regions of western North America (Arno and Hoff 1989). The species occurs in two distinct geographical distributions. The first extends through the Cascade Mountains in British Columbia, Washington, and Oregon, to the Sierra Nevada of central California (Figure 2). The second follows the major ranges of the Rockies from approximately 54°N in British Columbia, to 41°N in the Wind River Range in western Wyoming. This includes some of the higher interior ranges such as the Columbia Mountains in British Columbia. Towards the northern extent of its range in southern Alberta and British Columbia, whitebark pine is often found in smaller, more isolated populations on exposed ridges and rocky talus slopes up to approximately 2300 meters elevation (Ogilvie 1990). In contrast, stands further south in Montana and Idaho form more continuous forests extending over gentler, less extreme topography.
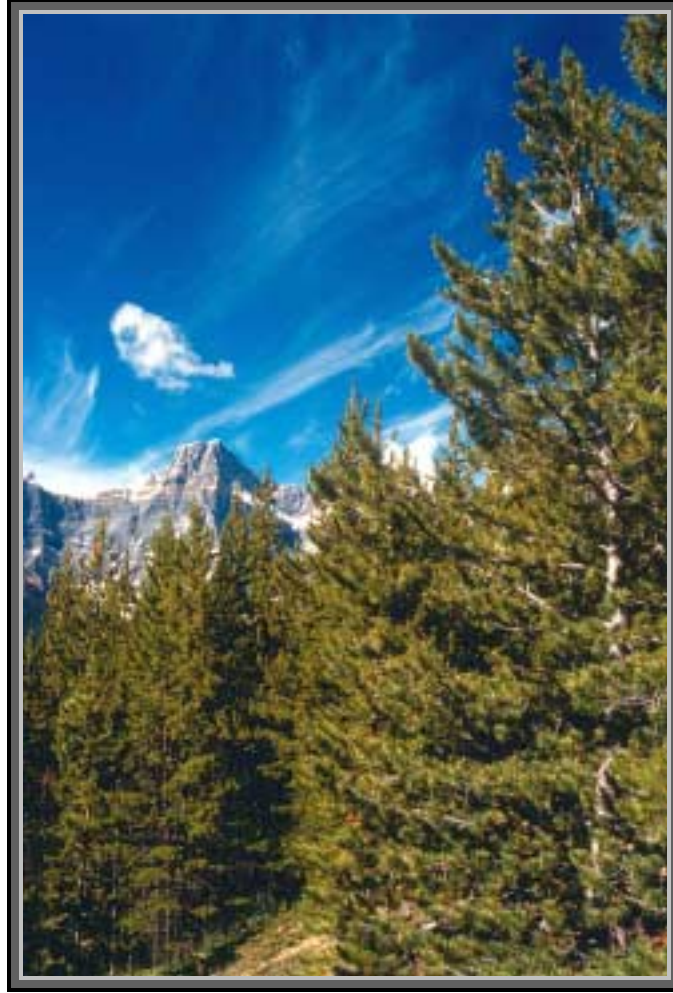
Figure 1. Young whitebark pine above Waterfowl Lake,
Banff National Park. Photo: B.C.Wilson.

Because of its high subalpine setting, it was not until 1863 that Engelmann described
whitebark pine (Engelmann 1863). Since then our understanding of the basic biology and
ecological role of whitebark pine has been limited, compared to the accumulated
knowledge on more economically important tree species. However, the importance of
whitebark pine is now starting to be appreciated for two main reasons. First, many
animals, from birds to bears, depend on whitebark pine not only for the shelter created by
its canopy but also on its energy rich seeds as a food source (Arno 1986). Second,
whitebark pine may aid in soil stability, prevent erosion (Arno and Hoff 1989), and aid in
facilitating a more rapid return to forested landscapes following disturbances (Callaway
1998).

Figure 2. Outline of the native range of whitebark pine (adapted from Arno and Hoff 1989).

1.3 Ecosystem interactions

Over its range, whitebark pine is an essential or "keystone" component of the subalpine ecosystem. Although there has been relatively little ecological research into the functional mechanisms of these high elevation ecosystems, whitebark pine has been linked both dir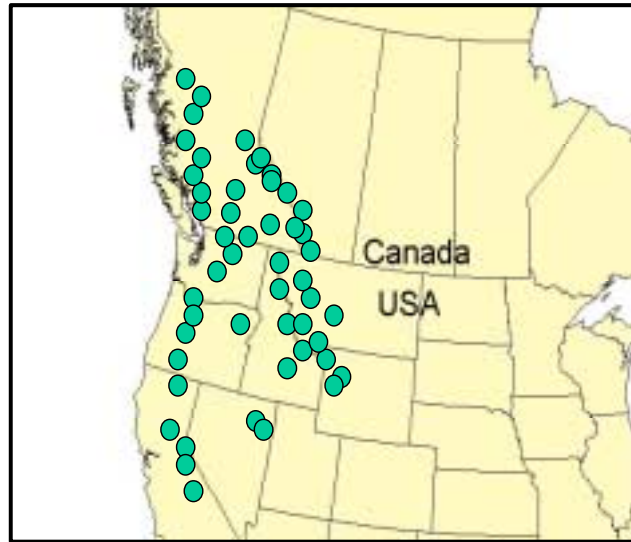ectly and indirectly with several important relationships. The most prominent and well researched example is the co-evolution with the Clark's nutcracker, *Nucifraga columbiana* (Figure 3) (Tomback et al. 1990). Clark's nutcrackers have a sublingual pouch that can hold up to 150 whitebark pine seeds, an adaptation that is unique among birds (Bock et al. 1973). With a full pouch, nutcrackers fly off to a suitable site where clusters of up to 15 seeds are cached 2 to 3 cm below the soil surface (Tomback 1982). Nutcrackers feed almost exclusively on whitebark pine seeds when they are available and store the seeds for use throughout the year (Tomback 1978). Caching sites are usually southern exposures where the lower snow depth facilitates seed retrieval during winter months (Hutchins and Lanner 1982). Nestlings hatch in the late winter and are fed almost exclusively from cached whitebark pine seeds (Lanner 1996). However, not all caches are remembered or fully exploited, giving the tree species an effective means of dispersal.

Figure 3. Juvenile Clark's nutcracker in a recent
prescribed burn. Photo: B.C. Wilson.

Similarly, whitebark pine has adaptations that accommodate seed dispersal by Clark's nutcrackers. The nutrient rich seeds of whitebark pine are wingless and remain in the cone after maturity. Cones are found on the tips of upswept branches, rather than close in to the core of the tree. This presentation allows the cones to be more easily seen by the passing birds (Lanner 1996). While the whitebark pine cones are still attached to the tree's branches, Clark's nutcrackers adeptly harvest the seeds by ripping open the cones with their long pointed beaks (Tomback 1978).

The cones of whitebark pine (Figure 4) are not serotinous, that is, fire is not required to open the cones to allow wind dissemination of the seeds. These indehiscent cones are a distinctive feature of the stone pine subsection of the genus *Pinus* - of which whitebark pine is the only North American member. All of the stone pines on other continents also show evidence of a mutualistic relationship with nutcracker species (Lanner 1996).

Figure 4. A female whitebark pine cone. Photo: G.J. Stuart-Smith.

Whitebark pine produces masts of seeds every 3 to 5 years (Morgan and Bunting 1992) with intervening years having very low, or no seed production. In the years with low seed production, nutcrackers have been known to erupt from their usual habitat and travel great distances in search of other food sources (Fisher and Myres 1979). One such event was documented in 1976 when nutcrackers appeared in the Cypress Hills of Southern Alberta, over 300 km from their usual habitat (Fisher 1979, Fisher and Myres 1979). Although Clark's nutcrackers depend heavily on whitebark pine seeds as a food source, the relationship between whitebark pine and this bird species is mutualistic (Tomback 1982). Without seed caching by nutcrackers, practically no whitebark pine regeneration would occur. The few seeds that remain in the cones eventually drop to the ground and, if rodents do not forage them on, they rot before they germinate (Hutchins and Lanner 1982). Lanner (1996) points to the heavy wingless seeds as evidence of the co-evolution of the bird-pine relationship because wind is no longer an effective method of seed dispersal.

The seeds of whitebark pine are not only important to Clark's nutcracker, but also to other animals such as red squirrels (*Tamiasciurus hudsonicus*) and bears (Arno and Hoff 1989). Red squirrels, in order to prolong seed storage time, hoard whole cones in underground middens (Mattson et al. 1992). Both black (*Ursus americanus*) and grizzly bears (*U. arctos*) have also been seen climbing into trees to remove cones, but more often, they will simply raid the already concentrated source in squirrel middens (Kendall 1983). Mattson

et al. (1992) found that in years with low cone yields, grizzly bears tend to move from the subalpine environment where whitebark pine is found to lower elevations where encounters with humans are more frequent. Therefore, whitebark pine habitat is also important to the survival of viable populations of bears, because bear-human encounters often result in bears being relocated or destroyed (Mattson et al. 1992). Although bears, squirrels, and other animals feed on its seeds, only Clark's nutcracker is significantly important to the regeneration process of whitebark pine (Hutchins and Lanner 1982, Tomback 1982).

1.3.1   The role of disturbance

Arno and Hoff (1989) indicate that whitebark pine is an early pioneer that provides structural modification to a site that allows for the establishment of other species in stands throughout the central Rocky Mountains. Successional development on whitebark pine sites is generally believed to follow a path starting from recently exposed glaciated terrain (primary succession), or more frequently at lower elevations, following a fire, pest attack, avalanche, or blowdown (secondary succession). As exposed areas created by fires are the most common of these large scale disturbance types, and are actively managed by various agencies, we will concentrate on describing general events that comprise this secondary succession pathway.

The openings created by fire are attractive to the nutcracker as these areas provide increased opportunities for seed caching (Tomback 1986, Tomback and Linhart 1990). Nutcrackers cache whitebark pine seeds around rocks and next to woody debris as a means of locating the cache for retrieval (Vander Wall and Balda 1977). Those seeds that remain un-retrieved may germinate and develop into seedlings, although germination may be delayed for up to several years (McCaughey 1993, Tomback et al. 2001). Meanwhile, seeds of other species that have either been blown in from the surrounding forest or have survived in the soil, or duff layer also begin to germinate. However, unlike whitebark pine, seedlings of other species such as Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*) and alpine larch (*Larix lyallii*) tend to prefer shade created by other plants and moisture that may not be found in the exposed mineral soil that is generally left after a fire (Beil 1966, Alexander and Shepperd 1990,

Alexander et al. 1990, Wilson 2001). Therefore, whitebark pine can dominate these sites for several decades or more, depending on the slope, aspect and rockiness of the site. In suitable timberline areas, the pine may also remain as the dominant climax tree species over the course of the fire-free period (Arno 1986).

After the regenerating whitebark pine on a burn site have reached sufficient height, they appear to create a microclimate that is more conducive to the germination and establishment of other tree species. This may include changes to the soil and air moisture and temperatures (Larcher 1983), and also protection from physical damage caused by winter snow and ice abrasion. For example, Callaway (1998) has shown that subalpine fir seedlings and saplings are more likely to be found adjacent to established whitebark pine than in open areas at high elevation sites.

However, understory vegetation development within young stands may also start to affect nutcracker caching. Recent work in the Canadian Rockies suggests that the bird species exhibits a high degree of selectivity in cache microsite characteristics. Wilson (2001) found that even on southern aspects in recently burned areas, younger seedlings were found in sites with distinctly less shrub cover compared to sites that contained older whitebark pine saplings. This suggests that some birds may actively seek out more open caching locations, even in relatively open sites.

Eventually, many stands that were initiated by whitebark pine become dominated by mature spruce and fir. In the absence of further disturbance, the pine may become replaced through this succession. However, with stand replacing fire return intervals estimated between 90 to 400 years for upper subalpine forests in the Canadian Rockies (Masters 1990, Johnson and Miyanishi 1991, Rogeau 1996), the model of fire, seed transport and caching, and subsequent whitebark pine regeneration appears to ensure that a dynamic equilibrium of whitebark pine stands is maintained at the landscape scale. Mixed fire regimes and low intensity fire, which may occur at shorter intervals, can also knock out competitors and promote whitebark pine, which is more fire resistant (Arno 1986).

There is also evidence of other successional pathways for whitebark pine within forests of southeast British Columbia. Campbell (1998) found that low numbers of the species were able to persist in regenerating subalpine forests dominated by lodgepole pine (*Pinus contorta*). These suppressed individuals showed evidence of release in maturing forest that became more open through natural thinning. Wilson (unpublished data) has also found whitebark seedlings and saplings growing under a closed canopy of older mixed subalpine forest containing mature Engelmann spruce, subalpine fir, lodgepole pine, and whitebark pine, in southeast B.C. In these stands there appears to be some release of smaller individuals in the larger tree fall gaps, although this requires more quantification.

Mountain pine beetle (*Dendroctonus ponderosae*) is also an important component in the successional cycle of whitebark pine, especially in the southern portion (USA) of its range (Perkins 2001). The probability of attack by pine beetle in lodgepole pine is directly related to phloem diameter, which is generally correlated with basal tree diameter (Cole and Amman 1980). Larger diameter trees in dense stands are more susceptible to beetle attack, a principle that is also true for beetle attack in whitebark pine (Perkins 2001). This appears to be less critical in the northern whitebark pine range (Ogilvie 1990, Stuart-Smith 1998, Campbell 1998), as the pine forms less continuous stands, reducing the probability of wide spread mountain pine beetle infestations, compared to the more continuous stands to the south.

1.4 The threats: blister rust

The keystone role of whitebark pine may be in jeopardy due to the introduction of white pine blister rust, *Cronartium ribicola* (Tomback et al. 1995). Although white pine blister rust is thought to have originated in Siberia, the rust species was introduced accidentally into North America, via Europe, at the turn of the 20th century (Peterson and Jewel 1968, Littlefield 1981, Millar and Kinloch 1991). A shipment of infected seedlings from Europe to a nursery near Vancouver, B.C. appears to be the point of introduction for the pathogen on the west coast (the disease was introduced separately on the eastern seaboard shortly afterwards). Regions of the coastal mountains dominated by western white pine (*P. monticola*) were quickly infected (Bedwell and Childs 1943).

Blister rust has since spread, often in long-range jumps between widely separated mountain ranges, throughout the distribution of the soft pines of western North America, including sugar pine (*P. lambertiana*), Foxtail pine (*P. balfouriana*), limber pine (*P. flexilis*), as well as western white pine and whitebark pine (Liebhold et al. 1995). Recently, blister rust reached interior states such as North and South Dakota and New Mexico (Draper and Walla 1993, Lundquist et al. 1992). The rust has reduced the prominent role of white pines in forest ecosystems throughout North America (Liebhold et al. 1995), and has become an epidemic on whitebark pine in parts of Idaho, western Montana and Wyoming and southern Alberta and British Columbia (Arno 1986, Keane and Arno 1993, Keane et al. 1994, Tomback et al. 1995, Stuart-Smith 1998). Stuart-Smith (1998) documented up to 76% blister rust infection in subalpine stands of the southern Canadian Rockies in Alberta and British Columbia near the US border. However, levels of infection within stands fell substantially, moving north along the Great Divide towards Jasper.

1.4.1 Blister rust life cycle

The extent of blister rust infection not only depends on the distribution of whitebark pine, but also on shrubs of the genus *Ribes*. The life cycle of white pine blister rust has five stages that alternate between two hosts, white pines and *Ribes* spp. (Zillar 1974). After the initial infection of pine needles, hyphae grow down the vascular bundle and enter the phloem in the branch or stem of the tree. Two to four years later cankers form and rupture the bark surface. Spermagonia, which produce haploid spermatia, form at the advancing edge of the canker. It is thought that insects, attracted to the nectar-like extrusions of the spermagonia, carry the spermatia to other cankers and facilitate cross-fertilization allowing for the production of dikaryotic cells through plasmogamy (Hunt 1985). Where spermatia grew the previous season, aecia develop that produce aeciospores, thick walled spores that are able to withstand desiccation. Aeciospores are carried by wind to the alternate host, *Ribes*, where another stage of the infection begins.

A minimum of 21 days after *Ribes* infection, uredinia develop on the under-surface of the leaves. Wind dispersed urediniospores develop from the uredinia. Urediniospores are able only to re-infect other *Ribes*. Thus, even if only a few plants are initially infected, the cycle of re-infection through urediniospores can rapidly spread blister rust throughout the *Ribes* in an area. During periods of hot dry weather or if infection intensity per leaf area is too high, *Ribes* leaves may be dropped thus decreasing the intensity of infection (Kinloch and Dulitz 1990). In the fall, a period of two weeks of cool weather (below 20° C) stimulates the development of telial columns from the aecia (Van Arsdel et al. 1956). The dikaryotic nuclei within the telial columns fuse and undergo meiosis to produce four haploid basidiospores. Due to their thin walls, basidiospores are very sensitive to environmental conditions (Van Arsdel 1965) and thus have been the focus of studies examining the climatic limitations to the spread of blister rust (Peterson and Jewel 1968). Basidiospores require 48 hours of saturated relative humidity (greater than 97%) and cool temperatures (less than $18^{o}C$) for release and germination. Bega (1960) found that the optimal temperature for germination was $16^{o}C$ and that exposure to sunlight for more than 5 hours or freezing significantly reduced basidiospore germination. Basidiospores, carried by wind, re-infect pine needles and thus complete the rust life cycle.

As the rust spreads through the phloem, the nutrient supply can be cut off to branches and portions of the upper stem. Flagging, brown or red-brown dead needles that droop to one side of the branch, are visible symptoms of branch death due to blister rust infection. Although a canker may become large enough to girdle and kill a tree, infection may not be the direct cause of death. The concentrations of nutrients in cankers attract rodents that chew the canker, thus removing vascular tissue that may girdle the tree and result in death. These losses of vascular tissue as well as invasion by secondary organisms are the main cause of mortality (Figure 5).

Figure 5: Girdling of a sapling at a blister rust canker.
Photo: B.C. Wilson

1.4.2   Blister rust resistance

Whitebark pine is more susceptible to blister rust than any other white pine (Bedwell and Childs 1943, Hoff and Hagle 1990, Hoff and McDonald 1993). For example, Tomback et al. (1995) found that whitebark pine seedlings had on average nearly double the number of cankers compared to that of western white pine. Despite this susceptibility, several sites in Montana and Idaho have been found where potentially rust resistant individuals exist. These sites are areas where blister rust mortality has been extremely high (greater than 90%) and so the one or two individuals that have survived this epidemic are potential candidates for resistance (Hoff and Hagle 1990). Although the presence of blister rust in the Canadian Rockies and mountainous regions of British Columbia had been noted in the past (Bedwell and Childs 1943, Forest Insect and Disease Survey 1959, 1968, 1970), it has only been recently quantified (Stuart-Smith 1998, Campbell and Antos 2000, Zeglen 2002). No effort has been made to seek out rust resistant individuals, but given the possibility of rust resistant individuals in the US and the high blister rust mortality in some locations in Canada, the likelihood would seem great that resistant individuals also exist here.

Resistance can be expressed in two ways: through mutations that give rise to dominant traits that convey resistance, or through sexual recombination that allows for the

expression of resistant non-dominant alleles that would otherwise be hidden within the genome. Since we cannot change the rate of mutation, increasing sexual recombination and the number of offspring is the only method available that will increase the probability of resistance. Presently, the reduction of fire in the Canadian Rockies (Tande 1979, White 1985, Hallett and Walker 2000) may be leading to a reduction in whitebark pine seed caching, and thus a reduction in the regeneration of the pine. By increasing the area suitable for nutcracker caching, the level of whitebark pine regeneration should also increase. This increase in regeneration may allow for the naturally occurring sexual recombination to be expressed (Stuart-Smith 1998). Consequently, dominant or recessive resistance alleles that are naturally present should be expressed and natural rust resistant populations may eventually develop.

In the life cycle of blister rust there is a much shorter time period between generations compared to the host species whitebark pine. Blister rust can complete its life cycle in as little as 3 years given the right conditions (Ziller 1974), whereas it can take 50-80 years before a whitebark pine produces seeds (Arno and Hoff 1989, Wilson and Stuart-Smith unpublished data). What consequences would this difference have on the expression of rust resistant alleles and the development of rust resistant populations? Because blister rust has such a comparatively short life cycle, it could be expected that the rust develop virulent genotypes that would be able to circumvent rust resistance mechanisms arising in whitebark pine. Although this may be a possibility, at present there is little regeneration in whitebark pine. Without effective regeneration to produce new combinations of genes there is a much lower chance that the species will be able to survive and develop rust resistant populations.

Even though the short life cycle of the rust would suggest that it should have the capacity to quickly develop virulent races under selection pressure, the low amount of genetic diversity that has been found in blister rust populations in North America, especially in western populations, should slow this process (Kinloch et al. 1998, Hamlin 1999). This lack of overall genomic diversity is encouraging for the effectiveness of resistance breeding programs. For example, Kinloch et al. (1998) found that the resistance

mechanisms in two separate *Ribes* cultivars were not overcome by blister rust, despite extensive field trials across North America. This suggests that it may be productive to select for resistant individuals through breeding programs or increasing the level of regeneration in whitebark pine and thereby increasing the chances of finding naturally occurring rust resistance. However, it should be remembered that studies of the genetic diversity of blister rust cannot be extrapolated to the variance in virulence (Kinloch et al. 1998).

The low level of genetic diversity of the rust also has important implications for the development of rust resistant breeding programs (Dekker-Roberstson and Bruederle 2001). Because of this low diversity, resistance genes isolated in the laboratory could be inserted into local pine genotypes with a high probability of success even if the pine population that served as the source for the gene was from a great distance away. Programs have already begun to look for resistant individuals in areas of Montana and Idaho (Burr et al. 2001). If the mechanism of resistance found to be responsible was determined to be a single gene, this gene could be incorporated into the genome of local populations in, for example, the Northern Rockies. This transfer could be made with only a low likelihood that the rust populations there may already have a mechanism of virulence that would circumvent the resistance supplied by the inserted gene.

1.5 Fire suppression

Recent studies in north western Montana have pointed to fire suppression as the cause of successional replacement of whitebark pine by the more shade tolerant conifers such as Engelmann spruce and subalpine fir (Arno 1986, Keane and Arno 1993, Keane et al. 1994). By measuring the basal area covered by whitebark pine, Keane and Arno (1993) have shown that the numbers of whitebark pine have decreased while those of subalpine fir have increased over a 20-year period.

As in Montana, there is concern that the past fire suppression practices of the Parks Canada may have altered the natural successional processes and may be contributing to a decline in whitebark pine populations in the Canadian Rockies. Parks Canada has had a

policy of fire suppression in the subalpine over the last century. However, this policy may have only been truly effective since around the 1960's, especially in the remote areas where whitebark pine is found. However, regardless of cause, there appears to have been a lot less fire in the areas of the southern Canadian Rockies over the last 100 years than there was over the last several hundred years (Hallett and Walker 2000). The mandate of Parks Canada is to maintain ecological integrity in the National Parks (Canadian Heritage 2000). In order to achieve this goal, there must be an understanding of the relationship between fire and its effect on the regeneration of whitebark pine.

1.6   Other factors influencing the health of whitebark pine ecosystems

Parks have increasingly become islands within a sea of growing industrial activity (Banff-Bow Valley Study 1996). Logging has occurred right up to the boundary of many national parks including Yoho, Banff, Kootenay and Waterton. Although whitebark pine is of little economic importance, co-dominant species, such as subalpine fir and particularly Engelmann spruce, are commercially valuable. As the remaining old-growth forest in British Columbia and Alberta dwindles and the efficiency of logging operations increases, the older mixed whitebark pine stands are becoming attractive to operators looking for untapped resources. In a number of forest regions, mature whitebark have been removed as part of the cut. This reduces the available seed sources for restocking disturbed areas within the local forest area and within the adjacent parks.

Furthermore, in logged areas that have the potential to sustain whitebark pine, the practice of the preferential planting of economic species, such as spruce and lodgepole pine, reduces the chance of natural whitebark pine regeneration occurring in these locations. Logging operations also increase the access to wilderness areas with the development of roads. Consequently, hunters and recreational users are more easily able to access these areas (Forman and Alexander 1998). The value of these areas for sensitive wildlife, such as grizzly bears, thereby decreases and subsequently the pressure on habitat within protected areas such as national parks increases.

Another threat to whitebark pine ecosystems comes from the potential changes to subalpine environmental conditions through rapid global climate change. Natural disturbances such as fire and avalanches are important agents of renewal in the subalpine ecosystems and successional relationships may greatly depend on the frequency and severity of these disturbance types (Agee and Smith 1984, Arno and Hammerly 1984). Human induced alterations to the global climate may drastically change these mechanisms by altering the regional temperature, moisture, and precipitation regimes (Beniston 1994, Hogg and Schwarz 1997). In turn, this may change the successional development of subalpine ecosystems (Grabherr et al. 1994, Kannitz and Kesting 1997).

1.7 *A whitebark pine conservation plan*

Recently, Parks Canada has initiated several research projects to assess the effects of reintroducing fire through prescription into the Canadian Rocky Mountain ecosystems (Wilson et al. 1998). Part of this program was in response to the findings of Stuart-Smith (1998) regarding the severe conservation problem of blister rust infected whitebark pine in the southern Canadian Rockies. Stuart-Smith (1998) made several recommendations that would help ensure the future survival of whitebark pine in this region. Among these was to assess the potential of prescribed fire as a means of enhancing whitebark pine conservation, primarily through increasing area available for whitebark pine seed caching by Clark's nutcrackers.

With this impetus, and the recognition that there was a need to have a focused approach to enable partnerships with other concerned agencies, a program was initiated in the Lake Louise, Yoho and Kootenay National Parks Field Unit to monitor the effects of prescribed fire on whitebark pine restoration using the vegetation monitoring methods developed in Wilson (1998). In 1999 Waterton Lake National Park also joined the effort and a research site was set up there with the goal of a prescribed burn. The results of this program to date are discussed in Wilson and Stuart-Smith (2000) and will not be examined here. The need to provide future direction for this project resulted in the development of this conservation plan.

2.0 Conservation plan

2.1 Goals

To implement a conservation strategy effectively for whitebark pine, a number of different approaches need to be carried out simultaneously. The program initiated by the Lake Louise, Yoho and Kootenay National Parks Field Unit (LLYK) in the mountain parks is a good start but there needs to be cooperation within Parks Canada, and with other agencies interested in whitebark pine ecosystem conservation. In this section, we explore the possibilities for integrating the present monitoring program in a broader research framework. There are a number of steps that need to be accomplished in the short term and other measures that will require a much longer time period to complete (Table 1).

Table 1. Time scale, potential partnerships and estimated initial costs associated with whitebark pine conservation goals.

Goal	*Time scale*	*Potential partners*	*Approximate cost*
Stand inventory	Short term	Selkirk College	$40 000 over two years
Seed collection	Short term	BCMoF, CFGC	$5 000
Adaptive traits study	Short/long term	Universities	$20,000/year for 3 years
Prescribed burns – Operations - Research and monitoring	Short term and long term	Selkirk College	$50 000 $20 000
Exploratory analyses of existing databases	Short term	Global Forest, SGRC	$10 000
Species at risk scoping.	Short term	MoF, WLAP, ABSRD	$10 000

SGRC = Selkirk Geospatial Research Centre.
BCMoF = British Columbia Ministry of Forests.
CFGC = Centre for Forest Gene Conservation.
BCWLAP = B C Ministry of Water Land and Air Protection
ABSRD = Alberta Sustainable Resource Development

2.1.1   Stand inventory

Presently, our knowledge of where whitebark pine occurs within the Canadian Mountain National Parks is limited to local knowledge and the Ecological Land Classification (ELC) database and associated maps (e.g., Holland and Coen 1982). The maps outline ecosites that may contain whitebark pine with the greatest possible resolution at the 1:50000 scale. The ELC was based on inferences from landform characteristics in relation to the more general plant community structure for similar physiographic areas, rather than inferences from the distribution of individual species. Therefore, to get an accurate assessment of the distribution and size of the whitebark pine population we need base maps that indicate where the species is located on the landscape at the highest possible resolution. It is possible that these maps may be developed using Geographical Information System (GIS) methods, such as supervised classification of existing remotely sensed data (such as performed by Keane at al 1994).

Following this mapping exercise, an appropriately designed reconnaissance level survey of the identified stands should be carried out to determine the extent of blister rust infection, and some basic stand structural characteristics. This is an important step; without a thorough inventory to obtain baseline data, we have no means of measuring the extent of the blister rust problem, or the success of any implemented strategy. For example, what do the demographics of uninfected stands, or stands with low blister rust mortality look like? Can we use these data to build recruitment targets, or predictions for the successional pathways of the badly infected prescribed burn units?

2.1.2   Seed Collection

Seed collection for gene conservation is also an important step that should not be delayed and could best be included as part of the inventory process. Programs to locate genetically resistant individuals have already commenced in British Columbia (Zeglen 2000) and outplanting programs of resistant progeny have already started in the most heavily hit areas of Montana and Idaho (Kendall and Keane 2001, McDonald and Hoff 2001). The stand inventory combined with a seed collection program within the National

Parks will be an important first step to enable participation in these types of programs and ultimately achieve the longer term conservation goals of germination and outplanting resistant stock. Although outplanting of genetically resistant stock may be a last resort, we should not exclude ourselves from the possibility that these types of measures will be required to maintain whitebark pine in the national parks.

2.1.3   *Distribution of Adaptive Traits*

Like many conifer species, the bulk of the genetic variation in whitebark pine is found within populations (Yandell 1992, Jorgensen and Hamrick 1997, Bruederle et al 1998, Stuart-Smith 1998, Krakowski 2001, Richardson et al. 2002). However, a small, but significant portion of variation is contained among populations with estimates ranging from 2.5 to 8.8 percent (Yandel 1992, Bruederle et al. 1998). However, to date, there has been little work done on how this "among" or "geographic" distribution of genetic variation is related to adaptive traits.

Recent work with mitochondrial DNA has suggested that the pattern of genetic variation may be in part due to the changes in glaciations brought about by climatic change (Richardson et al. 2002). The advance and retreat of glaciers in the western cordillera has dictated the relative location of whitebark pine populations, while Clark's nutcrackers have allowed for this movement through their dispersal of the pine's seeds (McCaughey and Schmidt 2001). Therefore, conservation programs must collect and use seed for restoration purposes with this genetic differentiation in mind (Dekker-Robertson and Bruderle 2001).

There is presently a lack of information available on how the patterns of genetic variation relate to phenotypic variation in whitebark pine. Some preliminary studies have been carried out in the United States (Howard 1999), but none have been conducted in Canada. Although whitebark pine does not play as dominant a role in the portion of its range found in Canada, the species still covers a large geographic area (Ogilvie 1990, Zeglen 2002). Adaptive variation may suffer if genetic stock is moved across this range, or

possibly further distances into the United States (Krakowski 2001). In order to determine how important these movements are, common garden type experiments need to be carried out. Parks Canada does not have the expertise or the facilities to carry out such a program. However, areas protected under the jurisdiction of Parks Canada cover a large area of the range of whitebark pine, and genetic stock from these areas should be an integral part of an adaptive traits study. Parks Canada should support such a project in conjunction with other governmental and private organizations that have the knowledge and experience necessary to carry out such a study.

2.1.4   Prescribed Burns

A prescribed burn program and associated monitoring program must be an integral part of Parks Canada's whitebark pine ecosystem conservation strategy. Other agencies in Canada and the United States have carried out prescribed burns for whitebark pine but few other agencies are able to execute a prescribed burn program that has a prime objective of restoring ecological integrity without the bias of economic timber production. This gives Parks Canada a mandate to explore the effects of fire and forest regeneration in the absence of the confounding effects of un-natural disturbance types. Further, it is through the quantitative monitoring of fire effects that the goals and objectives of a program may be assessed.

2.1.4.1   Operations

This component of the conservation plan is probably the most important and most expensive. Furthermore, managers are still wary of the risks associated with returning fire to the landscape and do not always understand that the risk of catastrophic fire may actually increase in the absence of smaller, controlled burns. More time and effort may be required before managers are fully on side with prescribed burning operations. Unfortunately, lack of managerial support can sometimes lead to delays of years when it comes to burning areas that have already had the whitebark pine pre-burn field assessments carried out. Presently, these is only one site that has actually been burned for whitebark pine in Canada, that is the Helen ridge site in Banff National Park (Figure 6).

This site was burned in 1998 and under the original design, is scheduled for a re-measurement in 2003. Because there are limited funds available for whitebark pine research, a balance must be achieved between the need to monitor previous burns such as the Helen Ridge site and the need for additional sites. Money has already been spent on the layout of three additional sites in the mountain parks, but these have yet to be burned. Continued agency support is needed so that these sites can be burned before the time and effort put into the layout and initial assessment is lost.

Figure 6: Field staff carrying out a prescribed burn (Helen Ridge) in the upper Bow Valley, Banff National Park. Photo: B.C. Wilson

2.1.4.2   Research and monitoring

To date, the permanent monitoring sites that have been set up to look at fire effects on the whitebark pine ecosystem provide only an initial sample of the apparent gradient of infection that occurs over the latitudinal distribution of Parks Canada's lands (Stuart-Smith 1998). To maximize the usefulness of these sites, replicate installations should be set up in the same regions with similar stand and environmental conditions to help determine whether the successional patterns observed are of a general nature. Following this, other options could be examined. The inventory procedure and ELC modelling will

likely generate a number of important questions about the relationships between stand conditions (age, structure, species composition), blister rust infection, and environmental factors. The database developed through the prescribed burn monitoring program will eventually provide the necessary confirmatory data with which to test many of these predictions, and through this process, provide new direction for the program.

2.1.5   Collaboration and partnerships

Currently there are a number of different government agencies, non-government organisations, and private individuals who are either currently working on, or interested in the restoration of whitebark pine ecosystems. Efforts should be made to form partnerships with these groups as a means to maximize the research output, and ultimately, to find more rapid solutions to the conservation problems facing whitebark pine ecosystems. For example, there are individuals in the British Columbia Ministry of Forests who are currently working on selective breeding programs for blister rust resistance in both western white and whitebark pine. Parks Canada presently has no infrastructure or expertise to effectively address this area of research. So, rather than embarking on a new research initiative, a better strategy would be to offer access to information, material (i.e., collected seeds and/or tissue from the Parks lands), and some kind of funding for work that would be of mutual benefit. Similarly, our American neighbours to the south already have years of research experience in genetic and ecological studies looking at these problems. Their advice and co-operation should be actively sought to further Parks Canada's contribution to the restoration effort.

Partnerships may also enable the exploration of important questions that need to be answered regarding the types of disturbance that are necessary to induce a caching response in the Clark's nutcracker. For example, is harvesting an option for creating acceptable caching sites (e.g., McCaughey 1993)? In certain situations this kind of manipulation may be possible within the parks boundaries. However, there are already areas available to complete chronosequence harvest studies in adjacent provincial lands (see below). Also, further harvesting treatment manipulations to examine the response of the Clark's nutcracker to a range of forest structural conditions could be completed

inexpensively and with less controversy in these existing forest management areas. This information may be useful in a Parks context for reintroducing disturbance in areas where different values (such as public safety) necessitate some other form of disturbance on the landscape to that of fire.

Some partnerships are developing. Global Forest, a non-government foundation for the advancement of forest science research, has provided seed funding for development of a subalpine research site in the West Kootenays, British Columbia. Currently, a number of issues that are of interest in context of National Parks conservation are being explored. These include whitebark population dynamics and root physiology, Clark's nutcracker biology, and a long term fire history. Parks Canada and Global Forest are also hoping to work on some joint fund raising activities for whitebark pine ecosystem conservation.

2.1.6   *Exploratory analysis of existing databases*

Currently there are several existing data sources that have some information on whitebark pine ecosystems other than the database associated with the recent work in LLYK. These include provincial forest cover maps, the Biogeophysical Ecological Classification (BEC) for British Columbia, and the previously mentioned ELC database. The most comprehensive of these is the ELC, as the provincial databases have poor coverage of non-commercial forest types. The ELC has also been recently updated into a relational database format (Wilson and Stuart-Smith 1999), making it more useful for extracting appropriate datasets for specific analytical purposes.

There are a number of questions about whitebark pine, *Ribes* spp. and the estimated level of blister rust infection that may be useful to explore in context of the relative distribution of these alternate hosts in the landscape. With further development of the ELC database, it may be possible to develop hypotheses about the occurrence of different size cohorts, or the shape of cohort size distribution given the associated environmental characteristics, such as stand age and cover or the various forest structural layers. Multivariate models may be used to develop predictions about the successional relationships with other vegetation (e.g., Campbell 1998).

2.1.7 Species at risk listing

The Canadian Government is about to pass the federal Species at Risk Act (SARA). The legislation will provide opportunities to pursue listing whitebark pine as endangered or threatened. Federal listing would enhance public awareness of the need for whitebark pine conservation and provide additional funding opportunities. An important unknown is whether federal listing would also impose constraints on our ability to manipulate whitebark pine ecosystems. A scoping exercise needs to be completed to determine whether the appropriate level of population description exists for whitebark pine to be considered in the listing process. Provincial listing of whitebark pine in both Alberta and British Columbia would also likely extend public awareness and increase opportunities for conservation of the species. Efforts need to be made to coordinate with the relevant provincial agencies.

2.2 The subalpine ecosystem: a holistic approach

Clearly, a conservation strategy for whitebark pine must extend to much more than just the tree itself. Actions (or lack thereof) we take to aid in the recovery and maintenance of this species' population will also directly affect Clark's nutcrackers, grizzly bears, red squirrels, and arguably the entire subalpine ecosystem over the natural range of the stone pine. To achieve anything like success in this endeavour, Parks Canada will have to commit to long term support of multidisciplinary research in the subalpine ecosystem. It will only be through a well thought out, holistic approach that the maintenance of true ecological integrity may be realised in these sensitive high elevation systems.

3.0 Acknowledgements

4.0 Literature cited

Agee, J. K. and Smith, L. 1984. Subalpine tree reestablishment after fire in the Olympic Mountains, Washington. Ecology. **65:** 810-819.

Alexander, R. R. and Shepperd, W. D. 1990. *Picea engelmannii* Parry ex Engelm. Pages 187-202 in: Burns R. M. and B. H. Honkala, Technical co-ordinators. Silvics of North America. **Agricultural Handbook 654**. US Department of Agriculture, Forest Service. Washington, DC, USA.

Alexander, R. R., Shearer, R. C., and Shepperd, W. D. 1990. *Abies lasiocarpa* (Hook) Nutt. Pages 60-70 in: Burns R. M. and B. H. Honkala, Technical co-ordinators. Silvics of North America. **Agricultural Handbook 654**. US Department of Agriculture, Forest Service. Washington, DC, USA.

Arno, S. F. 1986. Whitebark pine cone crops - a diminishing source of wildlife food? Western Journal of Applied Forestry. **1:** 92-94.

Arno, S. F. and Hammerly, R. P. 1984. Timberline: Mountain and Arctic Forest Frontiers. The Mountaineers. Seattle, USA.

Arno, S. F. and Hoff, R. J. 1989. Silvics of Whitebark pine (*Pinus albicaulis*). Intermountain Research Station. Ogden, UT, USA.

Banff-Bow Valley Study 1996. Banff-Bow Valley: At the crossroads. Summary report of the Banff-Bow Valley Task Force (Robert Page, Suzanne Bayley, J. Douglas Cook, Jeffrey E. Green, and J.R. Brent Ritchie). Prepared for the Honourable Sheila Copps, Minister of Canadian Heritage, Ottawa, ON, Canada.

Bedwell, J. L. and Childs, T. W. 1943. Susceptibility of Whitebark pine to blister rust in the Pacific Northwest. Journal of Forestry. **41:** 904-912.

Bega, R. V. 1960. The effect of environment on germination of sporidia in *Cronartium ribicola*. Phytopathology. **50:** 61-69.

Beil, C. E. 1966. An ecological study of the primary producer level of the subalpine spruce - fir ecosystem of Banff and Jasper National Parks, Alberta. M Sc thesis, University of Alberta, Edmonton, AB, Canada.

Bock, W. J., Balda, R. P., and Vander Wall, S. B. 1973. Morphology of the sublingual pouch and tongue musculature in Clark's Nutcracker. Auk. **90:** 491-519.

Bruederle, L. P., Tomback, D. F., Kelly, K. K., and Hardwick, R. C. 1998. Population genetic structure in a bird-dispersed pine, *Pinus albicaulis* (Pinaceae). Canadian Journal of Botany. **76**: 83-90.

Burr, K.E., Eramian, A. and Eggleston, K. 2001. Growing whitebark pine seedlings for restoration. Pages 325-345 in: Tomback, D. F., Arno, S. F., and Keane, R. E., editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C. USA.

Callaway, R. M. 1998. Competition and facilitation on elevation gradients in subalpine forest of the northern Rocky Mountains, USA. Oikos. **82:** 561-573.

Campbell, E. M. 1998. Whitebark pine forests in British Columbia: composition, dynamics and the effects of blister rust. MSc. Thesis. University of Victoria. Victoria, BC, Canada.

Campbell, E. M. and an l J. A. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Canadian Journal of Forest Research. **30:** 1051-1059.

Canadian Heritage 2000. Canada National Parks Act. Canada Gazette, Part III, Chapter 32. Queen's Printer for Canada. Ottawa, ON, Canada.

Cole, W. E. and Amman, G. D. 1980. Mountain pine beetle dynamics in lodgepole pine forests. Part: course of infestation. **GTR-INT-89**. USDA Forest Service. Ogden, UT, USA.

Dekker-Robertson, D. and Bruederle, L. P. 2001. Management implications of genetic structure. Pages 310-324 in: Whitebark pine communities: ecology and restoration. Tomback, D.F., Arno, S.F., and Keane, R.E., editors. Island Press, Washington, D.C. USA.

Draper, M. A. and Walla, J. A. 1993. First report of *Cronartium ribicola* in North Dakota. Plant Disease. **9:** 952.

Engelmann, G. 1863. *Pinus albicaulis* Engelm. Transactions of the Academy of St. Louis. **2:** 209.

Fisher, R. M. 1979. Eruption of Clark's Nutcracker in Cypress Hills. Blue Jay. **37:** 47.

Fisher, R. M. and Myres, M. T. 1979 . A review of factors influencing the extralimital occurrences of Clark's Nut Cracker in Canada. Canadian Field Naturalist. **94:** 43-51.

Forest Insect and Disease Survey 1959. Annual report. Queen's Printer, Ottawa, ON, Canada.

Forest Insect and Disease Survey 1968. Annual report. Queen's Printer, Ottawa, ON, Canada.

Forest Insect and Disease Survey 1970. Annual report. Queen's Printer, Ottawa, ON, Canada.

Forman, R. T. T. and Alexander, L. E. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics. **29:** 207-231.

Grabherr, G., Gottfried, M., and Pauli, H. 1994. Climate effects on mountain plants. Nature. **369:** 448.

Hallett, D. and Walker, R. C. 2000. Paleoecology and its application to fire and vegetation management in the Kootenay National Park, British Columbia. Journal of Paleolimnology. **24:** 401-414.

Hoff, R. J. and Hagle, S. K. 1990. Disease of whitebark pine with special emphasis on white pine blister rust. In: Schmidt W. C. and K. J. McDonald, compilers. Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. **GTR-INT-270:** U.S. Department of Agriculture, Forest Service, Intermountain Research Station. Ogden, UT, USA.

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

Hogg, E. H. and Shwarz, A. G. 1997. Regeneration of planted conifers across climatic moisture gradients on the Canadian prairies: implications for distribution and climate change. Journal of Biogeography. **24:** 527-534.

Holland, W. D. and Coen, G. M. 1993. Ecological (biophysical) land classification of Banff and Jasper National Parks. Alberta Institute of Pedology. Edmonton, AB, Canada.

Howard, J. 1999. Transplanted whitebark pine regeneration: The response of different populations to variation in climate in field experiments. M.Sc. Thesis, University of Montana, Missoula, MT, USA.

Hunt, R.S. 1985. Experimental evidence of Heterothallism in *Cronartium ribicola*. Canadian Journal of Botany **63**: 1086-1088.

Hutchins, H. E. and Lanner, R. M. 1982. The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. Oecologia. **55:** 192-201.

Johnson, E. A. and Miyanishi, K. 1991. Fire and population dynamics of lodgepole pine and Engelmann spruce forests in the southern Canadian Rockies. Pages 77-91 in: Nakagoshi N. and F. B. Golley, editors. Coniferous forest ecology from an international perspective. Academic Publishing. The Netherlands.

Jorgensen, S. M. and Hamrick, J. L. 1997. Biogeography and population genetics of whitebark pine, *Pinus albicaulis*. Canadian Journal of Forest Research. **27**: 1574-1585.

Keane, R. E. and Arno, S. F. 1993. Rapid decline of whitebark pine in western Montana: evidence from 20-year remeasurements. Western Journal of Applied Forestry. **8:** 44-47.

Keane, R. E., Morgan, P., and Menakis, J. P. 1994. Landscape assessment of the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness complex, Montana, U.S.A. Northwest Science. **68:** 213-229.

Kendall, K.C. and Keane, R.E. 2001. Whitebark pine decline: infection, mortality, and population trends. Pages 221-242 in: Whitebark pine communities: ecology and restoration. Tomback, D.F., Arno, S.F., and Keane, R.E., editors. Island Press, Washington, D.C. USA.

Kinloch, B. B. J. and Dulitz, D. 1990. White pine blister rust at Mountain Home Demonstration State Forest: a case study of the epidemic and prospects of genetic control. **PSW-204**. USDA Forest Service. Pacific SW Research Station, Berkeley, CA, USA.

Kinloch, B. B. Jr., Westfall, R. D., White, E. E., Gitzendanner, M. A., Dupper, G. E., Foord, B. M., and Hodgskiss, P. D. 1998. Genetics of Cronartium ribicola. IV. Population structure in western North America. Canadian Journal of Botany. **76:** 91-98.

Krakowski, J. 2001. Conservation genetics of whitebark pine (*Pinus albicaulis* Engelm.) in British Columbia. MSc. thesis. University of British Columbia, Vancouver, BC, Canada.

Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. Pages: 14-48 in: Dancik B. P. and O. Higginbotham, Compilers. Proceedings of the 6th North American Forest Biology Workshop. University of Alberta, AB, Canada.

Lanner, R. M. 1996. Made for each other. A symbiosis of birds and pines. Oxford University Press. New York, NY, USA.

Larcher, W. 1983. Physiological plant ecology. Springer-Verlag. Berlin.

Liebhold, A. M., MacDonald, W. L., Bergdahl, D., and Mastro, V. C. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. Forest Science Monographs. **30:** 1-49.

Littlefield, L. J. 1981. Biology of plant rusts. Iowa State University Press. Ames, IA, USA.

Lundquist, J. E., Geils, B. W., and Johnson, D. W. 1992. White pine blister rust on limber pine in South Dakota. Plant Disease. **76:** 538.

Macdonald, G. I. and Hoff, R. J. 2001. Blister rust: an introduced plague. Pages 196-220 in: Whitebark pine communities: ecology and restoration. Tomback, D.F., Arno, S.F., and Keane, R.E., editors. Island Press, Washington, D.C. USA.

Masters, A. M. 1990. Changes in forest fire frequency in Kootenay National Park, Canadian Rockies. Canadian Journal of Botany. **68:** 1763-1767.

Mattson, D. J., Blanchard, B. M., and Knight, R. R. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seeds crops. Journal of Wildlife Management. **56:** 432-442.

McCaughey, W. W. 1993. Delayed germination and seedling emergence of *Pinus albicaulis* in a high elevation clearcut in Montana, U.S.A. Pages 67-72 in: Edwards, D.G.W., compiler. Dormancy and barriers to germination. Proceedings of an International Symposium of IUFRO Project group P204-00. 23-26 April 1991. Forestry Canada. Victoria, BC, Canada.

McCaughey, W. W. and Schmidt, W. C. 2001. Taxonomy, distrubution, and history. Pages 29-40 in: Whitebark pine communities: ecology and restoration. Tomback, D.F., Arno, S.F., and Keane, R.E., editors. Island Press, Washington, D.C. USA.

Millar, C. I. and Kinloch, B. B., Jr. 1991. Taxonomy, phylogeny and coevolution of pines and their stem rusts. Pages 1-38 in: Hiratsuka, Y., Samoil, J., Blenis, P., Crane, P., and Laishley, B., editors. Proceedings of the IUFRO Rusts of Pines Conference, September 18-22, 1989 in Banff, Alberta, Canada, Canadian Forestry Service, Canada.

Ogilvie, R. T. 1990. Distribution and ecology of whitebark pine in Western Canada. Pages 54-60 in: Schmidt W. C. and K. J. McDonald, compilers. Symposium on whitebark pine ecosystems: ecology and management of a high mountain resource. GTR-INT-270. USDA Forest Service, Intermountain Research Station, Bozman, MT, USA.

Perkins, D. L. 2001. Ecology of treeline whitebark pine (*Pinus albicaulis*) populations in central Idaho: successional status, recruitment and mortality, and a spring temperature reconstruction from whitebark pine tree rings. Ph.D. Thesis. Utah State University, Logan UT, USA.

Peterson, R. S. and Jewel, F. F. 1968. Status of American stem rusts of pine. Phytopathology. **6:** 23-40.

Richardson, B. A., Brunsfled, S. J., and Klopfenstein, N. B. 2002. DNA from bird-dispersed seed and wind-disseminated pollen provides insights into postglacial colonization and population genetic structure of whitebark pine (*Pinus albicaulis*). Molecular Ecology **11**:215-227.

Rogeau, M. P. 1996. Understanding the age-class distribution in the southern Canadian Rockies. M.Sc. Thesis, Department of Forest Science, University of Alberta.

Edmonton, AB, Canada.

Stuart-Smith, J. 1998. Conservation of whitebark pine in the Canadian Rockies: blister rust and population genetics. MSc. Thesis. University of Alberta. Edmonton, AB, Canada.

Tande, G. F. 1979. Fire history and vegetation pattern of coniferous forest in Jasper National Park, Alberta. Canadian Journal of Botany. **57:** 1912-1931.

Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. Living Bird, 16th Annual. **1977:** 123-160.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. Journal of Animal Ecology. **51:** 451-467.

Tomback, D. F. 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. Madrono. **33:** 100-110.

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

Tomback, D. F., Clary, J. K., Koehler, J., Hoff, R. J., and Arno, S. F. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: the sundance burn of Northern Idaho (U.S.A.). Conservation Biology. **9:** 654-664.

Tomback, D. F., Anderson, A. J., Carsey, K. S., Powell, M. L., and Mellmann-Brown, S. 2001. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. Ecology. **82:** 2587-2600.

Van Arsdel, E. P. 1965. Micrometerology and plant disease epidemiology. Phytopathology. **55:** 945-950.

Van Arsdel, E. P., Riker, A. J., and Patton, R. F. 1956. The effects of temperature and moisture on the spread of white pine blister rust. Phytopathology. **46:** 307-318.

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

White, C. 1985. Wildland fires in Banff National Park 1880-1980. Occasional Paper No.3. Parks Canada. Ottawa, ON, Canada.

Wilson, B. C. 1998. Daer-Pitts prescribed burn research plan. **KKP05-98**. Cordilleran Ecological Research. Winlaw, BC, Canada.

Wilson, B. C. 2001. Regeneration Dynamics of *Larix lyallii* in the southern Canadian Rocky Mountains. PhD thesis. University of Alberta, Edmonton, AB, Canada.

Wilson, B. C. and Stuart-Smith, G. J. 1999. Conversion of the Mountain National Parks Ecological Land Classification database. **JNP01-99**. Cordilleran Ecological Research. Winlaw, BC, Canada.

Wilson, B. C. and Stuart-Smith, G. J. 2000. Draft whitebark pine conservation for the Canadian Rocky Mountain National Parks. **KNP03-00**. Cordilleran Ecological Research. Winlaw, BC, Canada.

Wilson, B. C., Stuart-Smith, G. J., and Walker, R. 1998. Ecosystem restoration in the Rocky Mountain National Parks [poster]. Ecosystem management of forested landscapes Symposium Nelson, BC, Canada.

Yandell, U. G. 1992. An allozyme analysis of whitebark pine (*Pinus albicaulis* Engl.). M.Sc. Thesis, University of Nevada, Reno, NV, USA.

Zeglen, S. 2000. Whitebark pine and white pine blister rust in British Columbia. Interim report. B.C. Ministry of Forests, Vancouver Forest Region, Nanaimo, BC, Canada.

Zeglen, S. 2002. Whitebark pine and white pine blister rust in British Columbia, Canada. Canadian Journal of Forest Research. **32:** 1264-1274.

Zillar, W. G. 1974. The tree rusts of Western Canada. Canadian Forest Service, Ottawa, ON, Canada.