GRAND TETON NATIONAL PARK

WHITE PINE BLISTER RUST AND MOUNTAIN PINE BEETLE SURVEY & ANALYSIS

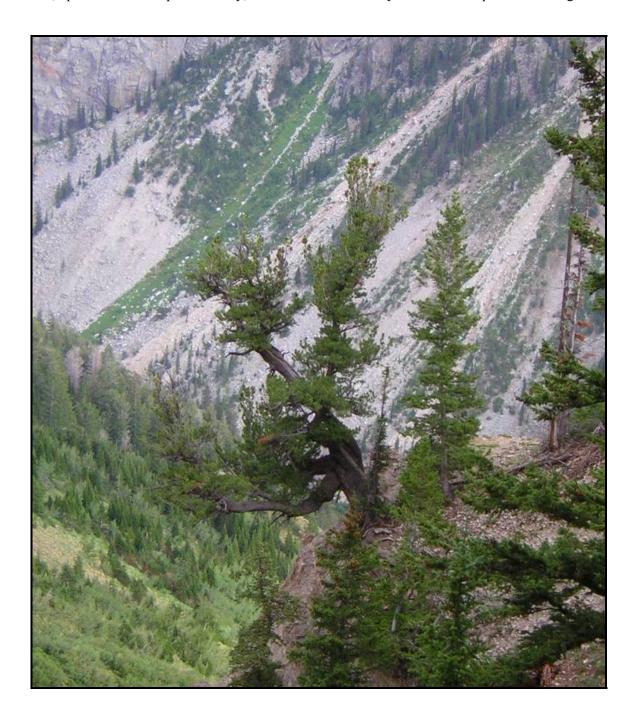
PREPARED BY

ΝΑΝΟΥ Κ ΒΟΟΚΙΝΟ

MAY **2008**

DEDICATION

I dedicate this project to the whitebark pine, whose tenacity reminds us to be rooted in place, patient, and nurturing. This ecosystem reveals that life is full of interwoven complexities, that the choices we make influence one another, and we must stand tall and endure. As we face imminent challenges to care for the natural world, upon which we depend entirely, the lessons embodied by the whitebark pine will emerge.



Abstract

The magnitude of current white pine blister rust (*Cronartium ribicola*) and mountain pine beetle (*Dendroctonus* ponderosae) impacts, combined with the effect of a changing climatic setting on beetle population dynamics in whitebark pine (*Pinus albicaulis*) ecosystems in the Greater Yellowstone Ecosystem (GYE) are placing this foundation species in a precarious state. This project conducted in Grand Teton National Park (GRTE) is a portion of an extensive monitoring and restoration project in the Intermountain West. Data reveal that within GRTE whitebark pine mortality, beetle activity, blister rust severity, cone production, and recruitment are spatially variable. Among whitebark pine sampled 17% were dead, 14% attacked by the beetle, 55% symptomatic for rust, and 30% bear cones. Whitebark pine regeneration was present on all sampled sites ranging from 20 to 1580 rust free seedlings per hectare. Beetle activity was greater than expected in individual whitebark pine with high severity blister rust, on sites <9500' and on south aspects. Blister rust severity was greatest on sites <9500', on south aspects, and on larger diameter whitebark pine. This information is critical to future monitoring efforts and successful restoration strategies.

TABLE OF CONTENTS

TITLE PAGE		i
DEDICATIO	N	ii
Abstract		iii
TABLE OF C	Contents	iv
INTRODUC	TION	1
Methods		3
Results		4
Discussio	N	5
	ON	9
ACKNOWL	EDGEMENTS	9
LITERATUR	e Cited	10
TABLE 1.	SITE NAMES & LOCATIONS	14
TABLE 2.	WHITEBARK PINE SUMMARY CONDITIONS 2007	14
TABLE 3.	CHI-SQUARE TEST RESULTS	15
TABLE 4.	CONDITIONS BY SITE 2007	16
FIGURE 1.	Site Locations	17
FIGURE 2.	DISTRIBUTION & SEVERITY OF MORTALITY	18
FIGURE 3.	DISTRIBUTION & SEVERITY OF MOUNTAIN PINE BEETLE ACTIVITY	19
FIGURE 4.	DISTRIBUTION & SEVERITY BLISTER RUST	20
FIGURE 5.	DISTRIBUTION MEAN # CANKERS	21
FIGURE 6.	DISTRIBUTION & ABUNDANCE CONES	22
FIGURE 7.	DISTRIBUTION & ABUNDANCE WHITEBARK REGENERATION	23

INTRODUCTION

The magnitude of current white pine blister rust (*Cronartium ribicola*) and mountain pine beetle (*Dendroctonus* ponderosae) impacts, combined with the effect of a changing climatic setting on beetle population dynamics in whitebark pine (*Pinus albicaulis*) ecosystems in the Greater Yellowstone Ecosystem (GYE) necessitates a deeper understanding of the spatial and temporal distribution of both of these agents of change on public lands. This project conducted in Grand Teton National Park (GRTE) is a portion of an extensive monitoring and restoration project in the Intermountain West. In addition, the Greater Yellowstone Inventory and Monitoring Program has identified threats to whitebark pine as "vital signs" within ecosystems. Goals of the Interagency Conservation Strategy Team include monitoring whitebark ecosystems.

Whitebark pine is a member of the genus *Pinus*, subgenus *Strobus*, and subsection *Cembra*, one of five stone pines worldwide (Critchfield & Little 1966). Although commercially insignificant, the value of whitebark pine rests in the realm of aesthetics, biological integrity, and ecosystem services. This slow growing, long-lived pine is often the only conifer species capable of establishment and survival on cold, harsh sites with poorly developed soil, high winds, and extreme temperatures (Arno & Hoff 1990).

Whitebark pine is a fundamental component of many high elevation ecosystems in the GYE and exhibits its influence at multiple scales throughout the western United States and Canada (Tomback et al. 2001a). A keystone species has an ecological role disproportionately large relative to its abundance, and a foundation species is one that defines ecosystem structure, function, and process (Tomback et al. 2001a). Characterized as both, the architectural, functional, and physiological characteristics of whitebark pine influence biodiversity and forest structure and process (Ellison et al. 2005). Specifically, these trees maintain hydrological quality by trapping snow, regulating snowdrift retention, spring melt and run-off, and erosion on steep sites (Arno & Hoff 1990; Farnes 1990). These influences affect agricultural lands and urban communities hundreds of miles away. Whitebark pine facilitate regeneration following disturbance, influencing community composition, structure, and succession (Tomback & Linhart 1990; Tomback et al. 2001a).

Whitebark pine exhibit several unique reproductive strategies that facilitate their foundational roles in forest structure, function, and resilience to disturbance-induced change and indicate they evolved in unpredictable and severe environments (Tomback & Linhart 1990). Recent findings reveal that whitebark pine exhibit delayed seed germination resulting in a soil seed bank not present in any other *Pinus* species (Tomback et al. 2001b). Their large, thick-coated seeds provide nutrients to a germinating seedling, allowing for rapid initial growth, and are an adaptation to xeric, cold conditions and short growing seasons (Tomback et al. 2001a).

Every three to five years, heavy cone crops produce abundant lipid-rich seeds which are an essential vegetative food source for some wildlife species, including the endangered grizzly bear (*Ursus arctos horriblis*) (Mattson et al.1994). The Clark's nutcracker is the primary dispersal vector for the wingless seeds and cache thousands throughout the landscape, transporting seeds several hundred meters up to over 12 kilometers

(Hutchins & Lanner 1982). Nutcrackers over wintering and courting in forests below the subalpine zone, and nestlings hatched in early spring depend on whitebark pine seeds as an energy-rich food source; nutcracker-pine interdependence is a nearly obligate mutualism (Tomback 1982; Tomback & Linhart 1990; Lanner 1996). Nutcrackers drive whitebark pine geographical distribution, genetic structure, and pioneer role on recently disturbed sites (Weaver & Dale, 1974; Lanner 1980; Tomback & Linhart 1990; Tomback et al.1995). AGENTS OF CHANGE

Although during the 20th century two significant mountain pine beetle events occurred in whitebark pine ecosystems, the extent and intensity of the current beetle outbreak, high incidence and severity of blister rust, and related mortality in whitebark pine is historically unprecedented (Kendall & Keane 2001; Logan & Powell 2001; Logan & Powell 2004; Westfall 2005; Smith et al. *In Press*). In the northern Rocky Mountains, mortality rates are as high as 90% (Gibson et al. 2007). In the Interior Columbia Basin, whitebark pine populations have declined by at least 45% (Keane & Kendall 2001). Data from the 2006 Forest Health and Protection aerial survey in the GYE indicated that approximately 41% of whitebark pine-dominated forest stands contained some level of beetle caused mortality, and 81% were infected with blister rust (Schwartz et al. 2007; Bockino 2008).

As agents of change, mountain pine beetle are considered regulators of ecosystem processes (Romme & Turner 1991). This native insect resides and reproduces within the subcortical tissues of coniferous trees and exhibits a broad range of aggressiveness in their host selection behavior, depending upon both host characteristics and beetle population dynamics (Wallin & Raffa 2004). Temporally coincident adult emergence enables beetles to collectively overcome tree defensive resin and supports epidemic populations (Safranyik et al. 1975). The coalescence of localized beetle activity is dependent on synchrony of critical bark beetle phenological events driven directly by temperature (Logan & Powell 2001). Conventional wisdom held that whitebark pine ecosystems were simply too cold for bark beetles (Amman & Schmitz 1988). Shifts in mountain pine beetle life cycles from maladaptive to adaptive seasonality and population transitions from endemic to epidemic, attributable to increased temperatures, has resulted in intensification of bark beetles within their historic range and expansion into high elevation ecosystems (Logan & Powell 2001).

In contrast, blister rust is a non-native pathogen accidently introduced into the western United States in the early 1900s. Spores enter through leaf stomata, fungal mycelia colonize living bark and cambial tissue, destroy the water and nutrient transport system, and form cankers or spore producing fruiting bodies. Blister rust decreases whitebark pine recruitment potential by extensive damage to cone bearing branches, seedlings and saplings (Tomback et al. 1995). Blister rust is continuing to spread throughout the GYE, and due to its perpetual presence, is considered the most damaging agent to whitebark pine.

As fundamental components of alpine and northern latitudinal habitats, where changes in climatic conditions and vegetative structure are occurring (Romme & Turner 1991), whitebark pines are significant "barometers of change". Disturbance-induced change is intricately linked to future stand structure and composition, successional trajectories, energy and nutrient fluxes, ecosystem function and services, and complex

spatial configurations on the landscape. The spatial pattern of biotic residuals inherently link patterns of successional change to disturbance. Shifts in these disturbance regimes may dramatically alter landscape structure and ecosystem function (Turner et al. 2001). Knowledge of the intensity, severity, duration, distribution and extent of beetle and blister rust is critical to effective management strategies. Understanding these dynamics has become vital to the conservation of this charismatic high elevation conifer. OBJECTIVES

The objectives of our project in GRTE were to track the status of the whitebark pine population through the: *i*) installation of permanent monitoring transects throughout the whitebark pine zone to be reread in order to detect temporal change; *ii*) quantification of the spatial distribution of blister rust and beetles; *iii*) to quantify the severity of blister rust and mountain pine beetle; *iv*) identification of areas of low beetle activity or rust infection; and *v*) description any relationships between edaphic factors and disturbance severity. In addition, we hope that our initial field survey will guide further studies to investigate current and potential whitebark pine recruitment and to identify potential target areas suitable for restoration.

METHODS

STUDY AREA

In 2005, a vegetation mapping project was completed and U.S. National Classification vegetation associations and alliances were attributed to all map units within GRTE. GRTE encompasses over 333,000 acres of which 53,000 or 16 % are coded as whitebark pine or subalpine forests (Nature Serve 2005). This study focused on whitebark pine found in the upper sub-alpine to tree line where stands are often patchy or form ribbon forests and krummholz that extend into the alpine. Whitebark pine often intermixes with spruce-fir and is often present as a minor component in high-elevation spruce-fir stands.

From June to August 2007, I randomly selected transect within GTRE using Hawth's tool in ArcGIS Version 9.2. Polygons established by the above mentioned 2005 vegetation map were used in a stratified random selection of potential transect locations. Two sets of polygons were established; those coded as whitebark pine (FWB) and those with whitebark pine present (FSF) and elevation > 8400'. Within each set, 100 polygons were randomly selected and then five random transect starting points (UTMs, NAD 83) were placed in each of the 200 polygons.

From among the random points in these polygons, based on the accessibility of the terrain in the field, I established and read 24 transects (Table 1; Figure 1). Transect data was collected based on a modified version of the Interagency Whitebark Pine Monitoring Protocol for the GYE (GYWPMWG 2007). Transect metadata recorded included: slope, aspect, elevation, UTM location, vegetation association, habitat type, cover type, presence and abundance of middens, and overstory tree composition by total % canopy cover and % canopy cover by species.

Within each polygon a random vector was used to lay out the 10 x 50 m transect. Transect monuments are comprised of 12" steel nails and large washers driven in at ground level at the beginning and end of the center of each transect. Within each transect all live whitebark pine >1.4 meters tall were tagged and examined. Dead whitebark pines were recorded, and only recently dead were tagged. Individual tree data recorded included: diameter breast height (DBH), height class, live/dead status, blister rust infection, mountain pine beetle activity, needle color, and cone presence.

To estimate individual tree blister rust infection each tree was visually divided into thirds. The total number of detectable cankers in each section of the bole and crown were recorded. Detectable cankers were placed in two categories, active or inactive. Active cankers were only recorded when white aecial blisters or orange aeciospores were present. The presence of two or more of the following denoted inactive cankers: *i*) branch flagging; *ii*) rodent chewing at canker site; *iii*) roughened, dead bark; *iv*) branch tissue with thin, smooth, or swollen sections, or *v*) oozing sap (Hoff 1992).

Mountain pine beetle activity was determined by the presence of: *i*) pitch tubes, which are mixtures of tree resin and beetle-produced boring dust; *ii*) boring dust in bark crevices particularly around root collar of tree; *iii*) entrance holes with inconspicuous pitch tubes; *iv*) small (\approx 2 mm diameter) emergence holes; or *v*) beetles actively chewing into bark (Safranyik et al. 1974).

DATA ANALYSIS

Two-dimensional chi-square tests of independence to determine statistical significance of the differences between two variables for a variety of host tree characteristics (SAS 2006). These tests corroborate relationships among variables, and the strength, direction and shape of the associations identified. Chi-square analyses compare observed frequencies to expected frequencies which were derived from my sample statistics, based on a model of complete independence.

RESULTS

SUMMARY OF WHITEBARK PINE CONDITIONS

Summary data for all transects shows that: 100% have seedlings, blister rust and cones; 58% middens; and 42% beetle activity (Table 2). Summary data for individual whitebark pine sampled (Table 2; n = 452) revealed that: 17% were dead, of which 4% were current beetle mortality, 10% old beetle mortality and 4% unknown; 14% mountain pine beetle activity; 55% symptomatic for blister rust; and 30% bear cones. Among sites, the proportion of dead whitebark pine ranged from zero mortality to 65% (Figure 2). The majority of whitebark pine mortality was related to beetle activity (Table 4).

MOUNTAIN PINE BEETLE ACTIVITY – SPATIAL DISTRIBUTION & INTENSITY

The intensity of mountain pine beetle activity varies among sites. Beetle activity is most intense on the eastern slope of the range, and conversely least intense near the Teton Crest (Figure 3). Beetles are present more than expected at lower elevation sites and on south (Table 3). In addition, on individual whitebark pine beetle activity is positively related to increased blister rust severity (Table 3).

BLISTER RUST - SPATIAL DISTRIBUTION & SEVERITY

Whitepine blister rust infection severity varies within Grand Teton Park. The proportions of live whitebark pine on each transect that exhibit blister rust symptoms range from 26 to 100% (Figure 4). Blister rust severity is positively related to elevations lower than 9500', south aspects, and larger diameter whitebark pine (Table 3). The mean number of blister rust cankers on individual whitebark pine rangeds from 1 to 22 and was greatest in the southern and eastern portions of the park (Figure 5).

WHITEBARK PINE CONE DISTRIBUTION & ABUNDANCE

Among sites, cone abundance ranges from 3 to 100% of individual whitebark pine bearing cones (Figure 6). Cone presence was positively related to blister rust severity. These results are counter intuitive and likely reflect the role of total branch abundance rather than the influence of blister rust on cone-bearing ability. Larger diameter whitebark pine have greater crown density and live crown ratios, and therefore more available branches for rust infection and cone production. When sampled trees are distributed into blister rust severity categories based on the number of cankers present, cones were present more often on whitebark pine with > 4 cankers (Table 3).

WHITEBARK PINE REGENERATION DISTRIBUTION & ABUNDANCE

Among sites, blister rust free seedling (whitebark pine <1.4 m in height) abundance ranges from 20 to 1580 per hectare. Seedling abundance varies spatially throughout the park.

DISCUSSION

ECOSYSTEM UNDERSTANDING

Data from this study facilitated the accomplishment of our original project objectives. We quantified the spatial distribution and severity of blister rust infection and beetle activity, identified areas of low rust infection and beetle activity. Results from this study also identified several relationships among mountain pine beetle activity, blister rust severity, and edaphic factors.

This study reveals that blister rust severity is positively related to mountain pine beetle activity. These results correspond to three studies reporting that whitebark pine exhibiting greater blister rust severity were more likely to be selected as host trees by the mountain pine beetle (Kegley et al. 2004; Six & Adams 2007; Bockino 2008). The role of host resistance is also fundamental to understanding mountain pine beetle selection patterns. Research clearly supports the idea that drought and disease compromise host tree vigor, which leads to reduced tree resistance to attack by mountain pine beetle (Cates & Alexander 1982; Mattson & Haack 1987; Lorio 1993). More recently, a single study in Montana, found a significant negative relationship between sapwood moisture content and blister rust severity, suggesting a reduction in tree defense capabilities (Six & Adams 2007).

Differences in host tree vigor may also be related to the presence and severity of white pine blister rust (Manion 1991; Tomback et al. 1995). Anatomical and cellular responses by trees infected with blister rust result in energetically costly processes. For example, cortical parenchyma and phloem polyphenolic parenchyma cells

divide to inhibit fungal colonization (Hoff et al. 2001; Hudgins et al. 2004). In addition, phenolic compound production is increased and concentrated around mycelial masses to kill or inactivate fungal hyphae (Beckman 2000). There is a potential feedback between altered or increased phenolic compounds and mountain pine beetle host colonization and population dynamics (Raffa et al. 2005; Seybold et al. 2006). The chemical composition of a tree responding to severe blister rust may provide the mountain pine beetle with greater quantity, quality, or variety of phenolic groups that serve as metabolic precursors to their aggregation and breeding pheromone system (Hudgins et al. 2004). Chemical defenses in pines are constitutive and inducible (Raffa et al. 2005; Seybold et al. 2006), suggesting that these defenses are limited. Perhaps whitebark pines responding to invasion by blister rust have less chemical resources available for defensive reactions to mountain pine beetle colonization. In addition, variable resource dynamics within an individual tree related to blister rust infection may play a role in cone production.

We also recorded mountain pine beetle activity and blister rust severity greater than expected at elevations <9500' and on sites with south aspects. These findings are supported by research indicating that beetle productivity is greatest at warmer temperatures (Bentz et al. 1991; Logan & Powell 2001). Mountain pine beetle are well-adapted for immediate and opportunistic response to changes in climatic conditions, due to the lack of a diapause phase in their life history (Bentz et al. 1991; Powell et al. 2000; Logan & Powell 2001; Powell & Logan 2004). A dramatic illustration of the thermally opportunistic nature of the mountain pine beetle is the increase in the proportion of univoltine synchronous mountain pine beetle brood, survivorship, and greater cold tolerance, due to increases in mean minimum temperatures since the 1980s (Bentz et al. 2001). Univoltinism is directly related to outbreak intensity and mountain pine beetle host colonization success (Logan & Powell 2007).

Field observations in the Intermountain West suggest unprecedented patterns of mountain pine beetle range expansion on the landscape (Logan & Powell 2001; Carroll et al. 2004; Gibson 2006; Logan & Powell 2004). In response to these circumstances, several veteran entomologists have initiated projects directed at the quantification of these novel observations. These studies will evaluate alterations in beetle phenology characterized by multiple host colonization and brood production by a single adult beetle. This appears to be occurring when an adult beetle over winters beneath the bark, re-emerges early the following spring to colonization an additional whitebark pine. This means in a single flight season, there are multiple cohorts of mountain pine beetle colonizing host trees (Bentz, personal communication). My study provides critical information to the global understanding of the present situation in whitebark pine ecosystems.

This study also demonstrates that rust severity was greater on larger diameter whitebark pine. This corresponds with findings from research conducted on a closely related five-needle pine species, limber pine (*Pinus flexilus*), relating increased whitepine blister rust infection with greater tree diameter (Hunt 1983; Campbell & Antos 2000; Kearns & Jacobi 2007). Related to this finding, this data revealed that live crown ratio is likely positively related to both blister rust severity and cone presence. Individual whitebark pines with larger

diameter had both greater cone abundance and, as mentioned above, blister rust severity. It is also possible that individual whitebark pine with severe blister rust infection are exhibiting cone masting phenology. ECOSYSTEM IMPLICATIONS

As both a foundation and keystone species occupying alpine and northern latitudinal habitats, where changes in climatic conditions and vegetative structure are occurring (Romme & Turner 1991; Walther et al. 2002) whitebark pine will become increasingly significant as a barometer of change. In particular, simulated vegetation change in the GYE project diminished whitebark pine range in response to climate change (Bartlein et al. 1997). Directional or differential selection on a keystone species will produce a ripple effect on biodiversity and ecosystem function. This trophic cascade will result in changes in ecosystem services such as key grizzly bear habitat component and watershed quality regulation, forest succession, and alpine vegetation biogeography (Callaway 1998; Tomback et al. 2001a; Schoettle 2004).

Whitebark pine ecosystem response and degree of resilience to alterations to the frequency and severity of disturbances will have profound effects on successional trajectories, stand composition and structure, landscape patterns, and future disturbance regimes (Romme & Turner 1991; Dale et al. 2002). As mentioned above, the combined effects of rust and beetles vary with the scale. On a stand-, ecosystem-, or landscape-level, as biogenic disturbance agents, mountain pine beetle and white pine blister rust influence autogenic and allogenic succession. This will result in altered patterns of ecosystem development and function, landscape structure and vegetative community composition (Kimmins 2004). In addition, mechanisms of allogenic succession respond to alterations in climatic setting, which influences the biotic components of succession (Kimmins 2004).

Whitebark pine occur in many community types depending on abiotic conditions such as moisture and temperature (Pfister et al. 1977), and biotic mechanisms such as dispersal and germination success. Recent work on successional trajectories of whitebark pine stands describe a broad range of successional roles filled by whitebark pine, and this range includes the well-documented early pioneer and climax roles, but also reveals a significant late-seral, shade tolerant role (Campbell et al. 2003). In addition, whitebark pine reproductive strategies enhance their ability to disperse, colonize, and persist on harsh sites (Tomback & Linhart 1990; Tomback et al. 2001a). For example, at the highest elevations krummholz whitebark pine facilitate timberline community expansion through creation of protected microclimates (Callaway 1998; Resler & Tomback 2008). In lower subalpine habitat types, whitebark pine is codominant with subalpine fir, lodgepole pine, and Engelmann spruce (Pfister et al. 1977).

The future distribution and abundance of whitebark pine on the landscape will reflect the inherent successional roles of whitebark pine, combined with the effects of the current blister rust and beetle disturbance. Limited propagule availability due to blister rust impacts on seed production may decrease future colonization rates (Resler & Tomback 2008). In mixed conifer stands, where whitebark pine is seral, beetle caused mortality may release suppressed whitebark pine and promote increased growth rates (Mattson & Addy 1975). Current

disturbances may promote this response in the GYE, as many stands contain several understory cohorts of whitebark pine (Bockino in prep).

TEMPORAL & SPATIAL CHANGE

Within Grand Teton Park, the intensity of blister rust infection and mountain pine beetle activity is spatially variable. It is also likely that rust and beetle activity vary temporally. Through the establishment of 24 permanent study sites, this work provides baseline data with which to compare further information. Overtime, these permanent transects will enable park managers to monitor the patterns and rates of spread of beetles and blister rust. Variation in stand conditions, and resulting heterogeneity, determine the pattern of connectivity and extent of susceptible trees and stands on the landscape (Raffa & Berryman1986; Bentz et al. 1996). This subsequently affects the pattern of spread and success of mountain pine beetle and blister rust on the landscape. For example, widespread and severe blister rust infection rates may lead to increased availability of whitebark pine with decreased vigor on the landscape (Ayres & Lombardero 2000).

As a result of this project we have increased our understanding of the extent, distribution, intensity, and severity of disturbance within the high elevation whitebark pine ecosystems in Grand Teton National Park. Knowledge of the location of residual stands of whitebark pine and areas with abundant whitebark pine

regeneration are critical to successful management strategies. Areas with low incidence of mountain pine beetle and blister rust should be targeted as potential restoration sites. In addition, areas of high blister rust infection rates should be surveyed more closely to identify potentially rust resistant individual whitebark pine.

Based on principles outlined in the "natural selection stand approach" proposed by Hoff et al. (1994), by selecting and killing whitebark pine with greater rust severity, in time mountain pine beetle host selection patterns will reduce the number of trees with severe rust available to recruit into subsequent populations. This idea reflects the potential for the interaction between mountain pine beetle and white pine blister rust to alter the genetic composition of whitebark pine populations remaining on the landscape. This alteration can occur rapidly, in as little as 50 years or one generation exposed to selection (Hoff et al. 1994).

A broad range of successional roles and reproductive strategies is an indication of the resilience of the whitebark pine as a species that will aid future restoration efforts. Whitebark pine exhibit several traits that indicate that they evolved in highly unpredictable and stressful environments (Tomback & Linhart 1990). Large, indehiscent, wingless, and thick-coated seeds provide nutrients, allow for rapid initial growth, and are an adaptation to xeric, cold conditions and short growing seasons (Baker 1972; Tomback & Linhart 1990). Furthermore, these seeds are stored in soil seed banks for up to eight years. Recruitment can occur continuously, even during years with no cone production and following severe disturbance events (Tomback 2001b). Reliance on bird dissemination provides whitebark pine with a pioneering advantage and a larger dispersal range. Whitebark pine's multi-trunk growth habit is not only a relic of nutcracker caching patterns, but because aggregated growth may provide protection, increased nutrient and water acquisition, and increased germination rates due to cross-pollination (Tomback & Linhart 1990).

CONCLUSIONS

In conclusion mortality, beetle activity, blister rust infection, and regeneration potential of whitebark pine in Grand Teton National Park varies spatially. Mountain pine beetle activity is greatest in whitebark pine with greater blister rust infection, at lower elevations and on south aspects. Blister rust severity is positively related to tree diameter and greatest at lower elevations and on south aspects. The majority of the current mortality rate of 17% is attributable to beetle activity and will continue to increase. The elimination and fragmentation of localized populations of whitebark pine is eminent, yet residual or legacy populations, propagule availability and distribution on landscape play a vital role of large-scale patterns of patches of different ages and a spatial configuration dissimilar from the present. The relative importance of certain variables and processes may shift with changes in disturbance regimes and climate.

The whitebark pine monitoring work performed in Grand Teton Park June to August 2007 provides vital information about whitebark pine ecology and conditions within the park. This information is critical to the direction and success of future monitoring and restoration strategies.

ACKNOWLEDGEMENTS

I would like to thank my invaluable field assistants John Carr, Dave Bywater, and Alida and Joe Bockino for their hard work and enthusiasm. I am grateful to the Jenny Lake Rangers, especially Scott Guenther, for their willingness to assist with this project. Thank you to Richard Easterbrook for his assistance with ArcGIS and map creation. I also thank Kelly McCloskey for logistical, emotional, and field support. Funding for the analysis and summary for this project was provided by the Rocky Mountain Cooperative Ecosystem Study Unit.

LITERATURE CITED

- Amman, G.D., and Schmitz, R.F. 1988. Mountain pine beetle lodgepole pine interactions and strategies for reducing tree losses. Am. Bio. 17: 62-68.
- Arno S.F., and Hoff R.J. 1990. Silvics of whitebark pine (Pinus albicaulis). USDA For. Serv. Gen. Tech. Rep. INT-253.
- Ayres, M.P., and Lombardero, M.J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Sci. Tot. Environ.. 262: 263-286.
- Baker, H.G. 1972. Seed weight in relation to environmental conditions in California. Ecology. 53: 997-1010.
- Bartlein, P., Whitlock, C. & Shafer, S. L. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. Conservation Biology. 11(3): 782-792.
- Beckman, C.H. 2000. Phenolic-storing cells: keys to programmed cell death and periderm formation in wilt disease resistance and in general defense responses in plants? Phys. and Mol. Plant Path.. 57: 101–110
- Bentz, B.J., Logan J.A., and Amman G.D. 1991. Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. Can. Ent. 123: 1083-1094.
- Bentz, B.J., Powell J.A., and Logan, J.A. 1996. Localized spatial and temporal attack dynamics of the mountain pine beetle in lodgepole pine. USDA For. Serv. Res. Pap. INT-RP-494.
- Bentz, B.J., Logan, J.A., and Vandygriff, J.C. 2001. Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size. Can. Ent. 133(3): 375-387.
- Bockino, N.K. 2008. Interactions of white pine blister rust, host species, and mountain pine beetle in whitebark pine ecosystems in the Greater Yellowstone. M.S. Thesis. University of Wyoming.
- Callaway, R.M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. Oikos, 82: 561-573.
- Campbell, E.M. & Antos, J.A. 2000. Disturbance and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Canadian Journal Forest Research. 30: 1051-1059.
- Campbell, E.M., and Antos, J.A. 2003. Postfire succession in *Pinus albicaulis-Abies lasiocarpa* forests of southern British Columbia. Can. J. Bot.. 81: 383-397.
- Carroll, A.L. Taylor, S.W. Regnierre, J., and Safranyik, L. 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. *Edited by* T.L. Shore, J.E. Brooks, and J.E Stone, J.E. Canadian Forest Service, Pacific Forestry Centre, Kelowna, B.C. pp. 223-232.
- Cates, R.G. & Alexander, H.1982. Host resistance and susceptibility. *In* Mitton, J.B. & Sturgeon, K.B (eds) Bark beetles in North American conifers. University Texas Press, Austin. 212-263.
- Critchfield, W.B. & Little, E.L. 1966. Geographic distribution of the pines of the world: U.S. Department of Agriculture Miscellaneous Publication. 991: 1-97.
- Ellison, A.M. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Fron. Eco. Environ. 3: 479-486.
- Farnes, P.E. 1990. SNOTEL and snow course data describing the hydrology of whitebark pine ecosystems. *In* Proceedings: Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High Mountain Resource. Edited by W.C. Schmidt and K.J. McDonald. USDA For. Serv. GTR-INT-207. pp. 302-304.
- Gibson, K., Steed, B., and Sturdevant, N. 2007. Mountain pine beetle-caused mortality 2001-2007. Nutcracker Notes 13: 12-15.
- Greater Yellowstone Whitebark Pine Monitoring Working Group (GYWPMWG). 2007. Interagency whitebark pine monitoring protocol for the Greater Yellowstone Ecosystem, Version 1.00. Greater Yellowstone Coordinating Committee, Bozeman, MT.
- Henigman, J., Ebata, T., Allen, E., Holt, J., and Pollard, A. 1999. Field guide to forest damage in British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre British Columbia Ministry of Forests, Victoria, B.C.
- Hoff, R.J. 1992. How to recognize blister rust infection on whitebark pine. USDA For. Serv. Res. No. INT-406.
- Hoff, R.J., Hagle, S.K., and Krebill, R.G. 1994. Genetic consequences and research challenges of blister rust in whitebark pine forests. *In* Proc. International Workshop on Subalpine Stone Pines and Their Environment: the Status of My Knowledge, September 5-11, 1992, St. Moritz, Switzerland, USDA For. Serv. INT-GTR-309. pp. 118-126.

- Hoff, R.J., Ferguson, D.E., McDonald, G.I., and Keane, R.E. 2001. Strategies for managing whitebark pine in the presence of white pine blister rust. *In* Whitebark pine communities. *Edited by* D.F. Tomback, S.F. Arno, and R.E. Keane. Island Press, Washington DC. pp. 346-366.
- Holdenrieder, O., Pautasso, M., Weisberg, P.J., and Lonsdale, D. 2004. Tree diseases and landscape processesthe challenge of landscape pathology. Tren. Eco. Evol. 19 (8): 446-452.
- Hudgins, J.W, Christiansen, E, & Franceschi, V. 2004. Induction of anatomically based defense responses in stems of diverse conifers by methyl jasmonate: a phylogenetic perspective. Tree Physiology. 24: 251-264.
- Hunt, R.S. 1983. White pine blister rust in British Columbia II. Can stands be hazard rated? Forestry Chronicles. 59: 30-33.
- Hutchins, H.E. & Lanner, R.M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201
- Jentsch, A., Berierkuhnlein, C., and White, P.S. 2002. Scale, the dynamic stability of forest ecosystems, and the persistence of biodiversity. Silva Fennica 36(1):393-400.
- Keane, R.E., Morgan, P., and Menakis, J.P. 1994. Landscape assessment of decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, Montana, USA. Northwest Sci. 68(3): 213-229.
- Kearns, H.S., & Jacobi, W.R. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Canadian Journal Forest Research. 37: 462-472.
- Kendall, K.C., and Keane, R.E. 2001. Whitebark pine decline: Infection, mortality, and population trends. *In* Whitebark pine communities. *Edited by* D.F. Tomback, S.F. Arno, and R.E. Keane. Island Press, Washington DC. pp. 221-242.
- Kimmins, J.P. 2004. Forest Ecology: A Foundation for Sustainable Forest Management and Environmental Ethics in Forestry. Prentice Hall. 611 p.
- Kinloch, B.B. 2003. White pine blister rust in North America: past and prognosis. Phytopathology. 93: 1044-1047.
- Lanner, R.M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. In Dancik, B.P. & Higginbotham, K.O. (eds) Proceedings of Sixth North American Forest Biology Workshop. University of Alberta, Edmonton, Alberta, Canada.
- Lanner, R.M. 1996. Made for each other, a symbiosis of birds and pines. Oxford University Press, New York, NY.
- Logan, J.A. & Powell, J.A. 2001. Ghost forests, global warming and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist. 47(3):160-172.
- Logan, J.A., & Powell, J.A. 2004. Modelling mountain pine beetle phenological response to temperature. *In* T.L. Shore, J.E. Brooks & Stone, J.E. (eds) Mountain Pine Beetle Symposium: Challenges and Solutions, October 30-31, 2003, Kelowna, British Columbia, Canada. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Information Report BC-X-399, p 210-222.
- Logan, J.A., & Powell, J.A. 2007. Ecological consequences of climate change altered forest insect disturbance regimes. *In* Wagner, F.H. (ed.) Climate change in western North America: evidence and environment effects. University of Utah. In press.
- Lorio, P.L. 1993. Environmental stress and whole-tree physiology. *In* Schowalter, T.D., & Filip, G.M. (eds), Beetle-Pathogen Interactions in Conifer forests. Academic Press, San Diego, CA. 81-101.
- Lorio, P.L. 1993. Environmental stress and whole-tree physiology. *In* Schowalter, T.D., & Filip, G.M. (eds), Beetle-Pathogen Interactions in Conifer forests. Academic Press, San Diego, CA. 81-101.
- Manion, P.D. 1991. Tree Disease Concepts. 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.
- Mattson, W.J. & Addy, N.D 1975. Phytophagous insects as regulators of forest primary production. Science. 190: 515-522.
- Mattson, W.J, & Haack, R.A. 1987. The role of drought in outbreaks of plant-eating insects. BioScience. 37(2): 110-118.
- Mattson, D.J., & Reinhart, D.P. 1994. Bear use of whitebark pine seeds in North America. *In* Schmidt, W.C., & Holtmeier, F.K. (eds) Proceedings International workshop on subalpine stone pines and their environment: The status of my knowledge. USDA Forest Service, Intermountain Research Station, GTR-INT-309. Ogden, UT. 221-220.
- McKinney, S.T., and Tomback, D.F. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. Can. J. For. Res. 37: 1044-1057.

- Mote, P.W., Hamlet, A.F., Clark, M.P., and Lettenmaier, D.P. 2005. Declining mountain snowpack in western North America. Bull. Amer. Meteorol. Soc. 86: 39-49.
- Nature Serve. 2005. Vegetation association descriptions for GRTE. International Ecological Classification Standard: Terrestrial Ecological Classifications. Nature Serve Central Databases. Arlington, VA.
- Pfister, R.P., Kovalchik, B.L., Arno, S.F., & Presby, R. 1977. Forest habitat types of Montana, USDA Forest Service, Intermountain Forest and Range Experiment Station, GTR-INT-34, Ogden, UT.
- Perkins, D.L., and Swetnam, T.W. 1996. A dendroecological assessment of whitebark pine in the Sawtooth-Salmon River region, Idaho. Can. J. For. Res. 26: 2123-2133.
- Powell J.A., Jenkins, J.L., Logan J.A. & Bentz B.J. 2000. Seasonal temperatures alone can synchronize life cycles. B Math Biol. 62: 977–98.
- Raffa, K.F., Aukema, B.H., Erbilgin, N., Klepzig, K.D., and Wallin, K.F. 2005. Interactions among conifer terpenoids and bark beetles across multiple levels of scale: an attempt to understand links between population patterns and physiological processes. Recent Advances in Phytochemistry. 39: 78-118.
- Resler, L.M., and Tomback, D.F. 2008. Blister rust prevalence in krummholz whitebark pine: implications for treeline dynamics. Ar. Ant. Al. Res. 40(1):161-170.
- Romme, W.H., and Turner, M.G. 1991. Implications of global climate change for biogeographic patterns in the Greater Yellowstone Ecosystem. Con. Bio. 5(3): 373-386.
- Safranyik, L., Shrimpton, D.M., and Whitney, H.S. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Canadian Forest Service, Tech. Rep.
- Safranyik, L., Shrimpton, D.M., and Whitney, H.S. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. *In* Management of lodgepole pine ecosystems. *Edited by* D.M. Baumgartner. Washington State University Cooperative Extension Service, Pullman, WA. pp. 406-428.
- SAS Institute. 2006. The SAS system for Windows. Release 9.1.3. SAS Institute, Cary, NC.
- Seybold, S.J., Huber, D.P., Lee, J.C., Graves, A.D., and Bohlmann, J. 2006. Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. Phytochem. Rev. 5: 143-178.
- Six, D.L., and J. C. Adams. 2007. Relationships between white pine blister rust and the selection of individual whitebark pine by the mountain pine beetle. J. Ento. Sci. 42: 345-353.
- Smith, C.M., Wilson, B., Rasheed, S., Walker, R., Carolin, T., and Dobson, B. *In Press*. Whitebark pine and blister rust in the Rocky Mountains of Canada and northern Montana. Can. J. For. Res.
- Schoettle, A.W. 2004. Ecological roles of five-needle pines in Colorado: potential consequences of their loss. *In*: Sniezko, R.A., Samman, S., Schlarbaum, S.E., & Kriebel, HB (eds) Breeding and genetic resources of fiveneedle pines: growth, adaptability, and pest resistance. Proc RMRS-P-32, USDA Forest Service, Rocky Mountain Research Station. Fort Collins, CO. 124-135.
- Schwandt, J.W., and Kegley, S. 2004. Mountain pine beetle, blister rust, and their interaction on whitebark pine at Trout Lake and Fischer Peak in northern Idaho from 2001-2003. USDA For. Serv. R1-FHP-049.
- Schwartz C.C., Haroldson M.A., and West K. 2007. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2006. USGS Nor. Roc. Mtn. Sci. Cen. Bozeman, MT.
- Taylor, S.W. and Carroll, A.L. 2003. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: a historical perspective. *In* Mountain Pine Beetle Symposium: Challenges and Solutions, Kelowna, B.C., 30-31 October 2003. *Edited by* T.L. Shore, Brooks, J.E., and Stone, J.E. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C.
- 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., and Linhart, Y.B. 1990. The evolution of bird-dispersed pines. Evol. Ecol. 4: 185-219.
- Tomback, D.F., and Kendall, K.C. 2001. Biodiversity losses: the downward spiral. *In* Whitebark pine communities. *Edited by* D.F. Tomback, S.F. Arno, and R.E. Keane. Island Press, Washington DC. pp. 243-262.
- Tomback, D.F, Clary, J.K., Koehler, J., Hoff, R.J., and Arno, S.F. 1995. The effects of blister rust on postfire regeneration of whitebark pine-the Sundance burn of northern Idaho (USA). Con. Bio. 9: 654-664.
- Tomback, D.F. Arno, S.F. and Keane, R.E. 2001a. The compelling case for management intervention. *In* Whitebark pine communities. *Edited by* D.F. Tomback, S.F. Arno, and R.E. Keane. Island Press, Washington DC. pp. 4-25.

- Tomback, D.F., Anderies, A.J., Carsey, K.S., Powell, M.L., and Mellman-Brown, S. 2001b. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. Ecology. 82(9): 2587-2600.
- Turner, M.G. & Dale, V.H. 1998. What have I learned from large, infrequent disturbances? Ecosystem. 1: 493-496.
- Turner, M.G., Gardner, R.H., and O'Neill, R.V. 2001. Landscape Ecology in Theory and Practice: Pattern and Process. Springer-Verlag, NY.
- Wallin, K.F. & K.F. Raffa. 2004. Feedback between individual host selection behavior and population dynamics in an eruptive insect herbivore. Ecol. Monogr. 74: 101-116.
- Walther, G.R., Post E., Convery, P. Menzel, A., and Parmesan, C. 2002. Ecological responses to recent climate change. Nature. 416: 389–95.
- Weaver, T. & Dale, D. 1974. Pinus albicaulis in central Montana: environment, revegetation, and production. American Midland Naturalist. 92: 222-230.
- Westfall, J. 2005. Summary of forest health conditions in British Columbia. BC Min. For. Range, Victoria, BC. Pest Management, Rep. 15.
- Zeglen, S. 2002. Whitebark pine and white pine blister rust in British Columbia, Canada. Can. J. For. Res. 32: 1265-1274.

TABLES

Table 1. Transec	t names, locations,	and metadata June-August 2007.	X = data unavailable.	UTMs are Nad 82,
Zone 12.		-		

Site	Elevation	Aspect	Easting	Northing
Amphitheater Lake	9866	160	517649	4842063
Boundary Lake	9889	300	510314	4853165
Carr Lake	9798	260	512978	4861719
Cascade	Х	Х	513382	4845553
DC Shelf	9647	132	507665	4832984
Delta Lake	9263	20	518556	4841876
Forellen	9729	30	514232	4872809
Garnet	9900	150	515949	4841084
Hanging Canyon	9104	110	519439	4848693
Holly Lake	9412	80	516451	4848195
JHMR	10076	300	510299	4827485
Lake Taminah	9802	142	515974	4841145
Marion	9256	155	506004	4829966
Mount Hunt	9700	115	511754	4830286
Mount Moran	Х	Х	519139	4852524
NFC Cache	9019	320	512967	4848351
Ortenberger Lake	9711	188	512699	4857740
SF Cascade	9822	68	514218	4844756
Static	9396	255	514407	4835194
Stewarts	9169	136	516327	4836470
Survey Peak	8494	104	513409	4876382
Teewinot Apex	9118	127	519075	4843205
Teewinot South	8950	18	519101	4842884
Upper Death	8745	280	508875	4833541

Table 2. Whitebark pine conditions in Grand Teton NP June-August 2007.

Variable	% Transects	% Whitebark
Total mortality	37	17
Current beetle mortality	29	4
1970s beetle mortality	13	10
Unknown mortality	21	3
Mountain pine beetle	42	14
Blister rust (live trees)	100	55
Whitebark Seedlings	100	Х
Cones Present (live trees)	100	30
Middens	58	Х

Variable	Categories	Frequency Ratios ^{t}	$\chi^{2^{\dagger \dagger}}$	Interpretation
Cone Presence		Cones Absent: Cones Present		
	# Cankers	Expected = $1:0.44$		
	0	1 : 0.26		Cone presence greater
	1-3	1 : 0.37		on wb with > 4 cankers
	4-15	1 : 0.92		
	>15	1 : 0.58	19.07; p=0.0003	
Elevation		Low:High		
Low (<9500') High (>9500')	# Cankers	Expected = 1 : 1.9		
5 (111)	0	1:3.3		Rust severity is greater
	1-3	1 : 3.5		at lower elevations (<9500")
	4-15	1 : 1.6		(
	>15	1:0.4	49.95; p<0.0001	
Aspect		North: South		
North	# Cankers	Expected = 1 : 1.70		
(0-70 & 280-360°) South	0	1 : 1.22		Rust severity is greater
(70-280°)	1-3	1 : 1.95		on south aspects (70- 280°)
	4-15	1 : 1.77		
	>15	1 : 3.80	11.07; p=0.113	
Rust Presence		Rust Absent: Rust Present		
	DBH (cm)	Expected = 1: 1.19		
	0.1-10	1: 0.46		
	10.1-20	1: 1.05		Rust presence
	20.1-30	1: 3.10		increases tree diameter
	30.1-40	1: 9.70		
	40.1-50	1: 10.5		
	>50	1: 10.5	84.81; p<0.0001	
MPB Presence		MPB Absent: MPB Present		
	# Cankers	Expected = $1:0.05$		
	0	1:0.02		MPB activity increases
	1-3	1:0.05		with rust severity
	4-15	1:0.07		
	>15	1 : 0.13	8.6650; p=0.0341	
MPB Presence		MPB Present: MPB Absent		
	Aspect	Expected = 1: 0.18		Mpb activity is greater
	North	1: 0.10		on south aspects (70- 280°)
	South	1: 0.23	7.490; p=0.0062	200)
MPB Presence		MPB Present: MPB Absent	<i>,</i> ,	
· · · · • •	- 1			Mpb activity is greater
	Elevation	EXDECLED = 1.0.10		
	Elevation <9500'	Expected = 1: 0.18 1: 0.50		at lower elevations (<9500')

Table 3. Rust severity frequency ratios by whole tree rust severity for individual whitebark pine. Rust severity categories where observed ratios exceed expected ratios are in bold.

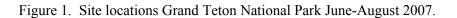
[†]Frequency ratios calculated by dividing the observed number of whitebark pine selected as hosts by the MPB by the observed number of whitebark pine not selected. We calculated this ratio for category indicated.

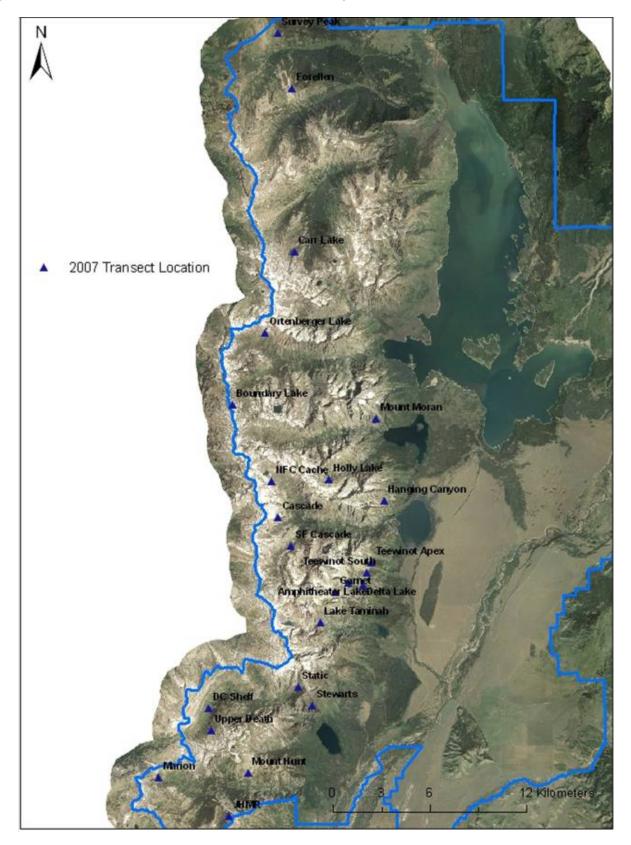
^{††}Pearson's chi-square calculates expected ratios based on the null hypothesis that all variables are independent.

Table 4.	Whitebark c	conditions by	v site Grand	l Teton NP	June-August 2007

Site	% wb dead	% wb with mpb	% live WB with rust	mean # cankers (live wb)	% live wb with cones	Rust-free Seedlings /ha
Amphitheater Lake	0	8	44	3.4	40	1240
Boundary Lake	0	0	33	0.9	4	700
Carr Lake	8	8	46	1.4	27	240
Cascade	20	0	63	6.1	Х	60
DC Shelf	0	0	45	8.5	35	620
Delta Lake	0	0	80	11.6	50	740
Forellen	32	47	28	1.5	62	840
Garnet	0	0	60	3.3	33	420
Hanging Canyon	47	47	90	19.4	10	1080
Holly Lake	0	0	80	10.8	60	320
JHMR	9	0	65	6.9	5	940
Lake Taminah	7	0	54	3.2	4	740
Marion	63	63	66	7.7	100	20
Mount Hunt	13	0	86	11.2	57	280
Mount Moran	8	0	26	0.4	Х	320
NFC Cache	0	0	30	1.5	30	320
Ortenberger Lake	2	21	82	7.0	64	160
SF Cascade	0	0	78	5.0	70	180
Static	33	67	92	17.2	58	220
Stewarts	0	24	88	22.2	18	1580
Survey Peak	3	3	58	6.8	3	900
Teewinot Apex	50	50	71	8.9	29	120
Teewinot South	63	79	100	18.9	14	280
Upper Death	22	44	29	11.0	14	100

FIGURES





Ν % Whitebark Dead ø 1 - 15 16 - 25 26 - 50 51 - 65 nometers

Figure 2. Whitebark pine mortality June-August 2007.

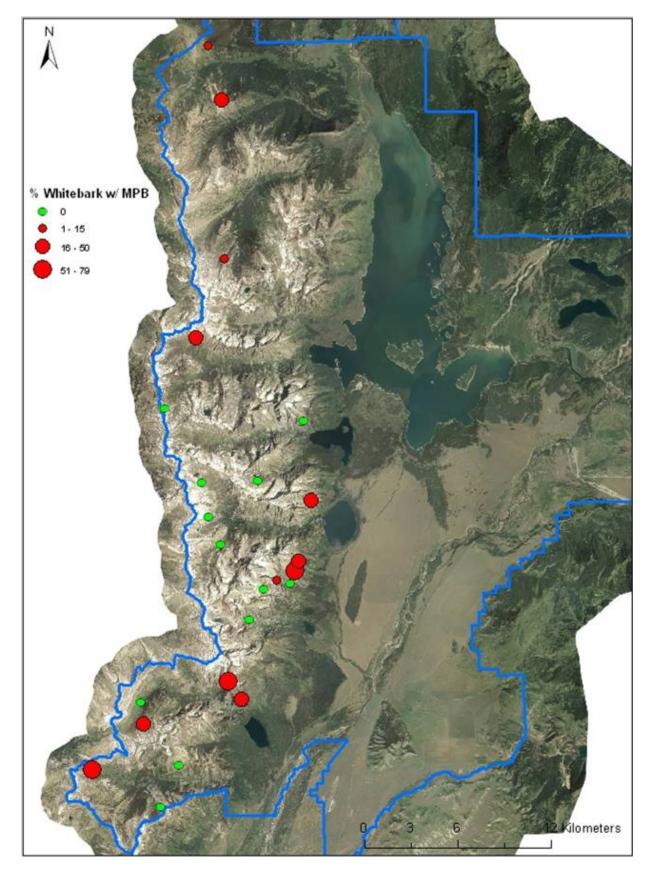


Figure 3. Mountain pine beetle activity in whitebark pine June-August 2007.

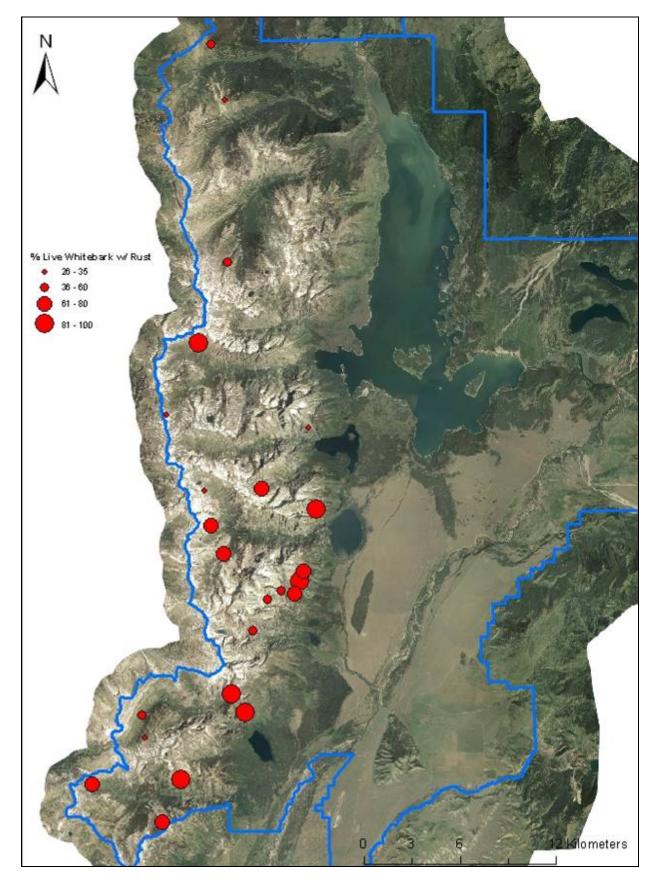


Figure 4. Proportion live whitebark pine with blister rust June-August 2007.

Figure 5. Mean number of blister rust cankers per tree.

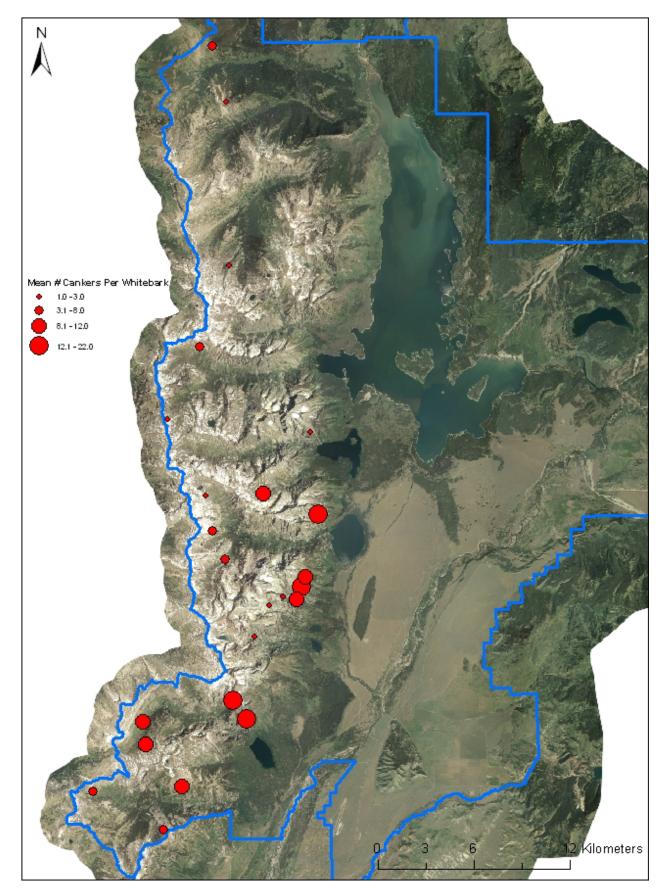


Figure 6. Proportion of live whitebark on each transect with cones present.

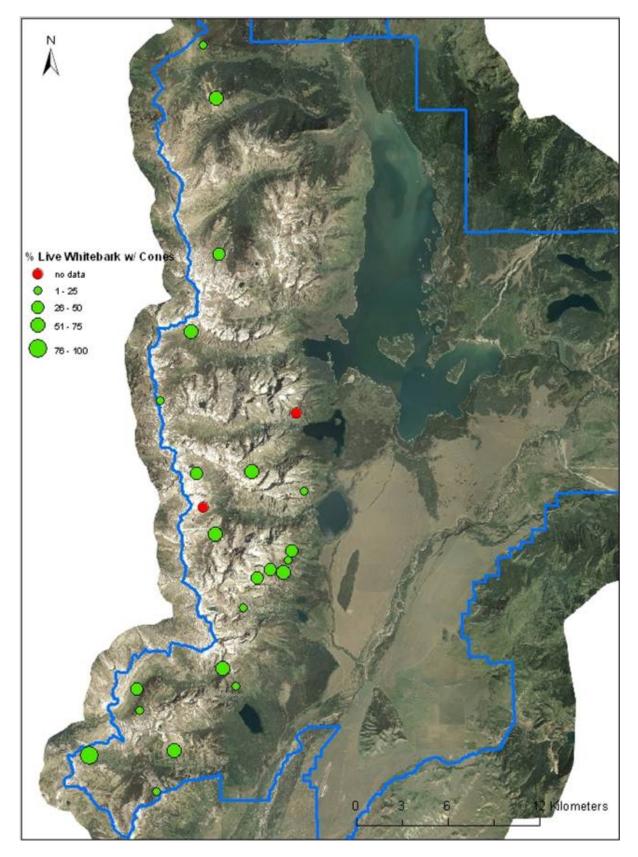


Figure 7. Whitebark pine seedlings (<1.3 m height) without blister rust per hectare.

