

# The influence of white pine blister rust on seed dispersal in whitebark pine

Shawn T. McKinney and Diana F. Tomback

**Abstract:** We tested the hypotheses that white pine blister rust (*Cronartium ribicola* J.C. Fisch.) damage in whitebark pine (*Pinus albicaulis* Engelm.) stands leads to reduced (1) seed cone density, (2) predispersal seed survival, and (3) likelihood of Clark's Nutcracker (*Nucifraga columbiana* (Wilson, 1811)) seed dispersal. We gathered data from two sets of paired forest sites in the Bitterroot Mountains of eastern Idaho and western Montana that were similar in topography, canopy structure, tree species composition, and successional stage, but differed in rust infection level, crown kill, and tree mortality. We counted initial (mid-July) and final (late August) seed cones, observed vertebrate seed predator activity, and documented nutcracker seed dispersal in study sites in 2001 and 2002. High-rust sites had higher rates of seed predation relative to cone abundance, lower predispersal seed survival, and fewer observations of nutcracker seed dispersal than paired low-rust sites. These findings suggest that as blister-rust-induced damage increases within stands in the Bitterroot Mountains, the likelihood of nutcracker seed dispersal decreases. We propose that whitebark pine in heavily rust-damaged forests may not self-regenerate and would therefore require planting of seeds or seedlings from genetically rust-resistant trees.

**Résumé :** Nous avons testé les hypothèses voulant que les dommages causés par la rouille vésiculeuse du pin blanc (*Cronartium ribicola* J.C. Fisch.) dans les peuplements de pin à écorce blanche (*Pinus albicaulis* Engelm.) entraîne la réduction (1) de la densité des cônes, (2) de la survie des graines avant leur dispersion et (3) de la probabilité de dispersion des graines par le casse-noix d'Amérique (*Nucifraga columbiana* (Wilson, 1811)). Nous avons ramassé des données dans deux groupes de stations forestières appariées situées dans les monts Bitterroot dans l'est de l'Idaho et l'ouest du Montana. La topographie, la structure de la canopée, la composition en espèces arborescentes et le stade de succession de ces stations étaient similaires mais le degré d'infection de la rouille, la portion de cime tuée par la maladie et la mortalité des arbres étaient différents. Nous avons compté les cônes au début (mi-juillet) et à la fin (fin août), observé l'activité des vertébrés prédateurs des graines et documenté la dispersion des graines par le casse-noix d'Amérique dans les stations expérimentales en 2001 et 2002. Les stations où l'incidence de la rouille était élevée avaient un taux plus élevé de prédation des graines relativement à l'abondance des cônes, un taux plus faible de survie des graines avant leur dispersion et moins d'observations de dispersion des graines par le casse-noix d'Amérique que les stations correspondantes où l'incidence de la rouille était faible. Ces résultats indiquent que la probabilité de dispersion des graines par le casse-noix d'Amérique diminue à mesure que les dommages causés par la rouille vésiculeuse du pin blanc augmentent dans les peuplements des monts Bitterroot. Nous croyons que le pin à écorce blanche pourrait ne pas se régénérer dans les forêts sévèrement endommagées par la rouille et qu'il serait par conséquent nécessaire de planter des graines ou des semis provenant d'arbres génétiquement résistants à la rouille vésiculeuse du pin blanc.

[Traduit par la Rédaction]

## Introduction

Many western North American coniferous forests are currently experiencing an unprecedented number of forest health challenges, including successional replacement, altered structure, and fuels accumulation from decades of fire suppression (Arno and Allison-Bunnell 2002); mountain

pine beetle (*Dendroctonus ponderosae* Hopkins, 1902) population upsurges possibly related to drought (Logan and Powell 2001); and epidemics of exotic pathogens, such as those causing sudden oak death (*Phytophthora ramorum* S. Werres, A.W.A.M. de Cock) (Rizzo and Garbelotto 2003) and white pine blister rust (*Cronartium ribicola* J.C. Fisch.) (McDonald and Hoff 2001). The fungal pathogen *C. ribicola* (division Basidiomycota, order Uredinales), native to Eurasia, exhibits a complex life cycle that includes five different spore types alternating between five-needled white pines (family Pinaceae, genus *Pinus*, subgenus *strobus*) and plants of the genera *Ribes*, *Pedicularis*, or *Castilleja* (Hummer 2000; McDonald and Hoff 2001; McDonald et al. 2006). White pine blister rust damages and kills five-needled white pines by girdling the branches and trunk. Since *C. ribicola*'s introduction to the Vancouver area in 1910, it has been spreading across western North American forests where previous attempts to control it, including elimination of one of its alternate hosts *Ribes*, were in

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vain (McDonald and Hoff 2001). In western North America, *C. ribicola* has infected seven of the eight five-needled white pines, reducing seed production and killing trees, which has resulted in altered successional processes and declines in forest community types and the biodiversity they harbor (McDonald and Hoff 2001).

Whitebark pine (*Pinus albicaulis* Engelm.), a subalpine and treeline forest species, ranges throughout the western United States and Canada. In general, whitebark pine occurs as a climax species on the coldest and driest sites — areas that are too harsh for its competitors to thrive — and occurs as a seral species on protected, lower elevation sites that favor its shade-tolerant competitors (Arno and Weaver 1990). Whitebark pine shows high susceptibility to blister rust (Hoff et al. 1980), and blister rust now occurs throughout the Canadian range of whitebark pine (Campbell and Antos 2000; Zeglen 2002) and throughout most of its US range (Kendall and Keane 2001). Mean mortality is 35% with a range on average of 8% to 58%, and mean infection is 66% with a range on average of 17% to 89% in stands sampled throughout the northwestern United States and southwestern Canada (Kendall and Keane 2001). Local extirpation of whitebark pine precipitates a cascade of consequences including reductions in soil stability and hydrologic regulation, altered plant successional pathways, and losses of biodiversity resulting from diminished wildlife carrying capacity and habitat and forest types (Arno 1986, 2001; Tomback et al. 2001a). The large, wingless seeds of whitebark pine, which are retained in indehiscent cones (Mirov 1967; McCaughey and Schmidt 1990), comprise an important wildlife food for granivorous birds and mammals, including grizzly (*Ursus arctos* Linnaeus, 1758) and black bears (*Ursus americanus* Pallas, 1780) in the Greater Yellowstone Area (Mattson et al. 2001; Tomback and Kendall 2001).

Whitebark pine depends on Clark's Nutcracker (*Nucifraga columbiana* (Wilson, 1811), family Corvidae) for seed dispersal. Nutcrackers store 1–15 seeds in small caches about 2 cm below the ground in late summer and fall for later retrieval (Tomback 1978; Hutchins and Lanner 1982). Nutcrackers often use recently disturbed areas such as burns and clearcuts for seed caching, which results in early successional establishment of whitebark pine (Tomback 1986; Tomback et al. 2001b).

Whitebark pine has additional challenges to its survival. Decades of fire suppression have resulted in successional replacement of seral whitebark pine communities in the Rocky Mountains and elsewhere by more shade-tolerant conifers, including subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) (Arno 1986; Keane and Arno 1993). Recent upsurges of mountain pine beetles, which may be related to warming trends, are now rapidly killing whitebark pine (Logan and Powell 2001). In areas where fire occurs and the whitebark pine seed source is nearly destroyed from earlier pine beetle infestations and blister rust, regeneration is slow and seedlings die from blister rust (Tomback et al. 1995).

*Cronartium ribicola* is acting as a selective force by causing differential survival among whitebark pine trees in rust-infested forests. Studies have shown that surviving whitebark pine trees from high-mortality stands possess higher levels of heritable resistance than trees from low-

mortality stands (Hoff et al. 1994) and that more than 40% of the progeny of high-mortality survivors display resistance to blister rust (Hoff et al. 2001). Increasing the frequency of genetic resistance to the blister rust pathogen within populations is the most promising management strategy for conserving whitebark pine. The most effective way to increase rust-resistance is by planting seedlings grown from stock with known genetic resistance (Bingham 1983). However, because this restoration can be costly and labor-intensive, a less demanding alternative is desirable.

Forest openings that provide caching opportunities for Clark's Nutcracker can be created in high-mortality stands by silvicultural thinning and prescribed burning. If nutcrackers harvest and disseminate seeds from the few remaining cone-producing trees, which are likely to have some resistance to blister rust, a new generation dominated by rust-resistant individuals could emerge. Hoff et al. (1994) termed this process the natural selection stand approach and predicted that it could occur in as little as 50 years. However, a possible complication to a solution based solely on natural selection and bird dispersal is the impact of seed predators on an inherently diminished cone crop.

Clark's Nutcracker consumes unripe whitebark pine seeds from early July until seed coats harden in mid- to late-August, at which time they become a seed disperser (Tomback 1978). Nutcrackers compete with the red squirrel (*Tamiasciurus hudsonicus* (Erxleben, 1777)), an efficient and voracious seed predator that cuts down conifer cones and stores them in middens for winter food. The squirrels feed first on the tree species with the greatest cone energy (Smith 1970) and thus prefer whitebark pine cones for their high energy seeds (Hutchins and Lanner 1982). Red squirrels can be responsible for even greater seed predation than nutcrackers, taking as much as 80% of the cone crop (Hutchins and Lanner 1982; Samano and Tomback 2003). Thus, in rust-damaged stands, predispersal seed predation by nutcrackers and squirrels could deplete cone crops before mid-August and cause fewer seeds to be cached in the ground, thereby reducing the potential for whitebark pine regeneration.

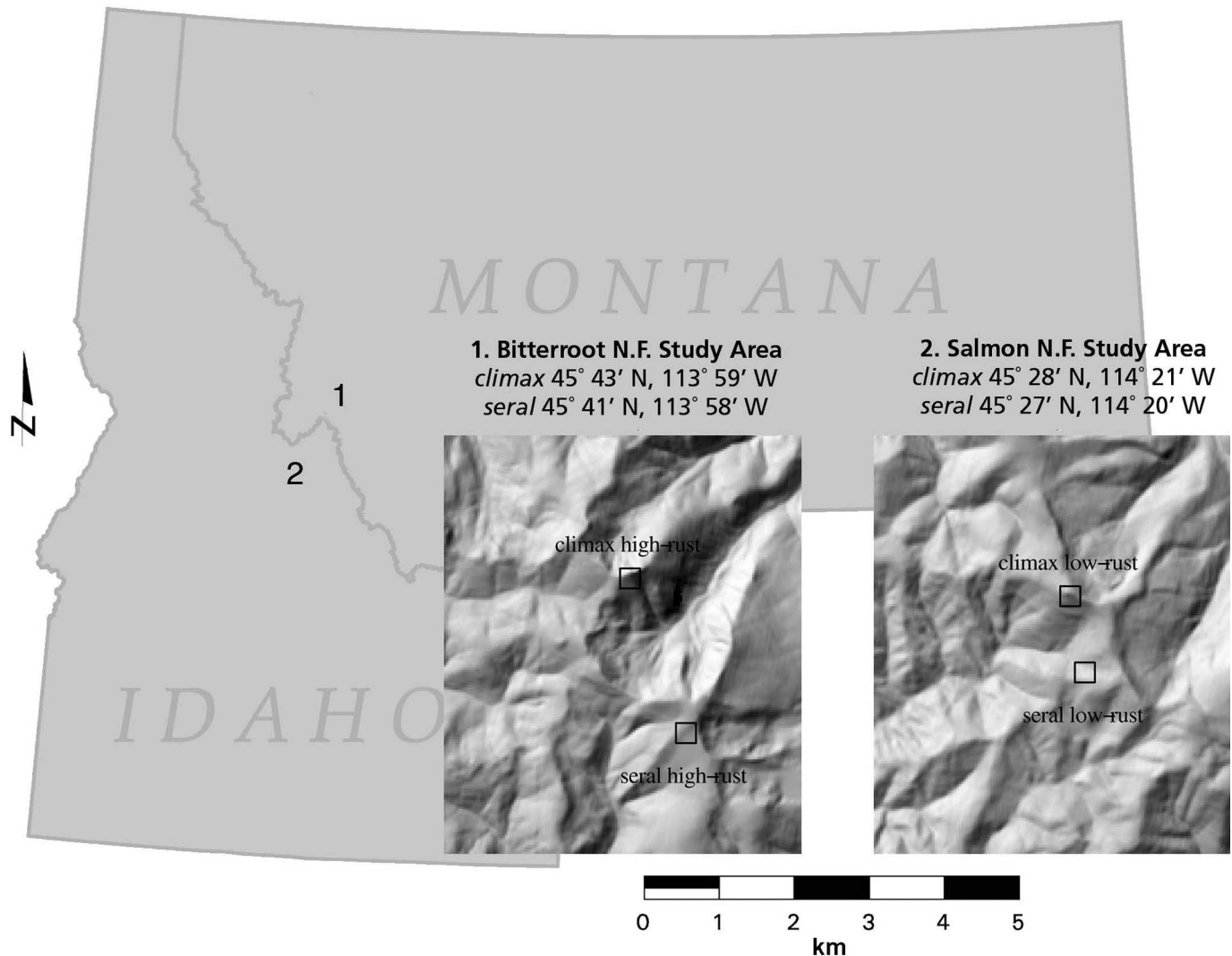
This study examines the influence of blister rust on whitebark pine cone density, predispersal seed survival, and the likelihood of seed dispersal across similar stands that vary in blister rust infection levels, crown kill, and tree mortality. We postulate that (1) stands with higher levels of blister rust infection and damage will have lower cone densities than similar stands with lower levels of rust infection and damage, (2) stands with lower cone densities will have a relatively smaller proportion of their cones survive to time of seed dispersal, and (3) stands with a lower proportion of cones surviving will be less likely to have seeds dispersed by nutcrackers.

## Materials and methods

### Study areas and sites

Using 1 ha forest sites as the sampling unit, we compared similar forest types that differed in levels of blister rust infection and damage to determine the effects of blister rust on whitebark pine predispersal seed survival and likelihood of seed dispersal. We chose two study areas, one located in

**Fig. 1.** Geographical locations and shaded relief maps of the two whitebark pine study areas in Montana and Idaho. Within the Bitterroot (1) and Salmon (2) National Forest Study Areas are the climax and seral high- and low-blister rust study sites.



the Bitterroot National Forest, Montana and another in the Salmon National Forest, Idaho (Fig. 1, Table 1). Each study area was comprised of two study sites — one site where whitebark pine was the climax species and one site where it was a seral species (Fig. 1). Each study site was a 1 ha parcel (100 m × 100 m) delineated from a larger, continuous forest. The climax sites were composed almost entirely of whitebark pine, located at high elevation, with steep slopes and rocky, poorly developed soils. The seral sites were composed of whitebark pine, subalpine fir, and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Englem.), located at lower elevation, with gentler slopes and moderately well-developed soils (Table 1).

Whitebark pine in the Bitterroot National Forest study area had high levels of blister rust infection and damage in both the seral and climax sites (Table 2). Hereafter we refer to these sites as seral high-rust and climax high-rust, respectively. Adjacent to this area was a large expanse of forest that burned in the 2000 Saddle Mountain fire. The Salmon National Forest study area had much lower blister rust infection levels in both the seral and climax sites (Table 2).

These sites are referred to as seral low-rust and climax low-rust. The Bitterroot and Salmon study areas were separated by a 40 km straight-line distance. Paired sites (e.g., climax high-rust and climax low-rust) were chosen to be similar in environmental characteristics, relative tree species abundance and size, and density of cone-bearing whitebark pine (Table 1).

#### Site description and cone inventories

Field sampling was conducted from 15 July to 4 September 2001 and from 15 July to 10 October 2002. At each study site in 2001, we established latitude, longitude, and midpoint elevation using a geographic positioning system cross referenced with US Geological Survey 7.5' maps; determined aspect with compass; and measured slope with a clinometer. For all trees in each site, we observed and recorded whether seed cones were present. We estimated tree height with a clinometer and measured stem diameter at 1.4 m above the ground (DBH) for all cone-bearing whitebark pine trees (single stem) and tree sites (≥2 stems joined below 1.4 m) that were ≥7.0 cm DBH. For all other tree

**Table 1.** Environmental, compositional, and structural characteristics of paired whitebark pine (*Pinus albicaulis* Engelm.) study sites in Montana and Idaho.

Characteristic	Study sites			
	Seral forest		Climax forest	
	Low-rust	High-rust	Low-rust	High-rust
<b>Environmental characteristics</b>				
Elevation (m)	2553	2451	2660	2574
Aspect (°)	180	176	184	158
Area (ha)	1	1	1	1
Slope (°)	5	7	28	22
<b>Compositional and structural characteristics*</b>				
Proportion and total number of trees <sup>†</sup>				
Whitebark pine	0.59   105	0.54   149	0.91   91	0.98   135
Subalpine fir	0.17   31	0.14   38	0.01   01	0   0
Lodgepole pine	0.24   43	0.32   87	0.08   08	0.02   02
Mean DBH (cm) <sup>‡</sup>				
Whitebark pine	22.5a (1.0)	20.5a (1.4)	16.2b (0.8)	15.6b (0.6)
Subalpine fir	16.3c (2.0)	22.8d (2.3)	9.2	—
Lodgepole pine	18.9e (1.4)	24.1f (1.2)	18.3g (2.4)	16.2g (5.9)
Number of cone producing trees in 2001 <sup>§</sup>				
Whitebark pine	28	27	30	32
Subalpine fir	28	34	1	0
Lodgepole pine	43	74	7	3

\*Trees  $\geq 7.0$  cm DBH.

<sup>†</sup>Sites were compared with  $\chi^2$  tests; distributions of tree species did not differ by blister rust condition ( $P > 0.05$ ).

<sup>‡</sup>Sites were compared using independent-sample  $t$  tests. Paired study sites (low-rust and high-rust) with the same letter are not different ( $P > 0.05$ ). Standard errors for site means are given in parentheses. Values for whitebark pine are for cone trees only. Values and contrasts not provided for subalpine fir in climax forests because only one tree was recorded.

<sup>§</sup>Includes single stem trees and tree sites with  $\geq 2$  stems joined below 1.4 m.

species, we measured DBH of all trees with diameters  $\geq 7.0$  cm.

Whitebark pine trees within each site were inspected for the presence of blister rust and tree damage from rust. A tree was considered to be infected if it exhibited active and (or) inactive branch or bole cankers (Hoff 1992). We estimated percentage crown kill for all infected whitebark pine, considering the crown to include the area from the highest point of the tree down to the lowest branches. Individual trees with  $>5\%$  crown kill were assigned the midpoint value of an 11% category range (Fig. 2). For example, if a tree was estimated to have from 5%–15% crown kill, it was assigned a 10% crown kill value; from 15%–25% crown kill, it was assigned 20%; from 25%–35%, it was assigned 30%; and so on. Trees with 1%–5% damage were recorded as having 3% crown kill. All dead whitebark pine trees were tallied and their cause of death recorded as white pine blister rust, mountain pine beetle, fire, or unknown.

All whitebark pine trees with seed cones were counted and individually tagged. In mid-July of 2001 and 2002, we counted all seed cones present on these trees. This count is referred to as the *initial number of cones* ( $C_i$ ) and was used to calculate mean initial number of cones (no./tree) and initial cone density (no./ha) for each study site. We used a tripod-mounted spotting scope with angular sight and 40 $\times$  eyepiece, 8  $\times$  32 binoculars, and a handheld counting device to survey and count cones. We marked and used three or four cone count observation points for each tree.

Seed dispersal dates were defined for each study site as

the date when the first nutcracker was observed harvesting seeds from whitebark pine and placing the seeds in its sublingual pouch for transportation to caching sites (for overview of nutcracker behavior and ecology, see Tomback 1998). At this time, we conducted another cone count for all cone-bearing whitebark pine within a study site. This count is referred to as the *final number of cones* ( $C_f$ ) for a given tree. For each study site,  $C_f$  was used to calculate the mean final number of cones (no./tree), final cone density (no./ha), and cone survival ( $C_f/C_i$ ).

### Seed predator observations

Vertebrate pine seed predators that frequented the study sites consisted primarily of Clark's Nutcracker and red squirrels. Sites were monitored for animal activity within the time period of 05:30 to 20:30 for 2–8 h per day throughout the summer (mid-July to September). One person observed and recorded seed predator activity within a site, and only one site was observed at any given time. Each of the four sites received an equal amount of observation time for each hour within the time period (05:30–20:30) and for total hours. During observation periods, we surveyed for animal activity by walking throughout a site and observing animals by means of binoculars, and surveying trees from vantage points with spotting scope and binoculars. Observed activities of red squirrels were divided into two categories: (1) cone harvesting and (2) present in study site, but not harvesting cones. Nutcracker activities were separated into three categories: (1) seed harvesting, (2) seed pouching (i.e., dispersal),

**Table 2.** White pine blister rust (*Cronartium ribicola* J.C. Fisch.) damage estimates and seed cone production in paired whitebark pine (*Pinus albicaulis* Engelm.) study sites in Montana and Idaho.

Site variable	Study sites			
	Seral forest		Climax forest	
	Low-rust	High-rust	Low-rust	High-rust
Blister rust infected (% of trees)*	24a	97b	54c	96d
Mean crown kill (%/tree)	2 (0.2)	79 (2.9)	13 (3.6)	38 (3.2)
With >50% damaged crown (% of trees)*	2e	65f	8g	32h
Dead (% of trees)*	2i	29j	2k	15l
Initial cone density (no./ha) <sup>†</sup>				
2001	623	433	724	226
2002	69	49	79	8
Mean initial cones (no./tree) <sup>†,‡</sup>				
2001	22.3m (5.1)	16.0m (2.5)	24.1n (4.5)	7.1o (1.3)
2002	2.5p (0.6)	1.7p (0.8)	2.6q (0.7)	0.2r (0.2)

**Note:** Paired study sites (low-rust and high-rust) with the same letter are not different ( $P > 0.05$ ). Data are for whitebark pine trees  $\geq 7.0$  cm DBH only. Standard errors for site means are given in parentheses.

\*Paired study sites were compared with  $\chi^2$  tests.

<sup>†</sup>Initial refers to the number of seed cones counted in mid-July.

<sup>‡</sup>Paired study sites were compared using independent-sample  $t$  tests.

or (3) within study site, but not harvesting seeds. Field data were converted into the number of sightings per hour for each seed predator and for its activity type. We then calculated an overall rate of seed predation (rSP) for each study site by summing the number of seed or cone harvesting observations of both nutcrackers and red squirrels and dividing by the total number of observation hours.

### Statistical analysis

Unless otherwise noted, data were analyzed with SPSS version 10.0 (SPSS, Inc. 1999), with a significance level of 5% ( $\alpha = 0.05$ ) for all statistical tests. Independent-sample  $t$  tests were used to determine if the population means of paired study sites (e.g., seral high-rust and seral low-rust) were different with respect to cone-bearing whitebark pine DBH, lodgepole pine DBH, the initial and final number of cones on whitebark pine trees, and postseed ripening occurrence of Clark's Nutcracker. Subalpine fir DBH was compared only in seral sites since only one tree of this species occurred in the climax sites. We used  $\chi^2$  tests to determine whether paired sites were different in population proportions of whitebark pine trees infected with blister rust, showing greater than 50% crown kill, or dead from all causes. Differences in tree species relative abundance and the proportion of whitebark pine cones surviving to time of seed dispersal were also evaluated between paired sites using  $\chi^2$  tests. No statistical tests were done on the 2002 final cone data because either too few or no cones remained in the high-rust sites for meaningful analysis.

We used simple linear regression models to quantify the relationship between the initial and final number of whitebark pine cones (cone survival) for each study site. We used Microsoft Excel (Microsoft Corporation 2003) to calculate one-way ANOVA to test for homogeneity of the slopes of the cone survival regression lines (Sokal and Rohlf 1995). We then performed post hoc multiple comparisons of the regression slopes by applying the Tukey-Kramer procedure and utilizing Gabriel's approximate method to construct

comparison intervals such that two regression slopes were significantly different if their intervals did not overlap (Sokal and Rohlf 1995).

We calculated a relative rate of seed predation for each site by scaling the overall rate of seed predation (rSP) to the initial number of cones ( $C_i$ ), then graphically analyzed the relationship between the final number of cones ( $C_f$ ) and the relative rate of seed predation ( $rSP/C_i$ ) for the 2001 and 2002 data. Linear regression models were used to quantify the strength of the relationship between  $C_f$  and  $rSP/C_i$  with  $rSP/C_i$  naturally log transformed for a better fit of the data to the model. Paired-sample  $t$  tests were used to compare the population mean differences between 2001 and 2002 in terms of the number of cone-producing whitebark pine trees and the number of initial cones per tree ( $C_i$ ).

## Results

### Site characteristics, blister rust, and cone production

We attempted to control for nonblister rust-related variables that might affect seed dispersal through our study site selection. Paired study sites were similar with regard to elevation, aspect, slope, area, and the number of trees producing seed cones in 2001 (Table 1). There was no statistical difference between paired sites in tree species relative abundance (seral,  $\chi^2 = 3.45$ ,  $P > 0.05$ ,  $df = 2$ ,  $n = 453$ ; climax,  $\chi^2 = 5.92$ ,  $P > 0.05$ ,  $df = 2$ ,  $n = 238$ ) and mean tree diameter of cone-bearing whitebark pine (seral,  $t_{111} = 1.0$ ,  $P = 0.318$ ; climax,  $t_{142} = 0.768$ ,  $P = 0.444$ ). Mean tree diameter of lodgepole pine also did not differ between climax sites ( $t_9 = 0.39$ ,  $P = 0.706$ ), but differed between seral sites ( $t_{128} = 2.49$ ,  $P = 0.014$ ). Subalpine fir mean tree diameter differed between the seral sites ( $t_{67} = 2.03$ ,  $P = 0.046$ ), and only one subalpine fir tree was recorded for the climax sites (Table 1).

We selected paired study sites based on their differences in blister rust infection and crown damage. High-rust study sites had significantly higher proportions of whitebark pine

**Fig. 2.** Examples of whitebark pine trees with varying degrees of crown kill. According to the methodology of this study these trees would have been assigned the midpoint values (in parentheses) of the following ranges: (A) 1%–5% (3%); (B) 15%–25% (20%); (C) 25%–35% (30%); and (D) 75%–85% (80%).

trees infected with blister rust (seral,  $\chi^2 = 114.64$ ,  $P < 0.001$ ,  $df = 1$ ,  $n = 196$ ; climax,  $\chi^2 = 34.85$ ,  $P < 0.001$ ,  $df = 1$ ,  $n = 144$ ); with more than 50% of crowns killed (seral,  $\chi^2 = 169.11$ ,  $P < 0.001$ ,  $df = 1$ ,  $n = 196$ ; climax,  $\chi^2 = 10.35$ ,  $P = 0.001$ ,  $df = 1$ ,  $n = 144$ ); and dead from all causes (seral,  $\chi^2 = 5.3$ ,  $P = 0.021$ ,  $df = 1$ ,  $n = 219$ ; climax,  $\chi^2 = 5.84$ ,  $P = 0.016$ ,  $df = 1$ ,  $n = 161$ ) (Table 2).

Our cone inventories in 2001 and 2002 documented extreme annual variation in whitebark pine cone production. In 2001, we followed the fate of 2006 cones produced in all study sites combined, whereas only 205 cones were produced in 2002. Likewise, in 2001, there were significantly more cone-producing trees in the study sites ( $t_3 = 3.776$ ,  $P = 0.033$ ), and more initial cones produced per tree ( $t_{116} = 8.364$ ,  $P < 0.001$ ) (Table 2). In both years, however, greater rust damage was associated with lower cone production between paired sites, and high-rust sites had both lower initial cone densities and fewer cones per tree (Table 2). This difference was significant between the climax sites in both years (2001,  $t_{60} = 3.681$ ,  $P < 0.001$ ; 2002,  $t_{60} = 3.575$ ,  $P < 0.001$ ), but not the seral sites (2001,  $t_{53} = 1.084$ ,  $P = 0.141$ ; 2002,  $t_{53} = 0.709$ ,  $P = 0.241$ ).

### Seed predators and seed predation

The greatest difference in mean observations of pre-dispersal seed predation (number of harvesting observations per hour) occurred for red squirrels in the seral whitebark pine forest sites (Fig. 3). In the climax sites, observations of red squirrel seed predation were similar, and mean observations of Clark's Nutcracker seed predation varied little among all sites (Fig. 3). However, when each site's overall rate of seed predation (rSP, combined nutcrackers and red squirrels) was scaled to its number of initial cones ( $C_i$ ) to calculate a relative rate of seed predation, the effects of blister rust damage became evident. The seral high-rust site had a relative rate of seed predation (rSP/ $C_i$ ) five and a half times greater than that of the comparable seral low-rust site (0.0067 and 0.0012, respectively). Likewise, the climax high-rust site had a ratio three and a half times greater than the climax low-rust site (0.0046 and 0.0013, respectively) (Fig. 3). In short, in the high-rust sites where blister rust killed relatively more cone-producing branches and entire whitebark pine trees, cone production was reduced, but the frequency of seed predation was not. Thus, in high-rust sites, there was a higher frequency of seed predation observations relative to the initial number of cones.

### Cone survival and seed dispersal

In 2001, in the seral whitebark pine sites, linear regression of cone survival was significant for the low-rust site (model,  $F_{[1,26]} = 464.95$ ,  $P < 0.001$ ), but not for the high-rust site (model,  $F_{[1,25]} = 2.85$ ,  $P = 0.104$ ) (Fig. 4). Although cone survival regression was significant for both climax sites (low-rust model,  $F_{[1,28]} = 70.72$ ,  $P < 0.001$ ; high-rust model,  $F_{[1,30]} = 12.76$ ,  $P = 0.001$ ), a similarly weaker relationship

between  $C_f$  and  $C_i$  was evidenced in the high-rust site (Fig. 4). We tested the cone survival regression lines for homogeneity of slopes with a one-way ANOVA (Sokal and Rohlf 1995), intending to perform analysis of covariance (ANCOVA), but found significant differences among the slope coefficients ( $F_{[3,68]} = 8.69$ ,  $P < 0.01$ ). A post hoc multiple comparisons test demonstrated that the low-rust sites had significantly greater slopes than the high-rust sites (Fig. 5). Thus, the magnitude of the strength of the response of  $C_f$  to changes in  $C_i$  differed greatly, indicating fundamentally different functional relationships in the low-rust and high-rust sites.

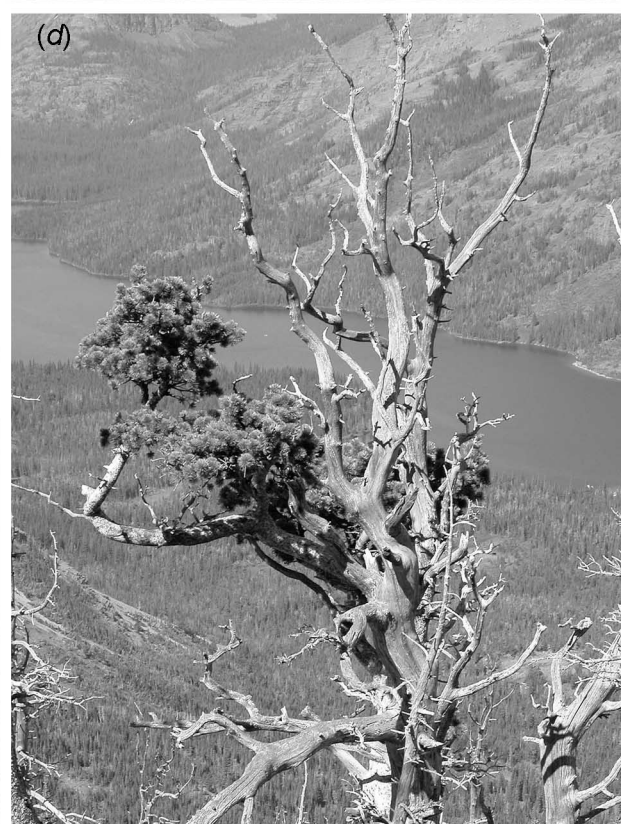
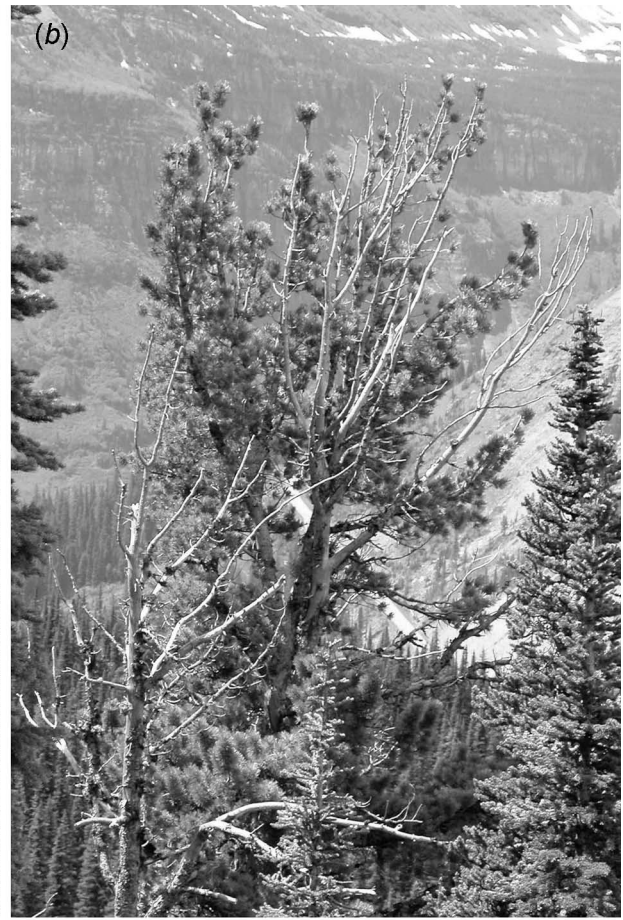
Linear regression models of the relative rate of seed predation (rSP/ $C_i$ ) against the final number of cones for both the 2001 and 2002 data were significant (2001 model,  $F_{[1,2]} = 26.48$ ,  $P = 0.036$ ; 2002 model,  $F_{[1,2]} = 60.82$ ,  $P = 0.016$ ). As the ratio of seed predation to initial cones increased, the number of cones remaining at time of seed dispersal decreased linearly (Fig. 6). In the high-rust sites in 2001, there were significantly lower proportions of cones surviving (seral,  $\chi^2 = 491.046$ ,  $P < 0.001$ ,  $df = 1$ ,  $n = 1,056$ ; climax,  $\chi^2 = 55.75$ ,  $P < 0.001$ ,  $df = 1$ ,  $n = 950$ ) and fewer cones per tree (seral,  $t_{53} = 3.387$ ,  $P = 0.001$ ; climax,  $t_{60} = 4.104$ ,  $P < 0.001$ ) when seeds ripened and nutcracker seed dispersal began (Table 3). In the low cone production year of 2002, the trend was the same: Higher rust was associated with fewer relative and absolute final cones (Table 3).

In 2001, the few remaining cones in the high-rust sites failed to attract many nutcrackers at the time of seed dispersal compared to the low-rust sites, and thus significantly fewer nutcrackers were observed per hour from the onset of seed dispersal to the end of the field season (seral,  $t_{32} = 2.056$ ,  $P = 0.048$ ; climax,  $t_{39} = 3.413$ ,  $P < 0.002$ ) (Table 3). Furthermore, we failed to observe a single seed dispersal event in the climax high-rust site. In the seral forests, we observed on average five times more seed dispersal events in the low-rust site than in the high-rust site (Table 3). In 2002, along with a significant reduction in cone production was a scarcity in nutcrackers in all of the study sites. In that year, the climax low-rust site, which had the greatest final cone density, was the only site where we observed nutcracker seed dispersal.

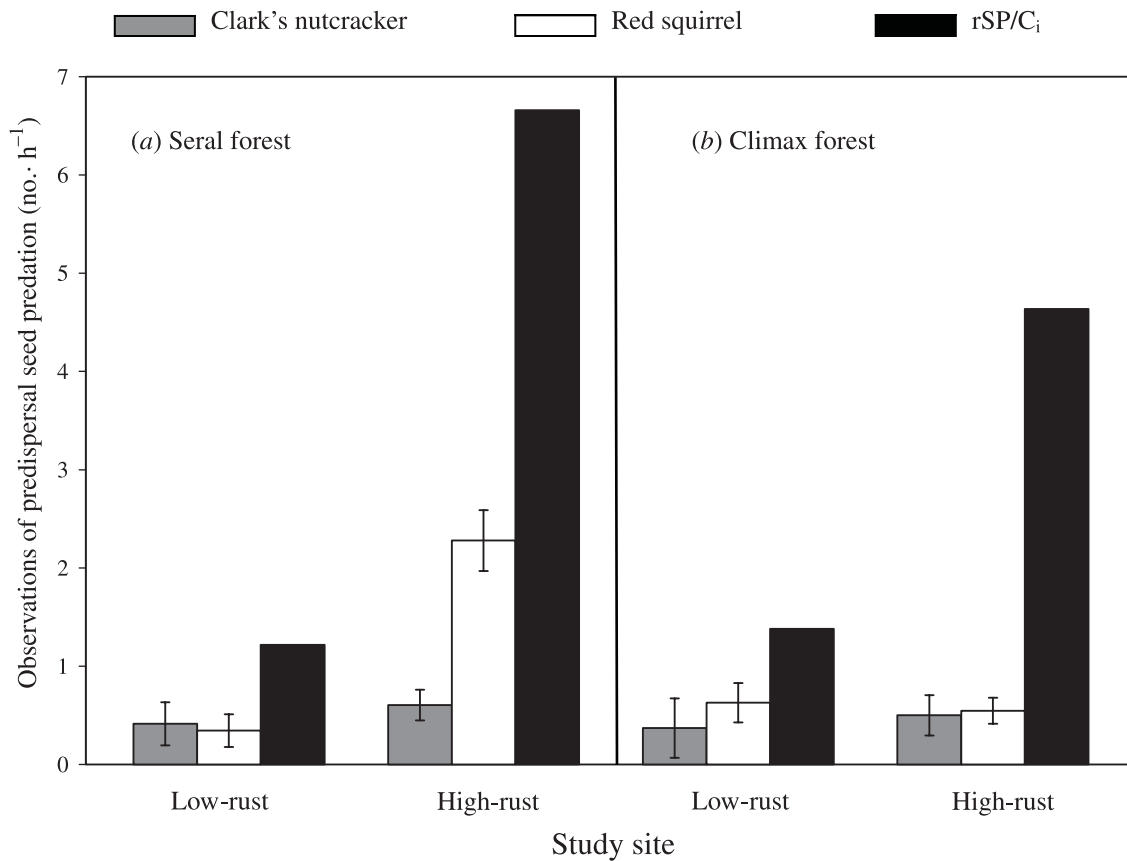
## Discussion

### Effects of blister rust on cone density, pre-dispersal survival, and seed dispersal

We originally hypothesized that (1) whitebark pine stands with higher levels of blister rust infection and damage will have lower cone densities than similar stands with lower levels of rust infection and damage, (2) stands with lower cone densities will have a smaller proportion of cones surviving to time of seed dispersal, and (3) stands with a lower proportion of cones surviving will be less likely to have seeds dispersed by nutcrackers. All three of these hypotheses



**Fig. 3.** Comparison of seed predator foraging observations (mean no./h  $\pm$  SE) for low- and high-blister rust-damaged whitebark pine sites in (A) seral and (B) climax forests in Montana and Idaho. Clark's Nutcracker values are for predispersal seed foraging observations only.  $rSP/C_i$  (relative rate of seed predation) is the combined seed predator foraging observation rate scaled to the initial (mid-July) number of cones (observations $\cdot$ h $^{-1}$  $\cdot$ cone $^{-1}$ ) and multiplied by 1000 for graphical presentation.



were supported by data from our four study sites in the Bitterroot and Salmon National Forests in 2001, a year of generally good cone production. The low cone production of 2002 actually supported these hypotheses as well, but in a more global sense: When cone production in general is low, few seeds are likely to survive to be dispersed if the community of seed predators is intact.

Seed dispersal of whitebark pine by Clark's Nutcracker varied among the four 1 ha forest study sites in western Montana and eastern Idaho. The differences in seed dispersal activity in 2001 corresponded to differences in stand conditions resulting from tree damage by blister rust, proportion of dead whitebark pine trees (Table 2), and relative differences in seed predator occurrence (Fig. 3), and not to differences in topography, tree species composition, number of cone-producing whitebark pine, or cone production due to DBH (Table 1). Blister rust infection of whitebark pine reduces cone density within a stand by killing cone-bearing branches and mature trees (McDonald and Hoff 2001). The two high-rust sites, characterized by significantly higher infection levels, crown damage, and mortality, had fewer cones per hectare and fewer initial (mid-July) cones per tree in both years of the study (Table 2).

Faster cone depletion rates were associated with greater rust damage (Tables 2 and 3). In 2001, at the time of seed dispersal in the climax forests, the low-rust site had 50% of

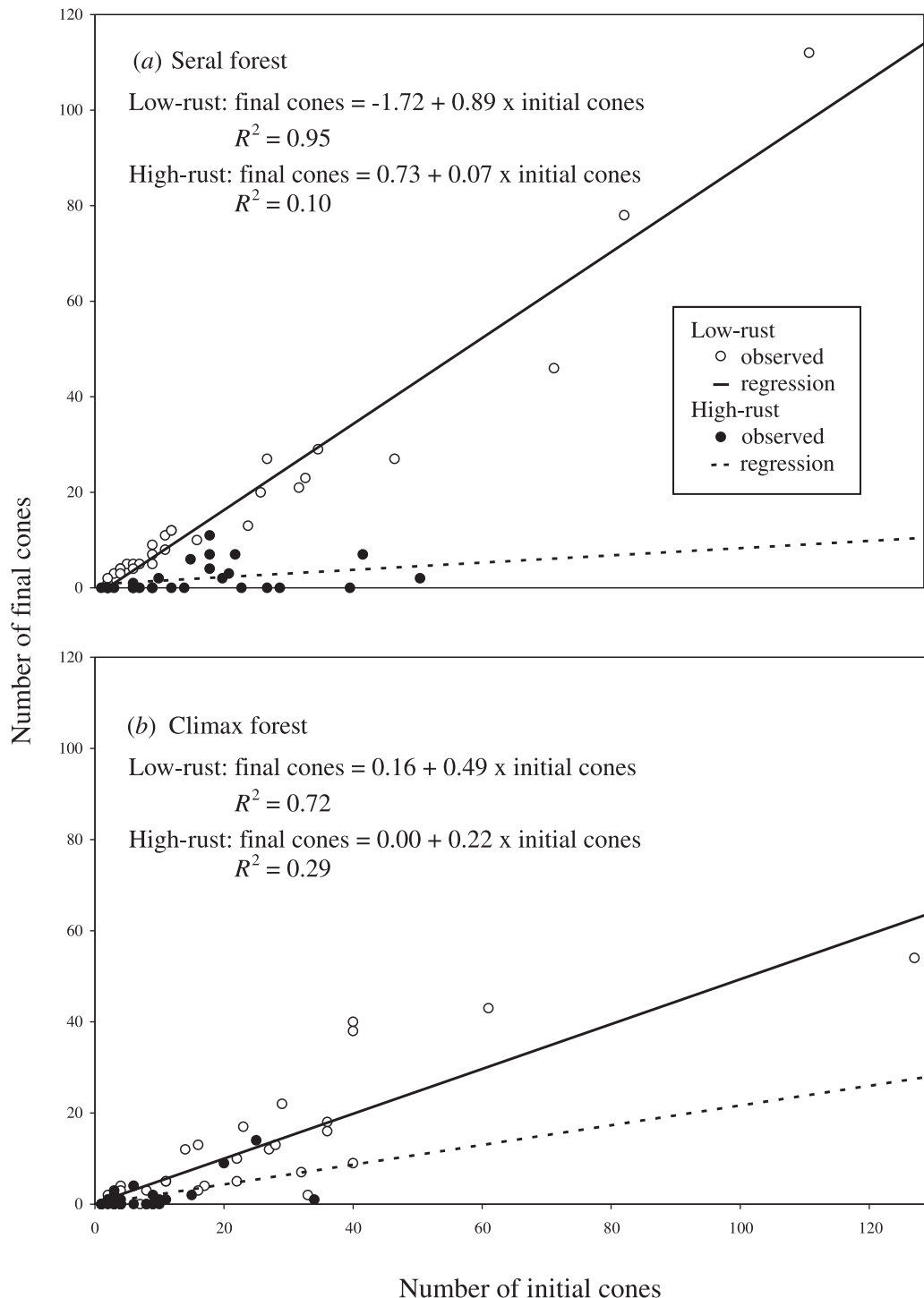
its cones remaining while the high-rust site had only 22% (Table 3). Likewise, 81% of the initial cones were available for seed dispersal in the seral low-rust site, but only 12% in the high-rust site (Table 3). Similar to our results, in a seral forest without blister rust during a high whitebark pine cone production year, Hutchins and Lanner (1982) reported only 50% cone depletion by the time of seed dispersal.

The relationship between the final and initial number of cones was also fundamentally different between low- and high-rust sites. In the low-rust sites, most of the variation in final cone number was explained by the initial cone number, but in the high-rust sites, the majority of this variation was left unexplained (Fig. 4). We believe that the accelerated rate of cone depletion and weak relationship between initial and final cone number in the high-rust sites is due, in part, to the higher mortality and blister rust levels in those sites. Mortality of cone-bearing branches by either crown kill or tree death from blister rust or mountain pine beetle caused a decrease in cone production without directly affecting seed predators, resulting in an increased seed predator to initial cone ratio. Furthermore, in both the high and low cone production years, the relationship between the relative rate of seed predation and the number of final cones was the same; as the ratio increased, the number of cones left at time of seed dispersal decreased (Fig. 6).

In the high-rust sites, fewer initial cones and faster rates



**Fig. 4.** Simple linear regression analysis comparing cone survival (the number of final cones against the number of initial cones) for low and high blister rust-damaged whitebark pine sites in (A) seral and (B) climax forests in Montana and Idaho in 2001. Initial refers to the number of seed cones counted on each tree in mid-July and final refers to the number remaining at time of seed dispersal in late August.

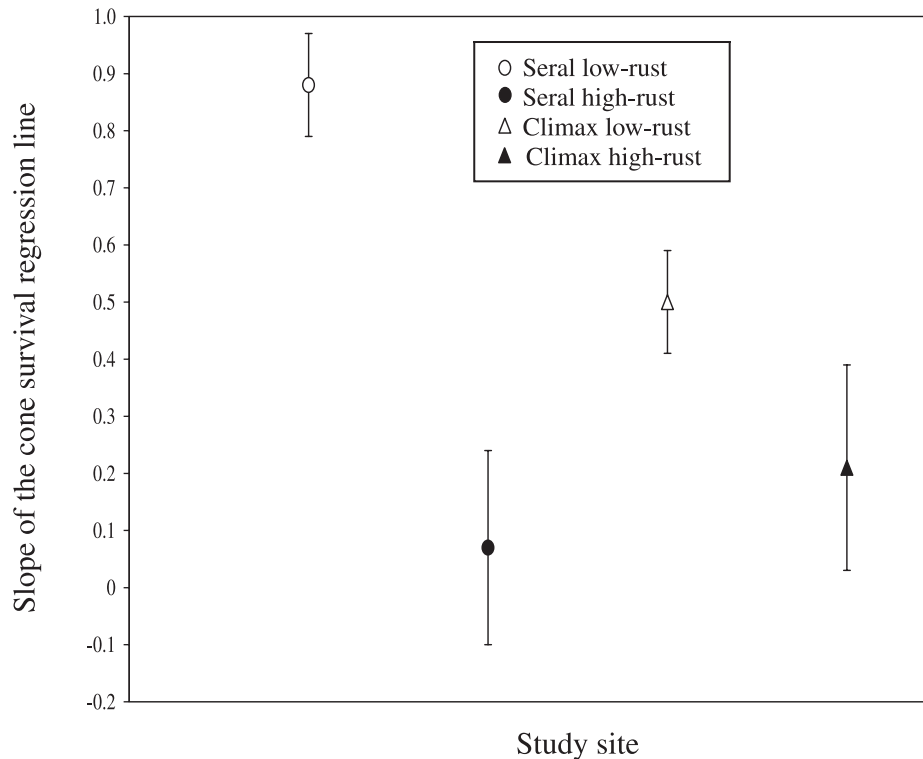


of cone depletion resulted in significantly fewer cones per tree and lower cone densities by the time nutcrackers began harvesting seeds for caching (Table 3). Cone densities were simply not high enough to accommodate both predispersal seed predation by nutcracker foraging and red squirrel cone harvesting with adequate seeds remaining for dispersal. Nutcrackers were infrequent visitors to the high-rust sites at the

time of seed dispersal in 2001, and in 2002, they were completely absent during this critical period. In 2 years of study at two high-rust sites, we observed nutcracker seed dispersal from only one site in 1 year, and this occurred at the high-rust site with the lowest seed predator to cone ratio.

Ultimately, initial cone density, and thus cone survival, influences the likelihood of whitebark pine seed dispersal

**Fig. 5.** Tukey–Kramer multiple comparisons test of cone survival regression slopes (the number of final cones against the number of initial cones) for four whitebark pine study sites in Montana and Idaho. Bars are 95% comparison intervals. Regression slopes whose intervals do not overlap are significantly different at  $\alpha = 0.05$ .



by Clark's Nutcracker. In this study, lower predispersal cone survival meant that there was a much lower chance of observing a nutcracker pouch and disperse seeds from a stand (Table 3). Therefore, the likelihood that a Clark's Nutcracker will disperse seeds from a given area appears to be inversely related to blister rust infection and damage at the stand level.

#### Trends in nutcracker foraging behavior

Our results raise questions about the impact of lower cone densities in formerly productive whitebark pine communities on Clark's Nutcracker foraging behavior both in the short and long term. Although some cones remained on trees in the high-rust sites, nutcracker seed dispersal was rarely observed and at only one high-rust site during the 2 year study. From the standpoint of foraging efficiency, it is likely that nutcrackers prefer whitebark pine communities with the highest cone densities for their caching activities. Previous studies show that nutcrackers tend to be sensitive to rates of energy gain, and adjust their foraging behavior accordingly (Tomback 1978; Vander Wall 1988). The possibility that seeds from isolated trees will eventually be dispersed by nutcrackers still remains; nutcrackers tend to continue to harvest and cache seeds late into the fall, moving through whitebark pine communities and then lower elevation communities with other relatively large-seeded conifers, such as ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) (Tomback 1978; Torick 1995). However, the remaining cones are more likely to be taken by red squirrels.

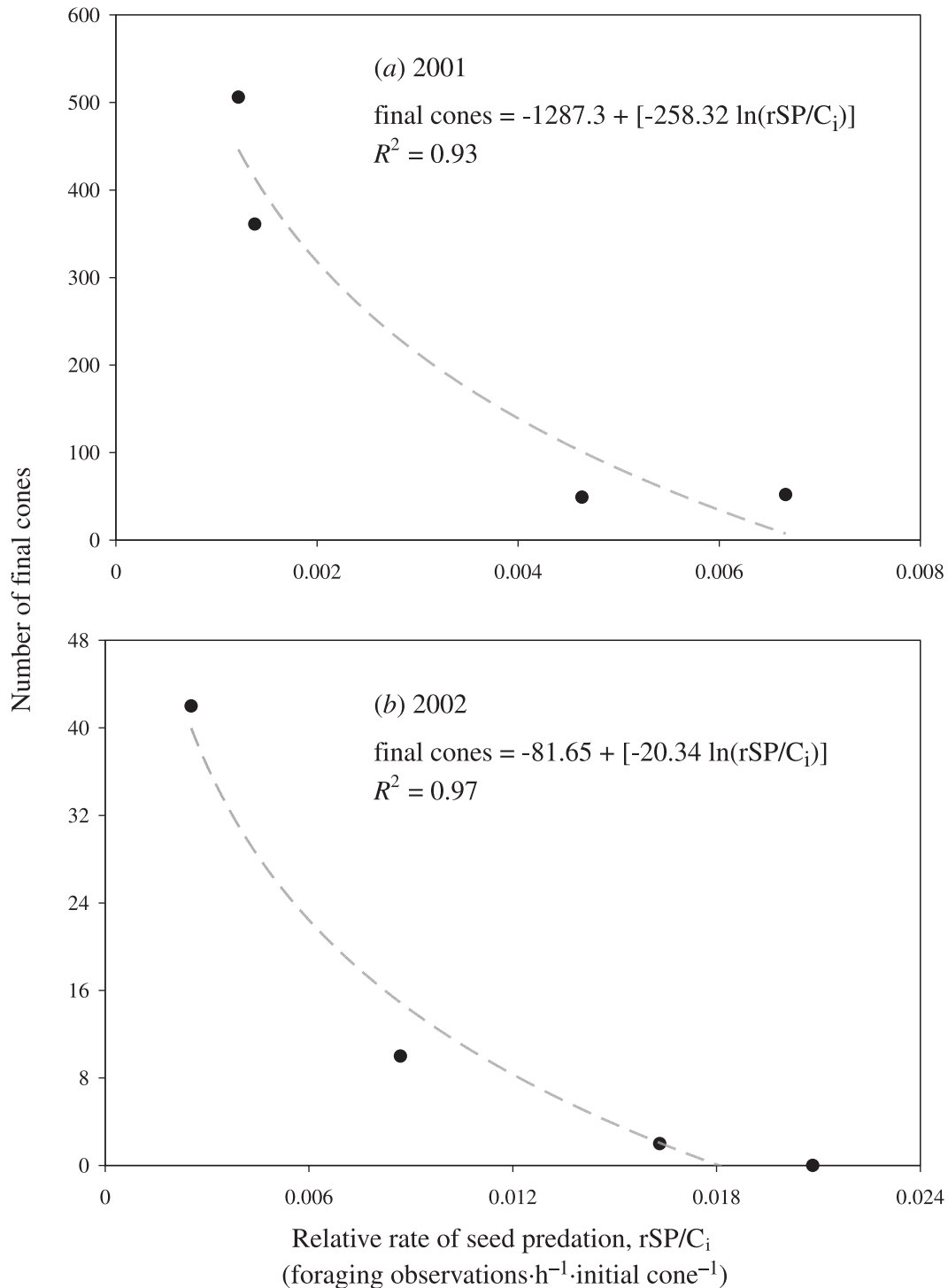
As the densities of cones decline in whitebark pine communities with more trees damaged and killed by both blister

rust and mountain pine beetle, it is likely that nutcracker visits will decline over time. Tomback and Kendall (2001) suggest that losses of whitebark pine will ultimately lead to declining carrying capacity for Clark's Nutcracker, lowered nutcracker populations, and possibly altered use of subalpine zone forest communities for seed caching. Because whitebark pine is essentially an obligate mutualist of the nutcracker, this trend would greatly reduce the possibility of future natural regeneration, even in areas with some cone production.

#### Trends in red squirrel populations

Reduced cone densities of whitebark pine in the high-rust study sites did not reduce the frequency of seed predator observations (Fig. 3). In fact, when the overall rates of seed predation (rSP) were scaled to initial cone density ( $C_i$ ), the relative rates of seed predation ( $rSP/C_i$ ) were much greater in the high-rust sites. When the adjacent forested areas burned in 2000, densities of red squirrels may have increased in the Bitterroot study area but not in all forest types: We observed more squirrels at the seral high-rust study site than we did at the low-rust site, but squirrel observations at the climax high- and low-rust sites were not different (Fig. 3). This effect was described for red squirrels in the Greater Yellowstone Area following the 1988 fires: Squirrels packed into the nearby unburned whitebark pine forest, and the mean linear abundance of active middens increased (Podruzny et al. 1999). With greater numbers of seed predators, the likelihood of seeds surviving to be dispersed drops. It remains to be seen whether the numbers of red squirrels and other seed predators adjust to available

**Fig. 6.** Regression analysis of the number of final cones against the relative rate of seed predation in four 1 ha whitebark pine study sites in Montana and Idaho in (A) 2001 and (B) 2002. Final refers to the number of cones remaining in a site at time of seed dispersal (late August). The relative rate of seed predation ( $rSP/C_i$ ) is the number of nutcracker and red squirrel seed and (or) cone harvesting observations per hour divided by the initial (mid-July) number of cones in each site. Dashed lines are the regression lines for the best-fitting equations given above. Note the different scales on the y and x axes in (A) and (B).



habitat over time after disturbance, returning to lower densities.

Another question is whether red squirrels decrease in numbers as whitebark pine seed production declines, given that carrying capacity diminishes. Red squirrels are the

most efficient predator on whitebark pine seeds because they remove cones from trees at a rapid rate, depleting the numbers available for nutcrackers (Hutchins and Lanner 1982). Previous studies in the Greater Yellowstone Area have shown that red squirrel densities increase as the basal

**Table 3.** Predispersal cone survival, final cone count, and Clark's Nutcracker (*Nucifraga columbiana* (Wilson, 1811)) occurrence in paired whitebark pine (*Pinus albicaulis* Engelm.) study sites in Montana and Idaho.

Site variable	Study sites			
	Seral forest		Climax forest	
	Low-rust	High-rust	Low-rust	High-rust
Whitebark pine cones				
2001				
Final density (no./ha)*	506	52	361	49
Survival (percentage of initial cones) <sup>†,‡</sup>	81a	12b	50c	22d
Mean final number (no./tree) <sup>*§</sup>	18.1e (4.7)	1.9f (0.6)	12.0g (2.6)	1.5h (0.5)
2002				
Final density (no./ha)*	10	2	42	0
Survival (percentage of initial cones) <sup>†</sup>	14	4	53	0
Mean final number (no./tree) <sup>*</sup>	0.36 (0.19)	0.07 (0.07)	1.4 (0.32)	0
Clark's Nutcracker observations (2001)				
Post seed ripening (no./h) <sup>§,  </sup>	4.36i (1.28)	1.85j (0.50)	1.92k (0.57)	0.39l (0.16)
Seed dispersal (no./h) <sup>¶</sup>	1.0 (0.54)	0.2 (0.09)	0.85 (0.37)	0

**Note:** Paired study sites (low-rust and high-rust) with the same letter are *not* different ( $P > 0.05$ ). Standard errors for site means are given in parentheses.

\*Final refers to the number of seed cones counted at time of seed dispersal.

<sup>†</sup>Survival was calculated as the number of cones remaining at time of seed dispersal divided by the initial mid-July number.

<sup>‡</sup>Paired study sites were compared with  $\chi^2$  tests.

<sup>§</sup>Paired study sites were compared by independent-sample  $t$  tests.

<sup>||</sup>Includes all observations of Clark's Nutcracker once seed dispersal had begun.

<sup>¶</sup>Observations of nutcrackers pouching and dispersing seeds.

area of lodgepole pine increases in whitebark pine habitat, suggesting the importance of alternative food sources for squirrels (Mattson and Reinhart 1997). Although the large seeds of whitebark pine are preferred by red squirrels, lodgepole pine and other conifers produce cones in years when whitebark pine does not, ensuring a dependable food supply. Research indicates that red squirrels occur in climax whitebark pine stands at lower densities in general than they do in mixed coniferous forest, and their presence is associated with large whitebark pine cone crops (Reinhart and Mattson 1990; Mattson and Reinhart 1997). These data suggest that even as whitebark pine declines in mixed conifer associations, squirrels may remain, and that squirrels may be attracted to climax stands when cones are produced. Thus, seed predation by red squirrels may not necessarily decline as whitebark pine basal area and cone production declines.

### Management implications

A natural restoration approach that relies on natural selection and bird dispersal of whitebark pine seeds into disturbed forest openings or into open climax forest communities is a lower cost management alternative for whitebark pine restoration than a nursery-production approach. For this natural approach to be effective: (1) genetically resistant trees must be located in stands with high levels of blister rust damage and mortality that are adjacent to disturbed forest openings or are within climax communities; (2) some cones of the rust-resistant trees must survive until their seeds ripen and are dispersed by nutcrackers; and (3) surviving seedlings in disturbed openings or in climax forests must result in offspring generations with higher frequencies of rust resistance than parental generations (Hoff

et al. 1994). Assuming that rust-resistant parental trees survive mountain pine beetle outbreaks, which are currently at extremely high levels (Gibson 2006), the natural restoration approach could enable whitebark pine populations to survive the challenges of blister rust and fire suppression, leading to increasingly greater proportions of rust-resistant whitebark pine trees over time (Hoff et al. 1994). Forest openings, which are created by wildfire or silvicultural treatments, reduce the density of competing species and create open areas for nutcracker caching, are essential to this process in successional whitebark pine communities. Thus, the primary management actions required under the natural restoration approach would be to open up areas suitable for nutcracker caching or permit natural disturbances when feasible.

The results of our study show that cone predation in our two high rust-damaged sites greatly limits seed dispersal opportunities and cast doubt on whether natural selection can lead to new generations of whitebark pine with higher frequencies of genetically rust-resistant individuals. Future studies with long-term monitoring will determine if our findings are supported over time among the various ecosystems where whitebark pine occurs.

Factors influencing whitebark pine predispersal seed survival and seed dispersal are likely to be more complex than assumed for this study. Two potential seed source stands that are similar in their density of cone-producing rust-resistant trees may be very different in terms of their likelihood of predispersal seed survival and seed dispersal based on their spatial configuration and neighboring conditions on the landscape. It is therefore imperative that during the site selection process of a restoration project, site-specific and landscape conditions are considered to select the resto-

ration approach that ensures the greatest chance for success at the least expense.

If the processes we found also occur in other areas of high rust damage, whitebark pine regeneration may be diminished because of high cone predation by red squirrels and nutcrackers. With white pine blister rust spreading geographically, with infection levels and mortality increasing in infected stands each year, and with the recent upsurges in mortality from mountain pine beetle, whitebark pine will be maintained on the landscape in large portions of its range *only* by means of restoration activities, such as thinning, burning, and planting rust-resistant seeds or seedlings. Stands not yet heavily damaged, however, will still have potential as natural seed sources. We are now challenged to determine the critical factors on different landscape scales that determine the probability of seed dispersal for different whitebark pine community types and different stand conditions, and to make use of any natural regeneration potential. It is likely that a small proportion of these naturally regenerated seedlings should have some genetic resistance to blister rust.

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## References

- Arno, S.F. 1986. Whitebark pine cone crops — A diminishing source of wildlife food? *West. J. Appl. For.* **1**: 92–94.
- Arno, S.F. 2001. Community types and natural disturbance processes. *In* Whitebark pine communities: ecology and restoration. *Edited by* D.F. Tomback, S.F. Arno, and R.E. Keane. Island Press, Washington, D.C. pp. 74–88.
- Arno, S.F., and Allison-Bunnell, S. 2002. Flames in our forest: Disaster or renewal? Island Press, Washington, D.C.
- Arno, S.F., and Weaver, T. 1990. Whitebark pine community types and their patterns on the landscape. *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. Gen. Tech. Rep. INT-GTR-270. pp. 97–105.
- Bingham, R.T. 1983. Blister rust resistant western white pine for the Inland Empire: the story of the first 25 years of the research and development program. USDA For. Serv. Gen. Tech. Rep. INT-GTR-146.
- Campbell, E.A., and Antos, J.A. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. *Can. J. For. Res.* **30**: 1051–1059. doi:10.1139/cjfr-30-7-1051.
- Gibson, K. 2006. Mountain pine beetle conditions in whitebark pine stands in the Greater Yellowstone Ecosystem, 2006. USDA Forest Service, Northern Region, Missoula, Mont. Report 06-03.
- Hoff, R.J. 1992. How to recognize blister rust infection on whitebark pine. USDA For. Serv. Res. Note INT-RN-406.
- Hoff, R.J., Bingham, R.T., and McDonald, G.I. 1980. Relative blister rust resistance of white pines. *Eur. J. For. Pathol.* **10**: 307–316.
- Hoff, R.J., Hagle, S.K., and Krebill, R.G. 1994. Genetic consequences and research challenges of blister rust in whitebark pine forests. *In* Proceedings — International Workshop on Subalpine Stone Pines and Their Environment: the Status of Our Knowledge. *Edited by* W.C. Schmidt and F.K. Holtmeier. USDA For. Serv. Gen. Tech. Rep. 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: ecology and restoration. *Edited by* D.F. Tomback, S.F. Arno, and R.E. Keane. Island Press, Washington, D.C. pp. 346–366.
- Hummer, K.E. 2000. History of the origin and dispersal of white pine blister rust. *Hortechonology*, **10**: 515–517.
- 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. doi:10.1007/BF00384487.
- Keane, R.E., and Arno, S.F. 1993. Rapid decline of whitebark pine in Western Montana: Evidence from 20-year remeasurements. *West. J. Appl. For.* **8**: 44–47.
- Kendall, K.C., and Keane, R.E. 2001. Whitebark pine decline: infection, mortality, and population trends. *In* Whitebark pine communities: ecology and restoration. *Edited by* D.F. Tomback, S.F. Arno, and R.E. Keane. Island Press, Washington, D.C. pp. 221–242.
- Logan, J.A., and Powell, J.A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *Am. Entomol.* **47**: 160–172.
- Mattson, D.J., and Reinhart, D.P. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. *J. Appl. Ecol.* **34**: 926–940. doi:10.2307/2405283.
- Mattson, D.J., Kendall, K.C., and Reinhart, D.P. 2001. Whitebark pine, grizzly bears, and red squirrels. *In* Whitebark pine communities: ecology and restoration. *Edited by* D.F. Tomback, S.F. Arno, and R.E. Keane. Island Press, Washington, D.C. pp. 121–136.
- McCaughy, W.W., and Schmidt, W.C. 1990. Autecology of whitebark pine. *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. Gen. Tech. Rep. INT-GTR-270. pp. 85–96.
- McDonald, G.I., and Hoff, R.J. 2001. Blister rust: an introduced plague. *In* Whitebark pine communities: ecology and restoration. *Edited by* D.F. Tomback, S.F. Arno, and R.E. Keane. Island Press, Washington, D.C. pp. 193–220.
- McDonald, G.I., Richardson, B.A., Zambino, P.J., Klopfenstein, N.B., and Kim, M.S. 2006. *Pedicularis* and *Castilleja* are natural hosts of *Cronartium ribicola* in North America: a first report. *For. Pathol.* **36**: 73–82. doi:10.1111/j.1439-0329.2006.00432.x.

- Microsoft Corporation. 2003. Microsoft Office Excel 2003. Microsoft Corporation, Redmond, Wash.
- Mirov, N.T. 1967. The genus *Pinus*. The Ronald Press, New York.
- Podruzny, S.R., Reinhart, D.P., and Mattson, D.J. 1999. Fire, red squirrels, whitebark pine, and Yellowstone grizzly bears. *Ursus*, **11**: 131–138.
- Reinhart, D.P., and Mattson, D.J. 1990. Red squirrels in the whitebark pine zone. *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. Gen. Tech. Rep. INT-GTR-270. pp. 256–263.
- Rizzo, D.M., and Garbelotto, M. 2003. Sudden oak death: endangering California and Oregon forest ecosystems. *Front. Ecol. Environ.* **1**: 197–204.
- Samano, S., and Tomback, D.F. 2003. Cone opening phenology, seed dispersal, and seed predation in southwestern white pine (*Pinus strobiformis*) in southern Colorado. *Ecoscience*, **10**: 319–326.
- Smith, C.C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecol. Monogr.* **40**: 349–371. doi:10.2307/1942287.
- Sokal, R.R., and Rohlf, F.J. 1995. *Biometry*. 3rd ed. W.H. Freeman, San Francisco, Calif.
- SPSS, Inc. 1999. SPSS 10.0 for Windows. SPSS, Inc., Chicago, Ill.
- Tomback, D.F. 1978. Foraging strategies of Clark's Nutcracker. *Living Bird*, **16**: 123–161.
- Tomback, D.F. 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. *Madrono*, **33**: 100–110.
- Tomback, D.F. 1998. Clark's Nutcracker (*Nucifraga columbiana*). *In* The birds of North America. *Edited by* A. Poole and F. Gill. The Birds of North America, Inc., Philadelphia, Penn. Number 331.
- Tomback, D.F., and Kendall, K.C. 2001. Biodiversity losses: the downward spiral. *In* Whitebark pine communities: ecology and restoration. *Edited by* D.F. Tomback, S.F. Arno, and R.E. Keane. Island Press, Washington, D.C. 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 post-fire regeneration of whitebark pine: the Sundance Burn of northern Idaho (U.S.A.). *Conserv. Biol.* **9**: 654–664. doi:10.1046/j.1523-1739.1995.09030654.x.
- Tomback, D.F., Arno, S.F., and Keane, R.E. (Editors). 2001a. The compelling case for management intervention. *In* Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C. pp. 3–25.
- Tomback, D.F., Anderies, A.J., Carsey, K.S., Powell, M.L., and Mellmann-Brown, S. 2001b. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. *Ecology*, **82**: 2587–2600. doi:10.2307/2679938.
- Torick, L. 1995. The interaction between Clark's Nutcracker and ponderosa pine, a "wind-dispersed" pine: energy efficiency and multi-genet growth forms. M.A. thesis, University of Colorado, Denver, Colorado.
- Vander Wall, S.B. 1988. Foraging of Clark's Nutcracker on rapidly changing pine seed resources. *Condor*, **90**: 621–631. doi:10.2307/1368351.
- Zeglen, S. 2002. Whitebark pine and white pine blister rust in British Columbia, Canada. *Can. J. For. Res.* **32**: 1265–1274. doi:10.1139/x02-049.