Forest Ecology and Management 280 (2012) 166–175

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Ecology of whitebark pine populations in relation to white pine blister rust infection in subalpine forests of the Lake Tahoe Basin, USA: Implications for restoration

Patricia E. Maloney [a,*], Detlev R. Vogler [b], Camille E. Jensen [a], Annette Delfino Mix [b]

[a] Department of Plant Pathology, Tahoe Environmental Research Center, University of California, One Shields Avenue, Davis, CA 95616, USA
[b] USDA, Forest Service, Pacific Southwest Research Station, Institute of Forest Genetics, 2480 Carson Road, Placerville, CA 95667, USA

ARTICLE INFO

Article history:
Received 15 February 2012
Received in revised form 15 May 2012
Accepted 20 May 2012
Available online 17 July 2012

Keywords:
Branch cankers
Cone production
Cronartium ribicola
Demographics
Environmental conditions
Fecundity

ABSTRACT

For over a century, white pine blister rust (WPBR), caused by the introduced fungal pathogen, *Cronartium ribicola* J.C. Fisch., has affected white pine (Subgenus *Strobus*) individuals, populations, and associated forest communities in North America. We surveyed eight populations of whitebark pine (*Pinus albicaulis* Engelm.) across a range of environmental conditions in subalpine forests of the Lake Tahoe Basin, California and Nevada, to determine how WPBR is influencing host fecundity (i.e., female cone production and recruitment), survival, and current population trends. In this region and throughout its range whitebark pine is an important component of subalpine ecosystems. In high-elevation forests of the Lake Tahoe Basin, the primary negative effect of this rust pathogen on whitebark pine is infection and mortality of cone-bearing branches.

Mean incidence of WPBR among whitebark pine populations was 35% and ranged from 1% to 65%. Given the high disease incidence, relationships were found between WPBR infection and reproductive output. Percent of individuals infected per population ($R^2 = 0.78$), average number of WPBR-infected branches per population ($R^2 = 0.71$), and severity of stem girdling ($R^2 = 0.76$) were all negatively related with cone production. A positive relationship was found between disease severity (i.e., extent of stem girdling) and available water capacity and a negative relationship was found between disease severity and % sand content. Environmental conditions, including soil properties, may affect pathogen growth and potentially influence the rate at which green infected trees lose the ability to produce female cones. Demographic trends for 7 of 8 whitebark pine populations were stable, with estimates of geometric growth rate (λ) $\geqslant$ 1.0. Population stability is a function of adequate population sizes, mixed-size structure, high survivorship, and moderate fecundity. Results show that WPBR is adversely affecting fecundity but having little effect on survivorship. Restoration strategies are designed to facilitate whitebark pine recruitment and deploy genetically diverse seedling material and potentially WPBR-resistant phenotypes. Our study highlights a need for long-term demographic data and monitoring of WPBR-infection to better understand population consequences and host responses in the future.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Consequences of invasive pathogens on forest tree populations in North America can be significant – from reduced population sizes to shifts in community structure and diversity (Paillet, 2002; Ellison et al., 2005; Burdon et al., 2006; Lovett et al., 2006; Tomback and Achuff, 2010). Such changes may occur over a few years to decades. Individual- and species-level effects include tree mortality, reduced fecundity and fitness, declining populations, as well as selective pressures on and evolutionary changes in host resistance (Gilbert, 2002; Paillet, 2002; van Mantgem et al., 2004; Maloney et al., 2005; Garnas et al., 2011). In addition, community-level changes can alter species composition, biodiversity, and biotic interactions (Tingley et al., 2002; Ellison et al., 2005; McKinney et al., 2009).

Invasive forest pathogens can have both subtle and profound effects on host reproduction, survival, and growth. The introduced fungal pathogen *Cronartium ribicola* J.C. Fisch. is a primary management concern in all five-needle white pine ecosystems in western North America. *C. ribicola* (cause of white pine blister rust; WPBR) was introduced into British Columbia around 1910 and arrived in northern California around 1929, the southern Sierra Nevada by 1961 (Smith, 1996), the Mt Rose area (north of Lake Tahoe) in the 1970s (Smith et al., 2000) and the Lake Tahoe region during the 1980s (K. Jones, pers. comm., USDA Forest Service). WPBR wave

* Corresponding author.
E-mail address: pemaloney@ucdavis.edu (P.E. Maloney).

0378-1127/$ - see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2012.05.025

years (i.e., infection periods) in the Mediterranean climate of California, particularly in lower-elevation forests of the Sierra Nevada on the western slopes, have a frequency of 7–14 years, and in some favorable microclimates possibly <7 years (Kinloch et al., 1996; Vogler unpublished data; Maloney personal observation). In high-elevation forests of the Sierra Nevada the current WPBR-infection observed on whitebark pine is possibly the result of initial infection approximately 25–40 years ago (Smith et al., 2000; Duriscoe and Duriscoe, 2002; D. Burton, pers. comm., USDA, Forest Service). These infections in the higher elevations may very well be the result of only one wave year. *C. ribicola* is a heteroecious rust that must alternately infect both white pines, the aecial host(s), and *Ribes* or other non-*Ribes* alternate hosts, the telial hosts, to complete its life cycle (Geils et al., 2010). Negative effects of the pathogen occur mainly on the pine host, in which branch infections are perennial (Kinloch et al., 1996; Geils et al., 2010). In California and other regions, WPBR may adversely affect reproductive output (female cone production) by infecting and killing cone-bearing branches (Maloney, 2000; McKinney et al., 2009; Maloney unpublished data). This species-level effect can poten-

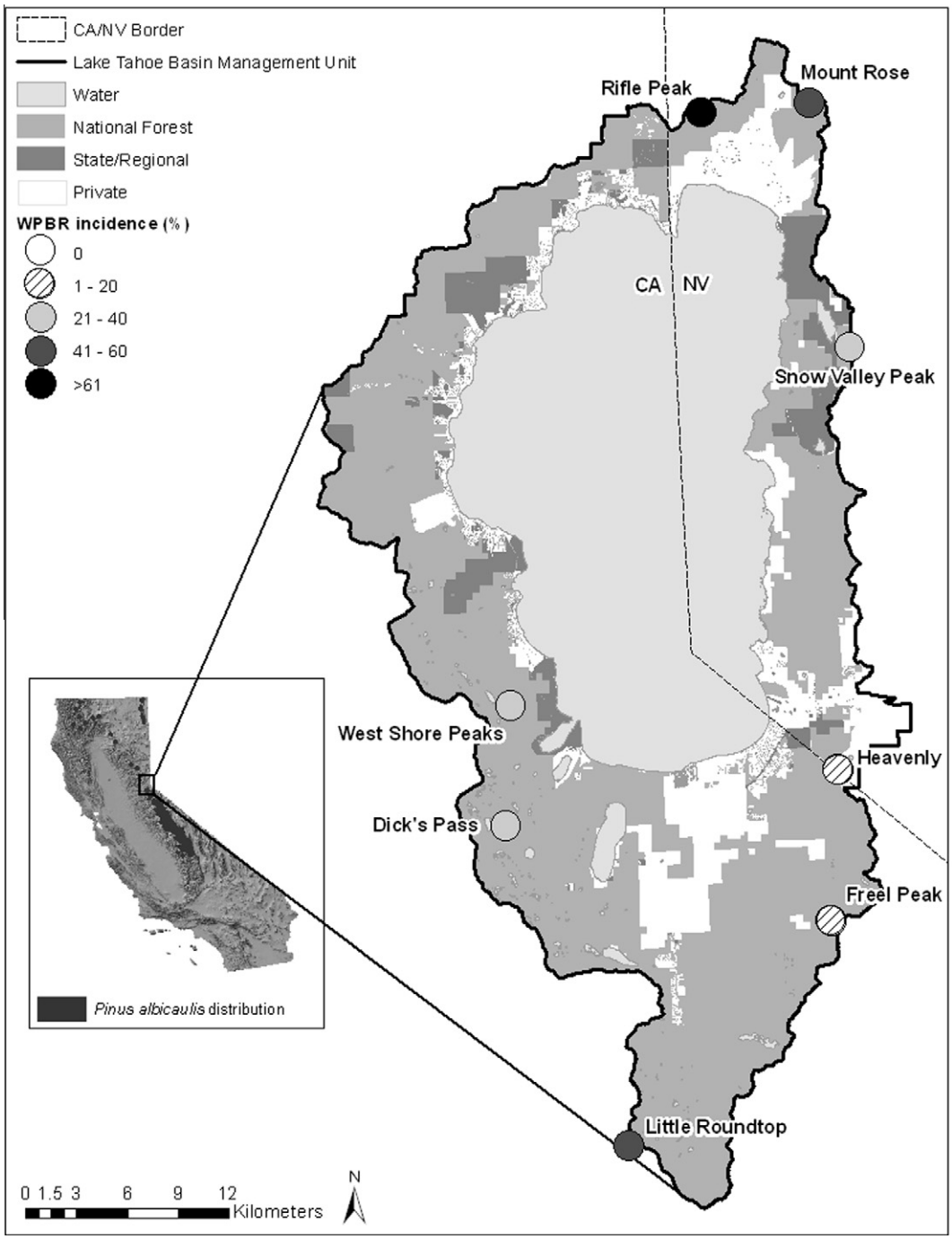


Fig. 1. Location of study area and whitebark pine populations in the Lake Tahoe Basin. Each location studied (circles) shows the average percent WPBR incidence for that population. *Pinus albicaulis* distribution in California is shown in insert (distribution map source: USGS (1999) Digital representation of "Atlas of United States Trees" by Elbert L. Little, Jr.).

tially have negative consequences on important community-level interactions, such as resource availability (e.g., cones and seeds) and dispersal of whitebark pine (Tomback et al., 2001 and chapters therein; McKinney et al., 2009).

Whitebark pine is an important tree species in subalpine watersheds throughout most of its range in Western North America. Its role in ecosystem function and services comprises multiple considerations: forest cover, food resource, watershed protection, protracting snowmelt, soil and snow stabilization, biodiversity, wildlife habitat, and greenhouse gas sequestration, as well as recreational, economic, and aesthetic values (Hutchins and Lanner, 1982; Farnes, 1990; Tomback et al., 2001; McKinney et al., 2009; Tomback and Achuff, 2010). Notable to whitebark pine is its wingless seed and its almost exclusive reliance on Clark's nutcracker, *Nucifraga columbiana* (Wilson), family Corvidae, for dispersal (Hutchins and Lanner, 1982; Lanner, 1982; Tomback, 1982; Hutchins, 1990). In the Northern Rocky Mountains (Northern Divide, Bitterroot Mountains, and Greater Yellowstone region), McKinney et al. (2009) found negative relationships between nutcracker occurrence and probability of seed dispersal and nutcracker occurrence and WPBR-infection of whitebark pine; they concluded that this bird-pine mutualism may be at risk in severely WPBR-infected sites. At these locations Mckinney et al. (2009) found high levels of WPBR ranging from 49% to 82% and mortality ranging from 14% to 68%.

In California, moderate levels of WPBR (% of trees infected per stand) are found on whitebark pine in the north-central Sierra Nevada (mean = 24%; range: 0 – 76%) (Maloney, 2011) and are a threat to this species in the Lake Tahoe Basin (Maloney, 2000). An important question is whether WPBR is affecting population parameters such as fecundity (by damaging and killing cone-bearing branches) and survival. We address this by (1) assessing whitebark pine population structure and trends, (2) determining levels of WPBR infection in populations and on individual trees, and (3) relating environmental conditions to host and pathogen characteristics. Restoration and management of whitebark pine is a current focus throughout the species range (Tomback et al., 2001; Schwandt, 2006; Keane and Parsons, 2010; Tomback and Achuff, 2010). Detailed ecological and epidemiological studies are essential to accurately assess WPBR impacts on whitebark pine populations and subalpine communities in western North America. The goal of our work was to provide baseline information on the population ecology, demography, and severity of WPBR infection on whitebark pine in the Lake Tahoe Basin. The baseline information and methods employed in this paper may become a foundation for monitoring and providing resource managers sufficient understanding of ecosystem status, trends, and vulnerabilities to develop appropriate restoration treatments.

2. Materials and methods

2.1. Study species and location

Whitebark pine, a principal component of high-elevation forests in California and Nevada, is continuously distributed in the Sierra Nevada, from Lake Tahoe south to Mt Whitney (2600–3600 m elevation). Whitebark pine's distribution is more fragmented in northern California from the Klamath region eastward to the Warner Mountains and in the southern Cascades (2200–2900 m). Whitebark pine's range extends northward into Oregon, Washington, British Columbia, and Alberta and eastward into northern Nevada, Idaho, Montana, and Wyoming (Critchfield and Little, 1966; Tomback and Achuff, 2010).

The Lake Tahoe Basin is located in the north-central Sierra Nevada at 120°W and 39°N within California and Nevada (Fig. 1). The Basin is flanked to the west by the Sierra Nevada crest and to the east by the Carson Range. The Lake Tahoe Basin Management Unit (LTBMU, USDA Forest Service) comprises 66,825 ha, ranging in elevation from 1890 m to 3292 m, with 85% of the Basin in National Forest. The climate is Mediterranean and characterized by warm, dry summers, and cool, wet winters. Most precipitation falls as snow between the months of November and April, with a strong gradient from west to east, with eastside locations influenced by the rainshadow effect of the Sierra Nevada. Average annual precipitation for subalpine forests is 1482 mm on the west slopes and 1046 mm in east-side locations (Table 2). Our study area is within the subalpine zone (2600–3200 m), which is a mix of whitebark pine, mountain hemlock (*Tsuga mertensiana*), lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*), red fir (*Abies magnifica*), and occasionally Jeffrey pine (*Pinus jeffreyi*). In some locations there are pure stands of whitebark pine. Mixed subalpine woodland is the most common forest type in the Basin's subalpine zone and covers approximately 10,000 ha (Manley et al., 2000). The geology of the region is dominated by igneous intrusive rocks, typically granodiorite, and igneous extrusive rocks, typically andesitic lahar, with small amounts of metamorphic rock (USDA NRCS, 2007). Study locations include a range of parent materials: andesite, granodiorite, tuff breccia, and volcanic (Table 2).

2.2. Population and pathogen sampling

During the summer of 2009, we selected eight study populations, with three permanent demographic plots per population, for a total of 24 plots. We define a population as an area in which gene flow (pollen and seed dispersal) occurs, which for lower mon-

Table 1
Stand, biological, and disease characteristics for eight locations of *Pinus albicaulis* in the Lake Tahoe Basin. Stands are listed clockwise from north, east, south, and west (reference Fig. 1).

Location	Rel. dens.	Density (inds.ha^{-1})	Basal area (m^2 ha^{-1})	Avg. no. stems cluster^{-1}	Cones (no. ha^{-1})	Recruit. (inds.ha^{-1})	WPBR (%)	Avg. no. branch cankers	Avg. stem girdle category	MPB (%)	Mortality (%)
Rifle Peak	0.96	446	16.7	6.8	960	44	65	4.89	1.35	1	2
Mt Rose	0.98	468	26.8	10.7	1477	199	56	4.99	1.00	3	3
Snow Valley Peak	0.99	458	17.7	8.3	2507	54	34	2.81	0.92	3	2
Heavenly	0.96	632	29.9	3.8	3144	296	13	0.50	0.17	4	3
Freel Peak	0.98	665	26.5	5.9	4632	173	1	0.06	0.02	2	4
Little Roundtop	0.95	508	18.6	10.0	2232	74	57	4.70	1.04	0	1
Dick's Pass	0.96	715	32.6	5.1	2349	158	38	2.76	0.60	1	4
West Shore Peaks	0.94	797	17.3	9.6	2353	114	19	1.19	0.39	1	3
Mean	0.97	586	23.3	7.5	2456	139	35.3	2.73	0.68	1.9	2.7
se	0.01	47	2.3	0.8	389	30	8.1	0.71	0.17	0.48	0.36

Notes: Relative density was calculated for each location as (total number of whitebark pine trees ⩾1.37 cm d.b.h.) ÷ (total number of all trees ⩾1.37 cm d.b.h.).

Table 2
Environmental summaries for 8 whitebark pine locations in the Lake Tahoe Basin.

Location	Elev. (m)	Ann. ppt. (mm)	T_{min} (°C)	T_{max} (°C)	Sept. GDD	AWC 0–50	% Sand content	Parent material
Rifle Peak	2819	1281	−7.4	22.7	13	3.48	70.8	Volcanic
Mt Rose	2711	1255	−7.5	22.6	58	2.75	90.6	Granodiorite
Snow Valley Peak	2740	891	−7.8	23.3	59	4.22	64.5	Volcanic
Heavenly	2848	782	−7.5	23.2	44	2.00	83.5	Granodiorite
Freel Peak	2865	1019	−8.8	21.6	0	2.51	88.7	Granodiorite
Little Roundtop	2875	1221	−8.0	21.5	3	2.93	66.2	Andesite/tuff breccia
Dick's Pass	2806	1686	−6.5	21.1	65	2.75	77.7	Granodiorite/volcanic
West Shore Peaks	2780	1538	−6.5	21.9	39	2.02	85.0	Granodiorite
Mean	2805	1208.7	−7.5	22.2	35.1	2.83	78.4	–
se	20.8	108.9	0.3	0.3	9.3	0.26	3.6	–

Notes: Climate averages for each population based on PRISM data for 30-year averages (Daly et al., 1994 and FHTET): Minimum temperature (January) and maximum temperature (July) in degrees celcius, total ppt = total annual precipitation in millimeters (mm), GDD = growing-degree days. AWC 0–50 = available water capacity in top 0–50 in. (inches of water per inch of soil) and % sand content (sand:silt:clay). Soil data source: USDA NRCS (2007).

tane conifers, has been estimated to be 3.98 ha (Neale, 1983; Adams and Birkes, 1988). However, for whitebark pine, seed can be dispersed long distances by Clark's nutcrackers, which may fly a few meters, a few hundred meters, or several kilometers to cache whitebark pine seed (Vander Wall and Balda, 1977; Tomback, 1978; Lanner, 1982; Hutchins and Lanner, 1982; Richardson et al., 2002a,b; Lorenz and Sullivan, 2009). Therefore, plot sampling for each population was done over landscapes ranging in size from 200 to 600 ha. Our plot network was established on National Forest and State Park lands surrounding Lake Tahoe (Lake Tahoe Basin Management Unit-LTBMU, Eldorado and Toiyabe National Forests, and Nevada State Parks).

Each of the eight populations was located in a distinct watershed and all were distributed around the Basin to capture variation in the physical environment (e.g., climate, geology, and topography). In each population a random starting point was chosen for the first plot and the second and third plots were sited 500–1000 m from the previous plot. The second and third plots were sited in a parallel or perpendicular direction so long as their locations remained within the subalpine forest type. Within a population, each of the three replicate plots was 40 m × 100 m (4000 m^2), with sampling covering approximately 1.2 ha (see Fig. 2). The following data were recorded for each demographic plot: GPS location, slope (in degrees), aspect, elevation (in meters), presence/absence of Clark's nutcracker, percent rock cover, signs of past fire (i.e., basal fire scar, bole scorch, lightning strike), slope position (ridge-top, upper slope, mid-slope, lower slope, valley bottom, or bench), and land-use history (e.g., historical logging, fire suppression, recent thinning, prescribed fire, wildland fire, recreation, unspecified).

Within each demographic plot, all whitebark pine ⩾1.37 m tall were measured for diameter at breast height (d.b.h. in cm). Seedlings and saplings (all stems <1.37 m in height) were also recorded. Tree positions (*x* and *y* coordinates from the centerline of the plot) were recorded and mapped. Individual tree data collected for status (live or dead), crown condition (rated 1–10 as follows: (1) ⩽10% dead, dying, damaged, or infected; (2) 11–20% dead, dying, damaged, or infected; (3) 21–30% dead, dying, damaged, or infected, etc.), and crown position (understory, suppressed, intermediate, codominant, dominant, or open-grown). Given the nature of Clark's nutcracker caching behavior, whitebark pine can often grow in clusters or clumps (Furnier et al., 1987). Cluster counts were made by counting the number of individual stems per cluster. Signs and symptoms of pathogens (including WPBR, dwarf mistletoe, and root diseases) and insects were recorded as well as abiotic agents of mortality (e.g., drought), where possible. Mountain pine beetle (MPB, *Dendroctonus ponderosae*) was confirmed when pitch tubes, frass, and characteristic galleries were present (Furniss and Carolin, 2002). In 2009 reproductive output was assessed, using binoculars, by counting the number of current and previous year's cones per tree (and then adding the two counts). Seedlings and saplings were counted and evaluated within each demographic plot by establishing three nested recruitment subplots (15 m × 15 m), for a total of nine regeneration plots/population (see Fig. 2). All recruitment was counted and identified to species. For whitebark pine recruitment, data were collected on basal diameter (cm), height (cm), crown condition (as evaluated above for trees), status (live or dead), disease condition (presence or absence of WPBR), and whorl count.

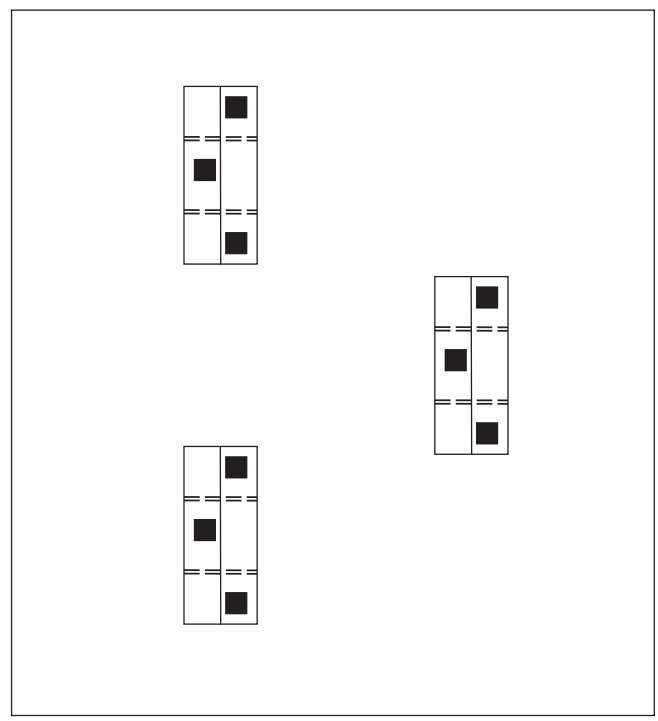


Fig. 2. Illustration of demographic plot layout for each population of whitebark pine. Each of the 3 plots per population were 40 m × 100 m (4000 m^2) with sampling covering approximately 1.2 ha. In white is the area in which all whitebark pine ⩾1.37 d.b.h. were measured and evaluated. In black are the three nested regeneration plots/plot (15 m × 15 m). The area between the double-dashed lines was the nested forest vegetation plot (40 m × 40 m).

A forest vegetation plot (40 m × 40 m) was nested within each of the three demographic plots per population to obtain data for other tree species besides whitebark pine (i.e., d.b.h., status, diseases, insects, crown condition, crown class, etc.) (see Fig. 2). All

tree and recruitment data at each plot were collected to quantify stand structure, composition, basal area, and density. Within the forest vegetation plot, positions of all associated trees were recorded and mapped.

For each demographic plot, mean, minimum, and maximum monthly and annual temperatures and precipitation from 1971 to 2000 were obtained from FHTET (USDA FS Forest Health Technology Enterprise Team, Fort Collins, CO) using the PRISM climatic model (Daly et al., 1994). Parent material and soil survey data (e.g., available water capacity in top 0–50 in. and % sand content as a percentage of sand:silt:clay) were obtained from the South Lake Tahoe office of the USDA Natural Resources Conservation Service (NRCS).

All live and recently dead whitebark pines within demographic plots were evaluated for symptoms and signs of WPBR. Rust infection was recorded on a tree when aecia (including aeciospores) were observed. Stem and branch canker locations and numbers were recorded for each infected tree; included in the canker counts were branches and stems with past signs of aecia such as symptomatic cracked bark and swelling, but only when aecia were confirmed on another part of the tree. If there were no signs of aecia, trees with conspicuous dead "flagged" branches and other symptoms of infection, including swelling, rodent gnawing, pitching, and cracked bark, were noted as suspect, though unconfirmed, WPBR. Stem cankers were assigned a stem-girdle category in which the horizontal circumference of stem cankers was estimated and rated: 1 = ⩽1/3 of stem girdled; 2 = >1/3–2/3 girdled; and 3 = >2/3-completely girdled (J. Dunlap, unpubl. protocol, USDA Forest Service).

Correlations and simple linear regression analyses were used to relate disease variables with whitebark pine cone production as well as soil properties. Regression and correlation analyses were conducted with the software program JMP, version 8.0.1 (SAS, 2009). For parametric analyses, assumptions of normality and homogeneity of variances were verified.

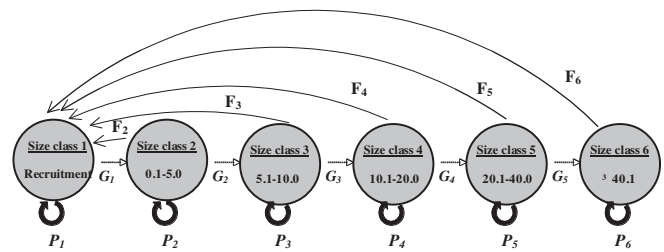
2.3. Current population trends

Population trends were assessed with transition matrix models for each of the eight populations of whitebark pine. We used transition matrices to describe and summarize current trends in survivorship, fecundity, and, to a lesser extent, growth. Transition matrix models of populations follow the Lefkovitch (1965) model:

$$\mathbf{n}_{t+1} = \mathbf{A}n_t$$

where $\mathbf{n}_t$ is a column vector corresponding to the size structure at time **t** of a population classified into **s** size classes, and **A** is the matrix representing population dynamics.

A is influenced by survival, growth, and reproduction. Entries in the transition matrix represent the contribution that each size class makes to every other size class during a specified time interval. We created sized-based models from six size classes: (1) recruits (individuals <1.37 m in height), (2) 0.1–5.0 cm d.b.h., (3) 5.1–10 cm d.b.h., (4) 10.1–20.0 cm d.b.h., (5) 20.1–40.0 cm d.b.h., and (6) ⩾40.1 cm d.b.h. In the diagram size classes are represented by circles with size class 1 at the left and proceeding to size class 6 at the right, as shown.



Transition probabilities for *growth* ($\boldsymbol{G}_1$–$\boldsymbol{G}_5$) are represented by the forward horizontal arrows, *survivorship* ($\boldsymbol{P}_1$–$\boldsymbol{P}_6$) by the bold circular arrows, and *fecundity* ($\boldsymbol{F}_2$–$\boldsymbol{F}_6$) by the long curved arrows from right to left. Transition probabilities were calculated and estimated from our field data. Fecundity was estimated from existing recruitment and cone production data collected for size classes 2, 3, 4, 5, and 6. We used the following formula to estimate fecundity for each of the five size classes:

$$\frac{(\text{No. of cones in size class}_i\ (t)/\text{no. of cones for population}\ (t)) \times \text{no. of recruits for population}\ (t))}{\text{No. of trees in size class}_i\ (t)}$$

where *i* is for each individual size class and *t* is time. This formula is similar to that used by Davelos and Jarosz (2004) for estimating fecundity for American chestnut (*Castanea dentata* Marsh.). For growth probabilities, we assumed that individuals will transition into the next size class if they are in the upper d.b.h. limit of their size class (height for seedlings/saplings). For example, an individual with a d.b.h. of 4.9 cm or 5.0 cm would be assumed to grow into the next size class in the next time step. Where there was mortality, survivorship was calculated using the number of standing dead trees (years dead ranged from 1 to 12 years, based on needle, bark, and branch retention) divided by current live and dead stems for each size class. In demographic studies of white pines where mortality was not observed, mortality has been assumed to be either 0% or 2% (Ettl and Cottone, 2002; van Mantgem et al., 2004). Where no mortality was observed, we assumed a minimal value of 1% mortality, an average of these published estimates.

The population growth rate (λ), estimated using the dominant eigenvalue of the transition matrix (Caswell, 2001), measures the rate of change in total population size. Population growth rate is a function of size- or age-specific rates of survival, growth and reproduction, with $\lambda > 1$ indicating growing, $\lambda = 1$ indicating stable, and $\lambda < 1$ indicating declining populations. Classical statistical tests using estimates of λ are inappropriate because demographic parameters and estimates of λ are not simple and their distributions are often not known (Caswell, 2001). Therefore, we computed 95% confidence intervals for λ by bootstrapping (n = 10,000) across survivorship, growth, and fecundity estimates comprising the transition matrix. All calculations and bootstrapping were performed in Matlab (Mathworks, 2009).

3. Results

3.1. Whitebark pine and stand characteristics

Whitebark pine is a dominant component in these subalpine forests and relative densities ranged from 0.94 to 0.99 (Table 1). Other associated species present, in lesser numbers, were mountain hemlock (*T. mertensiana*), lodgepole pine (*P. contorta*), western white pine (*P. monticola*), red fir (*A. magnifica*), and occasionally

Jeffrey pine (*P. jeffreyi*). Because whitebark pine tends to form clusters in subalpine environments, as a result of seed caching behavior, densities ranged from 446 trees ha^{-1} to 797 trees ha^{-1} (Table 1). Highest whitebark densities occurred in westside locations on the West Shore Peaks and Dick's Pass, and the lowest densities in eastside locations such as Rifle Peak and Snow Valley Peak (Table 1). Across locations mean basal area was 23.3 m^2 ha^{-1} (Table 1). In 2009 mean number of cones ha^{-1} was 2456 and ranged from 960 at Rifle Peak to 4632 at Freel Peak (Table 1). These data were comparable to data from Idaho, Montana, and Wyoming (McKinney et al., 2009). Average number of cones $tree^{-1}$ ranged from 0.38 for the smallest diameter size class (size class 2) to 20.75 for the largest diameter size class. Clark's nutcrackers were observed at all locations. Recruitment varied from location to location with a mean of 139 seedlings and saplings ha^{-1} and a range from 44 to 296 (Table 1). Mean recruitment reported by Larson and Kipfmueller (2010) was 2397 seedlings/saplings ha^{-1}, higher than what we found; they sampled a greater geographic range (Idaho, Montana, and Oregon) and more diverse environmental conditions.

White pine blister rust was found at all locations. Disease incidence (number of WPBR-infected whitebark pine trees/all whitebark pine trees in a population) ranged from 1% at Freel Peak to 65% at Rifle Peak (Fig. 1 and Table 1). Average number of branch cankers per population ranged from 0.06 to 4.99 (Table 1). Disease severity as measured by stem girdling category (1 = ⩽1/3 of stem girdled; 2 = >1/3–2/3 girdled; and 3 = >2/3-completelely girdled) ranged from a high of 1.35 at Rifle Peak and a low of 0.02 at Freel Peak, with three of eight populations having stem girdle categories ⩾1.0 (Table 1). Cumulative whitebark pine mortality was low, ranging from 1% to 4% (Table 1). Incidence of MPB was also low, ranging from 0% to 4% (Table 1). The primary causes of mortality at our sites were MPB, WPBR, and likely drought stress, and their interactions.

Sampled whitebark pine stands ranged in elevation from 2711 to 2865 m, and differed in climate, soil properties, and geology (Table 2). In subalpine stands mean January minimum temperature was −7.5 °C and July maximum temperature was 22.2 °C. Annual precipitation was highest at Dick's Pass (west) with 1686 mm compared to 891 mm at Snow Valley Peak (east). Diversity in parent material is reflected in soil properties (Table 2). Sites on andesite/tuff breccia or volcanics generally have higher available water capacity and lower percent sand content than sites on granodiorite (Table 2). Implications of these differences will be discussed.

Table 3
Means for estimated fecundity, survivorship, and growth from size-based transition matrices for eight whitebark pine populations. Estimated population growth rate, λ, is shown along with 2.5% and 97.5% confidence intervals (CI, in parentheses).

Population	Fecundity	Survivorship	Growth	λ (2.5%, 97.5% CI)
Rifle Peak	0.061	0.979	0.023	1.021 (0.729, 1.543)
Mt Rose	0.252	0.959	0.010	0.996 (0.290, 1.649)
Snow Valley Peak	0.090	0.988	0.040	1.033 (0.744, 1.497)
Heavenly	0.204	0.967	0.036	1.024 (0.370, 1.772)
Freel Peak	0.144	0.954	0.027	1.022 (0.431, 1.705)
Little Roundtop	0.108	0.970	0.047	1.032 (0.761, 1.486)
Dick's Pass	0.118	0.950	0.024	1.003 (0.527, 1.610)
West Shore Peaks	0.129	0.984	0.040	1.034 (0.631, 1.656)

3.2. Current population structure and trends

Multi-size structure was found for whitebark pine, with good representation in size classes 10.1–20.0 and 20.1–40.0 cm (Fig. 3). High proportions of large diameter trees (>40.1 cm) were found at Dick's Pass, Freel Peak, Heavenly, and Mt Rose (6.5%, 7%, 9%, and 13%, respectively) (Fig. 3). Relatively high proportions of trees in the smallest diameter class, 0.1–5.0 cm, were found at Freel Peak, Mt Rose, and Rifle Peak (Fig. 3).

Variation in fecundity, which is a function of cone production and the number of recruits that successfully established, was found among populations (Tables 1 and 3). Fecundity was highest at Mt

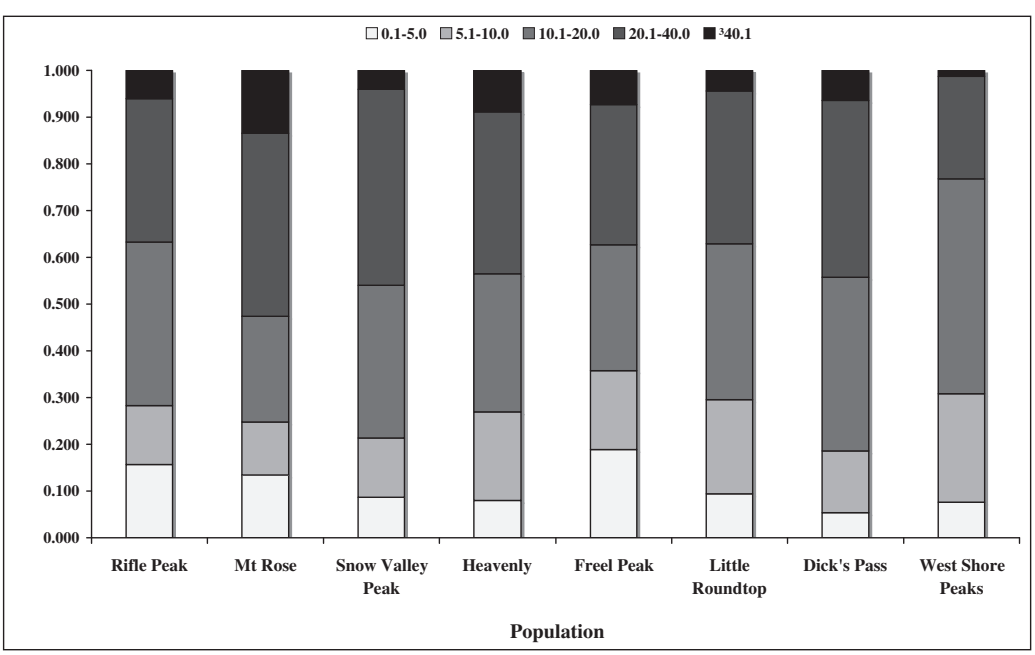


Fig. 3. Size structure for eight populations of *Pinus albicaulis* in the Lake Tahoe Basin. Population structure is represented by the proportion of stems in d.b.h. size classes 0.1–5.0 cm, 5.1–10.0 cm, 10.1–20.0 cm, 20.1–4.0 cm, and ⩾40.1 cm.

Rose (0.252), followed by Heavenly (0.204), and Freel Peak (0.144); this is attributable to a combination of good cone production and successful recruitment (Tables 1 and 3). The lowest fecundity was at Rifle Peak (0.061) and Snow Valley Peak (0.090) (Table 3 and Appendix 1). Because of low mortality at all sites survivorship ranged from 0.950 to 0.988 (Table 3 and Appendix 1).

Estimated growth rates (λ) for 7 of the 8 whitebark pine populations were $\geqslant$1.0, indicating that these populations appear to be stable (Table 3). Mt Rose had a $\lambda < 1.0$, indicative of a population that may, or may not be, in decline. All upper limit confidence intervals for λ were greater than 1, suggesting stability in all populations. However, for most populations the lower confidence interval was <1.0 (Table 3). There is no conclusive evidence at this point in time to say that these eight populations are either in decline or growing – currently they appear stable based on the criteria used for this one-time sampling.

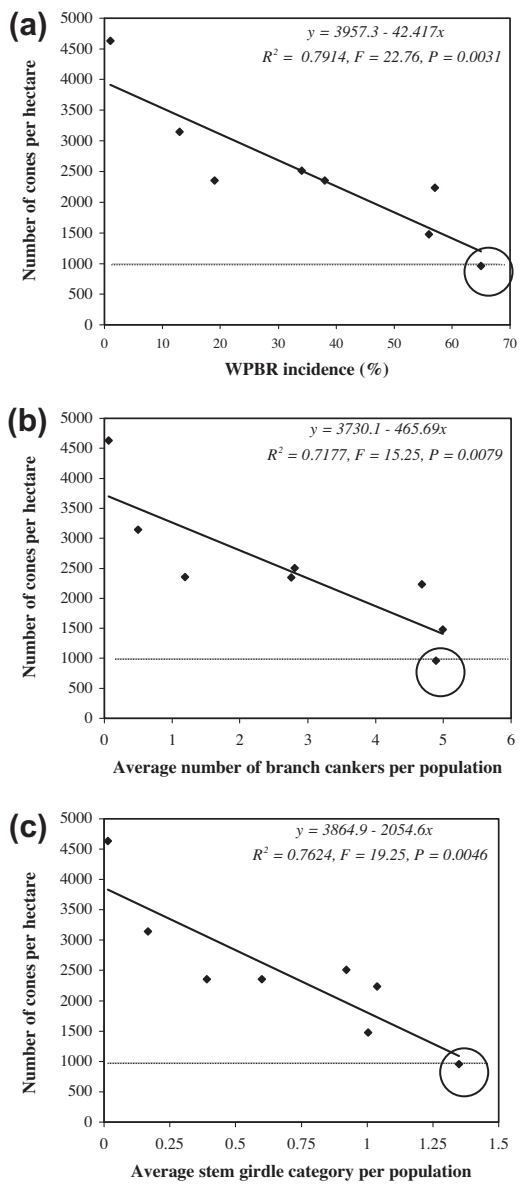


Fig. 4. Simple regression analysis of disease parameters and whitebark pine cone production. Negative relationships exist between (a) cone production and average WPBR incidence per population, (b) average number of branch cankers, and (c) average stem girdle category. Linear regression equations are shown along with R^2, F, and P values. A threshold number of $\geqslant$1000 cones ha^{-1} (hatched vertical line shown) have been estimated to maintain seed dispersal at a site by Clark's nutcracker (*Nucifraga columbiana*), a primary dispersal agent of whitebark pine (McKinney et al., 2009). Rifle Peak whitebark pine population (circled) falls just below this threshold number.

3.3. White pine blister rust, whitebark pine, and environment interactions

Negative relationships were found between cone production and disease incidence and severity (Fig. 4). Whether it is percent of individuals infected with WPBR (incidence), average number of *C. ribicola*-infected branches tree^{-1} population^{-1}, or average stem girdle category population^{-1}, all three disease measures were negatively related with cone production (Fig. 4a–c, respectively). A threshold number of 1000 cones ha^{-1} has been estimated to maintain seed dispersal by Clark's nutcracker at a site (McKinney et al., 2009). Rifle Peak falls just below this threshold; it produces the fewest cones, has the highest incidence and severity of WPBR (Fig. 4), and the fewest recruits of any population in the Basin (Table 1).

Environmental characteristics can influence host condition and pathogen interactions, and thus disease progress and severity. A moderate, positive relationship was found between stem girdle category and available water capacity, and a negative relationship was found between stem girdle category and percent sand content (Fig. 5a and b, respectively). Whitebark pine populations growing on parent material derived of andesite, tuff breccia, or volcanic tend to have higher available water capacities and lower percent sand content than those on granitic soils (Table 3).

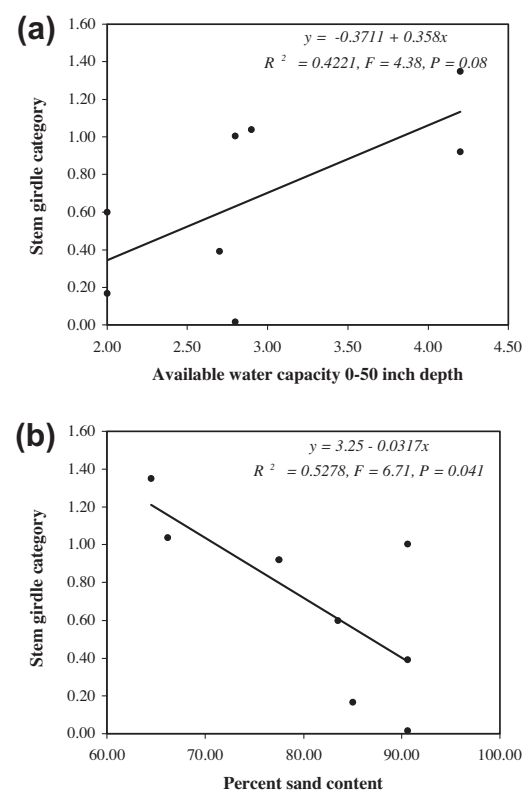


Fig. 5. Simple regression analysis of disease and environment interactions. Stem cankers and girdling are lethal to white pine species of all sizes. A positive relationship exists between (a) the mean severity of stem girdling per population and available soil water capacity while there is a negative relationship between (b) mean stem girdling and percent sand content. Linear regression equations are shown along with R^2, F, and P values.

4. Discussion

Our study indicates the most critical effect of *C. ribicola* on whitebark pine in the Lake Tahoe Basin is infection and mortality of cone-bearing branches. We found negative relationships between cone production and WPBR incidence and severity. Percent of individuals infected (incidence), average number of infected branches per population, and severity of stem girdling are all negatively related with cone production. This adverse demographic effect on reproduction (loss of cone and seed production) and potentially dispersal may lead to declines in whitebark pine numbers in the future. Conversely, white pine blister rust may also act as a selective agent by culling the most susceptible trees. Whitebark pine at Rifle Peak had the lowest female cone numbers [960 cones ha^{-1} (mean across sites = 2456)], lowest recruitment numbers [44 seedlings/saplings ha^{-1} (mean across sites = 139)], and the highest incidence of WPBR (65%) of all whitebark pine populations surveyed in the Lake Tahoe Basin. A threshold number of $\geqslant$1000 cones ha^{-1}, averaged over 2–3 years, resulted in a probability of seed dispersal of $\geqslant$80% within a forest stand by Clark's nutcracker (McKinney et al., 2009). Whitebark pine cone production at Rifle Peak falls below this threshold (see Fig. 4). Mckinney et al. (2009) found mean cone production ha^{-1} of 641, 1055, and 3635 in locations with mean WPBR incidence of 82%, 65%, and 49%, respectively. Our cone production estimates were based on a 1-year survey, and cone crops for whitebark pine can vary considerably from year to year (Crone et al., 2011). However, during our survey, all populations were producing cones. We lack data about seed dispersal by Clark's nutcracker and seed and cone predation at these sites. These are important factors in recruitment dynamics of whitebark pine that warrant further investigations to properly assess population- and community-level effects of WPBR in subalpine forests in the Lake Tahoe Basin.

While our study area is small relative to whitebark's distribution, we provide baseline data on the population ecology of whitebark pine in the north-central Sierra Nevada, at the southern, more arid, distribution of whitebark pine. Despite moderate to high WPBR incidence (mean = 35.3%), seven of eight whitebark populations were relatively stable, with estimates of $\lambda \geqslant 1.0$. They may be maintaining themselves because of adequate population sizes, mixed-size structure, high survivorship, moderate fecundity, and infrequent wave years. Relatively high survivorship across all diameter classes and low mortality are important in the demographic stability of these whitebark pine populations. In a recent study of sugar pine (*Pinus lambertiana*) from the Lake Tahoe Basin (Maloney et al., 2011), estimates of survivorship ranged from 0.621 to 0.987, whereas whitebark pine's range is 0.950–0.988. Mount Rose is the only whitebark pine population with an estimated $\lambda < 1.0$. This stand has the third highest incidence of WPBR (56%) and produces the second lowest number of cones (1477 ha^{-1}), yet has the second highest number of recruits (199 ha^{-1}). High recruitment success at this location may offset the lower than average cone production, resulting in relatively high fecundity. While not quantified, Clark's nutcracker's are abundant and active in this stand. Another important characteristic of this site is large areas of exposed, decomposed granite and high rock cover; Clark's nutcracker's are known to selectively cache seeds next to rocks (Tomback, 1978).

White pine blister rust stem cankers are often damaging or lethal by killing water conducting tissue (e.g., xylem), which can result in gradual or rapid wilting and dieback. The entry point for *C. ribicola* is through needles, hence branch cankers and branch mortality are often the first symptoms of establishment to be observed in woody tissues. In the northern Cascades, Ettl and Cottone (2002) estimated the annual mortality of infected adult whitebark with three classes of infection (branch, bole, and >50% crown loss) to be 1.6%, 2.1%, and 10.8% $year^{-1}$, respectively. These estimates of annual mortality are high, and are based on infection periods occurring once in every 18 years, with the first infection event having occurred in 1948 (Ettl and Cottone, 2002). These authors also assume mycelium growth rate in branches to be 8 cm $year^{-1}$ (Ettl and Cottone, 2002). However, the rate at which rust mycelium grows is mediated by environmental conditions in which hosts are growing (Buchanan, 1938; Kearns et al., 2009). We found relationships between soil properties and severity of stem girdling by *C. ribicola*. Subalpine environments are characterized by cold conditions, which will affect *C. ribicola*, but soil type may also influence pathogen growth. High available water capacities and soil properties that create favorable plant–soil water conditions may simultaneously benefit both host condition (e.g., tolerance to infection) and pathogen growth *in planta*. The rate at which disease progresses and eventually kills cone-bearing branches and main stems may be accelerated on non-granitic soil types (e.g., andesite, tuff, and other volcanic substrates). Both Rifle Peak and Little Roundtop have parent material of volcanic and andesite/tuff breccia, respectively, and the highest stem girdle categories, 1.39 and 1.037. The rate of WPBR mortality of cone-bearing branches may potentially vary depending on site geology and other environmental conditions (e.g., annual precipitation). The relationships are modest for just eight study sites; while nothing conclusive can be stated, the trends warrant further investigation on how site conditions such as geology might influence pathogen growth.

White pine blister rust in the Lake Tahoe Basin is currently exerting negative effects on susceptible whitebark pines via infection and mortality of cone-bearing branches. Yet WPBR may equally be exerting a positive effect on resistant or tolerant whitebark pine individuals, through natural selection. Additionally disease progress and severity may vary from one location to the next, given environmental heterogeneity and variation in host susceptibility. However, since population growth, λ, was calculated from a one-time sampling only, our estimates may not reflect intrinsic variation in rates of survivorship, fecundity, or growth. Year to year fluctuations in climate, cone production, seed dispersal, recruitment success, cone and seed predation, tree mortality, and conditions favorable for WPBR-infection may be considerable. Our intent in this study was not to predict future population dynamics of whitebark pine in the Lake Tahoe Basin, but to describe current population status and disease conditions. A limitation of our study is that the confidence intervals are large for λ, as it was estimated from a one-time sampling that likely generated large variances around the point estimate. Long-term demographic data, monitoring of whitebark pine infection, and studies on Clark's nutcrackers will be needed to adequately assess trends in population dynamics, disease, and host responses, as well as community-level effects in the future.

5. Restoration implications

Field studies and methods that incorporate both ecological and disease condition assessments are necessary to identify whitebark pine populations that may require intervention and restoration. Our restoration strategy is to facilitate whitebark pine recruitment at Rifle Peak to maintain both adequate species numbers and to enhance resistance and/or tolerance to white pine blister rust.

Our initial restoration efforts will be directed toward planting of seedlings. Season of planting, microhabitat, and herbivore pressure will be tested. Spring is the standard planting time for reforestation in the LTBMU and yields average survival of 60% from container-grown seedlings (D. Fournier, pers. comm., USDA Forest Service). We will also test the efficacy of fall planting. Greenhouse-grown

Plate 1. Whitebark pine conservation and restoration activities: caging whitebark pine for seed collection, 2-year old container-grown whitebark pine seedlings, and spring test plantings at Rifle Peak with protective mesh to determine herbivore pressure. Photo credits: D. Vogler and M. Frye.

seedlings from containers may have higher survival in a fall planting when both above- and below-ground tissue (i.e., shoots and roots) are entering winter dormancy (A. Delfino Mix, pers. comm.). Fall plantings may allow roots to successfully establish before they initiate active growth in the spring under favorable soil moisture conditions. Three microhabitats will be tested for seedling survival: rock shelter, open canopy, and closed canopy. Replicate plantings for each season, microhabitat, as well as planting seedlings enclosed in plastic mesh tubing will be made. Enclosures will allow us to determine if there is significant browsing by deer (aboveground) or pocket gophers (belowground).

Source seeds and seedlings for restoration are from 6 of the 8 study populations which include: Rifle Peak, Mt Rose, Snow Valley Peak, Freel Peak, Little Roundtop and Dick's Pass. Each test seedling will have been evaluated for white pine blister rust resistance, phenology, water-use efficiency, root:shoot ratio, and growth (Maloney et al., unpublished data). Deploying disease resistance can have long-term positive effects for white pine survival in high-risk sites; preliminary data from resistance evaluations suggest that it may be inherited complexly (multigenic) (Vogler and Delfino-Mix, pers. comm.). If *C. ribicola*-resistant whitebark pine is not available or found only in a limited number of families, deploying early bud-set phenotypes may be an effective alternate strategy as a disease-escape mechanism. A trait such as early bud-set may protect white pines (particularly in cold, dry, and high environments) from *C. ribicola* infection (see Maloney, 2011; Maloney et al., study in progress). If individuals initiate winter dormancy in late August when basidiospores begin to discharge, early bud-set phenotypes may not be receptive hosts because stomatal closure prevents inoculation and subsequent infection. Such phenotypes should be considered in restoration plantings of whitebark pine.

Restoration of whitebark pine requires considerable effort and can be costly (Plate 1). We have designed a restoration trial to evaluate important components of outplanting strategies (including season of planting, favorable microhabitat conditions for planting, determine herbivore pressure, and diverse seedling material) to develop effective and successful restoration protocols. Our ultimate goal is to maintain whitebark pine numbers on the landscape, both currently and in the future.

Acknowledgements

We thank Tom Burt for field assistance and cone collections and Clay DeLong for GIS maps. Additionally, we thank David Fournier, Don Lane (USDA Forest Service – LTBMU), Bill Champion (Nevada State Parks), Woody Loftis (USDA NRCS, South Lake Tahoe, CA) and Audrey Newman (Heavenly Mountain Resort) for site information, permission to work on Federal and State lands, and access to Heavenly Mountain ski area. We thank Brian Geils and Erik Jules for critical comments on an earlier draft. This work was supported by the Southern Nevada Public Lands Management Act – Round 7, sponsored by the USDA, Forest Service, Pacific Southwest Research Station.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.05.025.

References

Adams, W.T., Birkes, D.S., 1988. Estimating mating patterns in forest tree populations. In: Hattemer, H.H., Fineschi, S. (Eds.), Proceedings International Workshop on Plant Biology, Biochemical Markers in Population Genetics of Forest Trees, Porano-Orvieto, Italy. Inst. Agroforestry Nat. Res. Council Italy (CNR). SPB Academic Publishing, The Hague, pp. 152–172.

Burdon, J.J., Thrall, P.H., Ericson, L., 2006. The current and future dynamics of disease in plant communities. Ann. Rev. Phytopathol. 44, 19–39.

Buchanan, T.S., 1938. Annual growth rate of *Cronartium ribicola* cankers on branches on *Pinus monticola* in northern Idaho. Phytopathology 28, 634–641.

Caswell, H., 2001. Matrix Population Models, second ed. Sinauer Associates, Sunderland, MA, USA.

Critchfield, W.B., Little, E.L., 1966. Geographic Distribution of the Pines of the World. USDA Forest Service Miscellaneous Publication 991.

Crone, E.E., McIntire, E.J.B., Brodie, J., 2011. What defines mast seeding? Spatio-temporal patterns of cone production by whitebark pine. J. Ecol. 99, 438–444.

Daly, C., Neilson, R.P., Phillips, D.L., 1994. A statistical model for mapping climatological precipitation over mountainous terrain. J. Appl. Meteorol. 33, 140–158.

Davelos, A.L., Jarosz, A.M., 2004. Demography of American chestnut populations: effects of a pathogen and a hyperparasite. J. Ecol. 92, 675–685.

Duriscoe, D.M., Duriscoe, C.S., 2002. Survey and Monitoring of White Pine Blister Rust in Sequoia and Kings Canyon National Parks—Final Report of 1995–1999 Survey and Monitoring Plot Network. Science and Natural Resources Management Division, Sequoia and Kings Canyon National Parks.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3, 479–486.

Ettl, G.J., Cottone, N., 2002. Whitebark pine (*Pinus albicaulis*) in Mt. Rainier National Park, Washington, USA: response to blister rust infection. In: Akçakaya, H.R. (Ed.), RAMAS GIS. Applied Mathematics, Setauket, NY, pp. 36–48.

Farnes, P.E., 1990. SNOTEL and snow course data describing the hydrology of whitebark pine ecosystems. In: Schmidt, W.C., McDonald, K.J. (Eds.), Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource. Gen. Tech Rep. INT-270. Intermountain Research Station, USDA Forest Service, Ogden, UT.

Furnier, G.R., Knowles, P., Clyde, M.A., Dancik, B.P., 1987. Effects of avian seed dispersal on the genetic structure of whitebark pine populations. Evolution 4, 607–612.
Furniss, R.L., Carolin, V.M., 2002. Western Forest Insects. Misc. Publ. 1339. USDA Forest Service, Washington, DC.
Garnas, J.R., Ayres, M.P., Liebhold, A.M., Evans, C., 2011. Subcontinental impacts of an invasive tree disease on forest structure and dynamics. J. Ecol. 99, 532–541.
Geils, B.W., Hummer, K.E., Hunt, R.S., 2010. White pines, *Ribes*, and blister rust: a review and synthesis. For. Pathol. 40, 147–185.
Gilbert, G.S., 2002. Evolutionary ecology of plant diseases in natural ecosystems. Ann. Rev. Phytopathol. 40, 13–43.
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.
Hutchins, H.E., 1990. Whitebark pine seed dispersal and establishment: Who's responsible? In: Schmidt, W.C., McDonald, K.J. (Eds.), Symposium on Whitebark Pine Ecosystems: Ecology and management of a High-Mountain Resource. Gen. Tech Rep. INT-270. Intermountain Research Station, USDA Forest Service, Ogden, UT, pp. 245–255.
Kearns, H.S., Jacobi, W.R., Geils, B.W., 2009. A method for estimating white pine blister rust canker age on limber pine in the Central Rocky Mountains. For. Pathol. 39, 177–191.
Keane, R.R., Parsons, R.A., 2010. Management Guide to Ecosystem Restoration Treatments: Whitebark Pine Forests of the Northern Rocky Mountains, USA. USDA Forest Service, Rocky Mountain Research Station, General Technical, Report RMRS-GTR-232.
Kinloch, B.B. Jr., Marosy, M., Huddleston, M.E. (Eds.), 1996. Sugar Pine: Status, Values, and Roles in Ecosystems: Proceedings of a Symposium presented by the California Sugar Pine Management. University of California, Division of Agriculture and Natural resources, Davis, CA. Publication 3362.
Lanner, R.M., 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Can. J. For. Res. 12, 391–402.
Larson, E.R., Kipfmueller, K.F., 2010. Patterns in whitebark pine regeneration and their relationships to biophysical site characteristics in southwest Montana, central Idaho, and Oregon, USA. Can. J. For. Res. 40, 476–487.
Lefkovitch, L.P., 1965. The study of population growth in organisms grouped by stage. Biometrics 21, 1–18.
Lorenz, J.T., Sullivan, K.A., 2009. Season differences in space use by Clark's nutcracker in the Cascade Range. Condor 111, 326–340.
Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., 2006. Forest ecosystem responses to exotic pests and pathogens in Eastern North America. Bioscience 56, 395–405.
Maloney, P.E., 2000. Topics in Forest Pathology and Ecology in the Sierra Nevada and the Sierra San Pedro Martir, Baja. Ph.D. Dissertation, University of California, Davis.
Maloney, P.E., Lynch, S.C., Kane, S.F., Jensen, C.E., Rizzo, D.M., 2005. Establishment of an emerging generalist pathogen in redwood forest communities. J. Ecol. 93, 899–905.
Maloney, P.E., Vogler, D.R., Eckert, A.J., Jensen, C.E., Neale, D.B., 2011. Population biology of sugar pine (*Pinus lambertiana* Dougl.) with reference to historical disturbances in the Lake Tahoe Basin: implications for restoration. For. Ecol. Manage. 262, 770–779.
Maloney, P.E., 2011. Incidence and distribution of white pine blister rust in the high-elevation forests of California. For. Pathol. 41, 308–316.
Manley, P.N., Fites-Kaufman, J.A., Barbour, M.G., Schlesinger, M.D., Rizzo, D.M., 2000. Biological integrity. In: Murphy, D.D., Knopp, C.M. (Eds.), Lake Tahoe Basin Watershed Assessment, Gen. Tech Rep. PSW-GTR-175, vol. 1. Pacific Southwest Research Station, USDA Forest Service, Albany, CA, pp. 403–600.
Mathworks, Inc., 2009. 3 Apple Hill Dr. Natick, MA 01760, USA.
McKinney, S.T., Fiedler, C.E., Tomback, D.F., 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecol. Appl. 19, 597–607.
Neale, D.B., 1983. Population Genetic Structure of the Douglas-Fir Shelterwood Regeneration System in Southwest Oregon. PhD Dissertation, Oregon State University.
Paillet, F., 2002. Chestnut: history and ecology of a transformed species. J. Biogeogr. 29, 1517–1530.
Richardson, B.A., Klopfenstein, N.B., Brunsfeld, S.J., 2002a. Assessing Clark's nutcracker seed-caching flights using maternally inherited mitochondrial DNA of whitebark pine. Can. J. For. Res. 32, 1103–1107.
SAS Institute, 2009. JMP Start Statistics: JMP Statistics and Graphics Guide, Release 8.0.1. SAS Institute Inc., Cary, NC.
Schwandt, J.W., 2006. Whitebark Pine in Peril: A Case for Restoration. USDA Forest Service Forest Service, Rocky Mountain Region (R-1), Forest Health Protection, Report No. R-1-06-28, 20pp.
Smith, J.P., Hoffman, J.T., Sullivan, K.F., VanArsdel, E.P., Vogler, D.R., 2000. First report of white pine blister rust in Nevada. Plant Dis. 84, 594.
Smith, R.S., 1996. Spread and intensification of blister rust in the range of sugar pine. In: Kinloch, B.B. Jr., Marosy, M., Huddleston, M.E. (Eds.), Sugar Pine: Status, Values, and Roles in Ecosystems: Proceedings of a Symposium presented by the California Sugar Pine Management. University of California, Division of Agriculture and Natural resources, Davis, CA. Publication 3362, pp. 112–118.
Richardson, B.A., Brunsfeld, S.J., Klopfenstein., 2002b. DNA from a bird-dispersed seed and wind-disseminated pollen provides insights into postglacial colonization and population genetic structure of whitebark pine (*Pinus albicaulis*). Mol. Ecol. 11, 215–227.
Tingley, M.W., Orwig, D.A., Field, R., Motzkin, G., 2002. Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations. J. Biogeogr. 29, 1505–1516.
Tomback, D.F., 1978. Foraging strategies of Clark's nutcracker. Living Bird 16, 123–161.
Tomback, D.F., 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. J. Anim. Ecol. 51, 451–467.
Tomback, D.F., Arno, S.F., Keane, R.E., 2001. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, DC.
Tomback, D.F., Achuff, P., 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. For. Pathol. 40, 186–225.
United States Geological Survey, 1999. Digital Representation of "Atlas of United States Trees" by Elbert L. Little, Jr. <http://esp.cr.usgs.gov/data/atlas/little/>.
United States Department of Agriculture, Natural Resources Conservation Service, 2007. Soil Survey of the Tahoe Basin Area, California and Nevada.
Vander Wall, S.B., Balda, R.P., 1977. Coadaptations of the Clark's Nutcracker and the piñon pine for efficient seed harvest and dispersal. Ecol. Monogr. 74, 89–111.
van Mantgem, P.J., Stephenson, N.L., Keifer, M., Keeley, J., 2004. Effects of an introduced pathogen and fire exclusion on the demography of sugar pine. Ecol. Appl. 14, 1590–1602.