Impacts of black stain root disease in recently formed mortality centers in the piñon–juniper woodlands of southwestern Colorado

H.S.J. Kearns and W.R. Jacobi

Abstract: Thirty discrete black stain root disease (BSRD) mortality centers, caused by *Leptographium wageneri* (Kendr.) Wingf. var. *wageneri*, were examined in 1999 to determine the effects of BSRD on the composition and structure of piñon–juniper woodlands at the tree, shrub, and herbaceous plant levels and on tree-seedling regeneration. In these recently formed mortality centers, the majority (68%) of all piñon (*Pinus edulis* Engelm.) was dead, 76% of piñon were affected by BSRD, and 70% had evidence of piñon ips bark beetle (*Ips confusus* Leconte) attack. BSRD mortality centers had a mean area of 0.28 ha (range 0.07 to 0.63 ha). There were no statistically significant ($p > 0.05$) differences in shrub composition, cover, or diversity between mortality centers and the unaffected surrounding woodlands. Herbaceous plant cover was significantly greater ($p < 0.001$) within mortality centers and frequency responses were species specific. There were no significant ($p = 0.629$) differences in the density of piñon regeneration inside mortality centers compared with outside mortality centers. The pathogen was regularly isolated from piñon roots dead for 5–8 years and once from a root dead for 16 years. The rate of radial expansion of mortality centers averaged 1.1 m/year (0.07 SE). The rate of mortality center expansion was not significantly ($p > 0.05$) related to available water-holding capacity, percent organic matter, pH of soils, piñon density, or any other site data recorded.

Résumé : Trente zones discrètes de mortalité associées au noircissement des racines causé par *Leptographium wageneri* (Kendr.) Wingf. var. *wageneri* ont été étudiées en 1999 pour déterminer les effets de la maladie sur la composition et la structure des forêts de pin du Colorado et de genévrier au niveau des arbres, des arbustes et des plantes herbacées ainsi que sur la régénération. Dans ces zones de mortalité récemment formées, la majorité (68 %) des pins du Colorado (*Pinus edulis* Engelm.) étaient morts; 76 % des pins du Colorado étaient affectés par la maladie et 70 % montraient des signes d'attaque par le scolyte du pin du Colorado (*Ips confusus* Leconte). Les zones de mortalité avaient une dimension moyenne de 0,28 ha (écart de 0,07 à 0,63 ha). Il n'y avait pas de différences significatives ($p > 0,05$) dans la composition des arbustes, le couvert ou la diversité entre les zones de mortalité et les forêts environnantes non affectées. Le couvert de plantes herbacées était significativement plus élevé ($p < 0,001$) dans les zones de mortalité et les réponses en fréquence étaient propres à chaque espèce. La densité de la régénération du pin du Colorado n'était pas significativement différente ($p = 0,629$) à l'intérieur et à l'extérieur des zones de mortalité. Le champignon pathogène a régulièrement été isolé des racines du pin du Colorado mortes depuis 5–8 ans et une fois d'une racine morte depuis 16 ans. Le taux d'expansion radiale des zones de mortalité atteignait en moyenne 1,1 m/an (erreur type = 0,07). Le taux d'expansion des zones de mortalité n'était pas significativement ($p > 0,05$) relié à la capacité de rétention de l'eau disponible, au pourcentage de matière organique, au pH du sol, à la densité du pin du Colorado, ni à aucune autre donnée recueillie au sujet de la station.

[Traduit par la Rédaction]

Introduction

Piñon–juniper woodland is the largest forest cover type in Colorado, covering more than 1.8×10^6 ha (Landis and Helburg 1976), most of which grows on the western slope of the Continental Divide. Increased recreational and housing activity in piñon–juniper woodlands has been accompanied by a heightened awareness of mortality of piñon (*Pinus edulis* Engelm.). Primary mortality agents of piñon include (1) the fungal pathogen *Leptographium wageneri* (Kendr.) Wingf. var. *wageneri*, which causes black stain root disease (BSRD), a vascular wilt disease of piñon, and (2) the piñon ips bark beetle (*Ips confusus* Leconte) (Eager 1999). BSRD was first identified in Colorado at Mesa Verde National Park in 1942, but may have been observed as early as 1906 (Wagener and Mielke 1961). Local spread of the disease occurs primarily through root contacts and grafts between infected and healthy trees (Hessburg and Hansen 1986). Mortality of piñon attributable to BSRD often has different appearances on the landscape, typically appearing as discrete mortality centers, but in areas that are heavily infested, disease centers merge and appear as a mosaic of mortality covering extensive areas (Landis and Helburg 1976). Insects may act as vectors, and although Bishop and Jacobi (2003) identified potential vectors of the piñon variant of the fungal pathogen *L. wageneri*,

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they did not demonstrate that insects could vector the pathogen. Insect vectors have been identified for both the Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and hard pine variants of *L. wageneri* (Goheen and Cobb 1978; Harrington et al. 1985; Witcosky and Hansen 1985). Ips bark beetles often attack piñons affected by BSRD; the most common species found on piñon is *Ips confusus*. Ips beetles act as agents of thinning and recycling by attacking and feeding on declining and dying trees, but when population levels are high, such as the current outbreak in the southwestern United States, ips beetles may be associated with widespread mortality (Eager 1999; Landis and Helburg 1976; Wagener and Mielke 1961).

Previous research on BSRD has focussed predominantly on the two varieties of *L. wageneri* that infect hard pines and Douglas-fir because of the hosts' commercial value as timber species. The disease in piñon has been studied less intensively. Consequently, very little is known about the short-term or long-term impacts of BSRD on piñon–juniper woodland ecosystems. Piñon is highly susceptible to *L. wageneri* var. *wageneri* infection, which typically results in mortality, while junipers are not susceptible and are not directly affected by BSRD. Continued mortality of piñon could potentially shift the species composition of these forests towards dominance by juniper species. Removal of piñon by BSRD could have detrimental effects on wildlife and ecosystem properties by altering species composition and stand structure, and through changing nutrient cycling and hydrologic regimes.

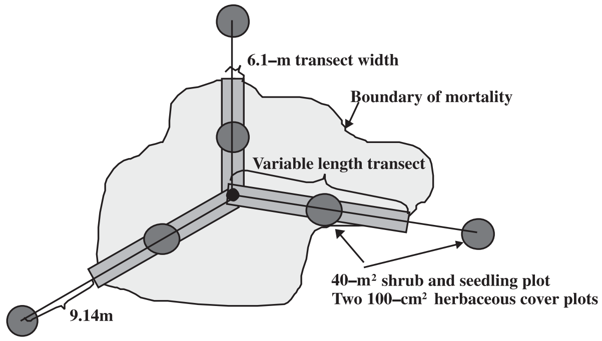
In 1999, a study was undertaken to examine the effects of *L. wageneri* var. *wageneri* on piñon–juniper woodlands in southwestern Colorado. The objectives of this study were to examine the short-term effects of *L. wageneri* var. *wageneri*, where discrete areas of mortality (BSRD mortality centers) occurred in piñon–juniper woodlands, by answering the following questions: (1) Does BSRD significantly impact the composition and structure of piñon-juniper woodlands at the tree, shrub, or herbaceous levels? (2) Does BSRD significantly alter tree regeneration within mortality centers? (3) How long can the pathogen remain viable within the roots of dead piñon putting subsequent piñon generations at risk? (4) At what rate are discrete BSRD mortality centers expanding? and (5) Are there site characteristics that influence the rate of expansion?

Materials and methods

Study sites

Thirty BSRD mortality centers were surveyed. A combination of aerial photographs and ground surveys was used to locate piñon mortality centers within the study areas. From this population of piñon mortality centers, we sampled mortality centers that fit the following criteria: a pattern of expanding mortality with dying or newly dead piñons defining edges surrounded by green, healthy piñons, and visually confirmed BSRD in at least one tree. Piñon mortality centers that did not meet the above criteria were excluded from the sample. Twenty-two mortality centers were located near McPhee reservoir, north of Cortez, Colorado, in an area occupying approximately 96 km^2 within the western portion of the San Juan National Forest. Eight mortality centers were located in a second study area occupying approximately 44 km^2, which straddles the boundary of the Southern Ute Reservation and the San Juan National Forest, east of Ignacio, Colorado, and is approximately 113 km east of the McPhee sites. A 1998 ground survey of the two study areas found that 2%–3% of piñon sampled were dead because of BSRD (W.R. Jacobi, unpublished data). Elevations of mortality centers ranged from 1945 to 2334 m, essentially covering the middle portion of the elevational range of piñon in Colorado (Ronco 1990). Mortality center attributes including percent slope, slope position, aspect, general topography, UTM coordinates, elevation, area, and circumference of disease centers were recorded.

Fig. 1. Plot sampling scheme for black stain root disease mortality centers in piñon–juniper woodlands.



To supplement time of mortality of dead piñon data, which were used to determine pathogen viability and mortality center expansion rates, BSRD monitoring plots established in 1978 within Mesa Verde National Park by US Forest Service personnel were relocated and visited. Mesa Verde is a 21 045 ha national park located in the high plateau country of southwestern Colorado, between the Cortez and Ignacio sites. Piñon–juniper woodlands occupy elevations from approximately 1700 to 2500 m within the park (Floyd et al. 2003*a*).

Mortality center characteristics

At each mortality center, plot center was established at the location of the oldest piñon mortality, based on the condition of the snags or logs within the plot. The edges of the mortality center were defined at the midpoint between the last chlorotic or dead piñon and the first green, nonsymptomatic piñon encountered around the entire circumference of the mortality patch. All boundaries and plot centers were georeferenced and measured using Trimble Navigation's GeoExplorer II global positioning system (GPS) unit (Sunnyvale, California).

Three belt transects were established within each mortality center. Transects radiated out from plot center with a minimum of 45° between the centerline of transects (Fig. 1). Whenever possible, transects were placed so as to include declining piñon. When only one transect included chlorotic piñon, remaining transect centerlines were located at 120° intervals. Transects were 6.1 m wide and varied in length from 7.9 to 74.4 m, with a mean transect length of 33.2 m, ending at the first green, nonsymptomatic piñon beyond all declining and dead piñons. For every tree, snag, or log whose base fell within the transect, the following were recorded: location (measured as the distance along the center line from plot center); species; height (total standing height or total length of log segments to estimate height when standing and

Table 1. Tree status rating system applied to black stain root disease centers in piñon–juniper woodlands.

Tree status	Description
1	No chlorosis; tree foliage appears normal green color, healthy
2	One-third of crown displays chlorotic foliage (based on no. of branches)
3	Two-thirds of crown displays chlorotic foliage (based on no. of branches)
4	All branches exhibit chlorotic foliage (general yellowing, some red needles but majority are yellow)
5	Crown with red and (or) brown foliage; tree dead; foliage remaining on twigs
6	Few to no needles, many fine twigs, intact bark, sound heartwood
7	No needles, many twigs, bark may be missing in patches, relatively intact crown, sound heartwood
8	No needles, few twigs, 5%–33% branches broken, bark loose or missing in places, crown broken
9	Very few twigs remaining, crown broken, >33% branches broken, bark loose or missing
10	Fallen, few twigs, 5%–33% branches broken, bark loose or missing in places, like tree status 8
11	Fallen, very few twigs remaining, >33% branches broken, bark loose or missing, like tree status 9
12	Fallen, stem broken into pieces, few branches
13	Well deteriorated, extensive loss of original mass, original shape apparent to undistinguishable, becoming incorporated into soil
14	Cut stump

Note: Modified from Sharon (1985); Omdal, D.W. personal communication.

whole); diameter at root crown (measured as the average of two caliper measurements taken at 90° from each other); tree status (based on a 14-class system designed to describe tree, snag, and log conditions (Table 1)); presence of damaging agents; and symptoms and signs of BSRD and ips bark beetles.

Statistical analyses were performed utilizing the SAS (Cary, North Carolina) Mixed and GLM statistical procedures. Summary statistics were calculated for tree measurements, including height, diameter at root crown, status, and BSRD infection. Analysis of variance, correlation, and *t*-tests were used to compare the composition and structure of BSRD mortality centers, at the tree, shrub, and herbaceous levels, with the communities found in adjacent nonaffected woodlands. Relationships between variables including tree measurements, tree and seedling density, number of trees infected, tree location along transects, and mortality center size were evaluated by analysis of variance, correlation, and *t*-tests. The present study was considered a randomized block design for statistical evaluation.

Shrub cover and tree seedlings

A 40-m^2 circular shrub and seedling plot was established at the midpoint of each transect, representing conditions within the mortality center, and at 9.14 m beyond the end of each transect, representing the unaffected forest. Shrub cover by species was visually estimated, including all nonconiferous woody plants >30 cm tall, and the number of piñon, juniper, and ponderosa pine seedlings (height <1.37 m) were recorded. Because of the minimum of 45° between transect centerlines and the varying lengths of transects in each mortality center, at no time did the 40-m^2 plots overlap. The three plots either inside or outside each mortality center were averaged to estimate mean shrub cover by species for inside each mortality center and its outside, adjacent woodland. Using the 30 paired observations from each mortality center, paired *t*-tests were performed to determine differences in shrub cover and occurrence and tree-seedling density.

To determine the effect of *L. wageneri* var. *wageneri* infection on shrub-layer vegetation, we utilized species richness and diversity indices. Three indices of diversity were utilized, Shannon's index, Simpson's index, and Hill's ratio of evenness (Ludwig and Reynolds 1988), to examine differences in diversity between BSRD mortality centers and surrounding areas.

Herbaceous vegetation and ground cover

Two 0.1-m^2 rectangular (Daubenmire 1959) herb subplots were established within each of the 40-m^2 circular shrub and seedling plots at the midpoint and at 9.14 m beyond the end of each transect to represent conditions within the mortality center and in the adjacent unaffected forest, respectively. Herbaceous cover (%) by species, including all nonwoody plants and woody plants <30 cm tall, and cover (%) by bare soil, litter, and rock on all herb subplots were visually estimated by the same two observers. Cover was defined as the percentage of ground that could not be seen by an observer viewing it from directly above. Herbaceous plants, except grasses and mosses, were identified when possible to the rank of species. The six 0.1-m^2 herb subplots either inside or outside each mortality center were averaged to estimate mean cover by species for inside each mortality center and its outside, adjacent woodland. Using the 30 paired observations from each mortality center, paired *t*-tests were performed to determine differences in cover and occurrence.

Pathogen viability

Piñon root and root crown samples were collected and taken to the laboratory for isolation and confirmation of *L. wageneri* var. *wageneri* and to determine the pathogen's viability in dead piñon. The sampled tissues were kept cool after collection in the field until processed, then cut into thin (<1 cm thick) slices with a band saw after which the bark was removed. Water agar (1.5%) amended after autoclaving with 200 mg/L cycloheximide and 100 mg/L streptomycin was used as the selective medium (Harrington 1992). Cultures were kept at 15 to 17 °C in a dark growth chamber then transferred to 4.5% malt extract agar after approximately 3 weeks. Cultures were identified on the basis of mycelial and conidiophore characteristics (Kendrick 1962; Harrington and Cobb 1986).

Age of mortality and rate of mortality center expansion

Tree increment cores and (or) stem cross sections were obtained from sound piñons in all tree-status classes present within individual mortality centers to date mortality and determine expansion rates of mortality centers. Crossdating, conducted using the skeleton plot technique (Stokes and Smiley 1968) based on chronologies developed from live trees on each site, was utilized to determine the date of mortality, which was assumed to be the last year in which a growth ring was added (Kearns 2001). To supplement snag and coarse woody debris data collected from the McPhee Reservoir and Ignacio study sites, BSRD monitoring plots established within Mesa Verde National Park by US Forest Service personnel were located and visited. In 1978, US Forest Service personnel established seven variable radius plots to examine mortality rates. Trees were tagged, referenced to plot center, and the condition and cause of death, if applicable, were recorded (Sharon 1985). The plots were all revisited in 1980, 1982, 1984, and 1986. Three of the seven plots were remeasured in 1992. We visited five of the plots in 1999, one in 2000, and were unable to relocate the seventh plot. The six Mesa Verde plots contained between 17 and 113 tagged piñon, and a total of 293 piñon were re-examined and classified according to snag or log status based on the 14-class system. The number of years dead was then determined for each tree based on Forest Service records as the midpoint between last year recorded as live and first year recorded as dead. These data on number of years dead, as categorized by snag or log status class, were then compared with the data assembled from tree-ring analyses at the two study sites and used to determine mean years dead as categorized by status class. Student's *t*-tests were applied to determine significant differences between piñon status classes in number of years dead. Analysis of variance was performed to determine the effect of site (McPhee, Ignacio, and Mesa Verde) on mean ages of piñon snags and logs (Kearns 2001).

The first dead piñon in each transect was treated as the initiation point for disease in that transect. For all other piñon in an individual transect, the change in distance and the change in number of years dead relative to the first dead piñon was calculated. The mean rate of expansion was calculated using a split-plot design (where the transects were the split-plot units) and analysis of covariance to determine the relationship between the change in distance and the change in number of years dead within each transect for the 30 BSRD mortality centers examined. Rates of expansion for infected and recently killed piñon (status classes 2–7) were determined in addition to overall expansion for all piñon (status classes 2–12) within individual mortality centers. Analysis of covariance and correlation analysis were performed to examine effects of physical and chemical soil properties, percent slope, aspect direction, slope position, general topography, mean stand age, and tree density on the rate of expansion. Soil properties including pH, permeability, mean bulk density, available water-holding capacity, cation exchange capacity, percent organic matter content, and percent clay content were derived from USDA Natural Resources Conservation Service (NRCS) Soil Survey Geographic database GIS layers and USDA NRCS map unit descriptions. These soil property data were averaged for each horizon from the range of values provided, and a weighted average of the relative contribution each of the horizons made was determined for three cumulative soil depths (0.0–0.3 m, 0.3–0.6 m, and 0.6–0.9 m).

Results

Mortality center characteristics

BSRD centers varied in size, shape, and general site characteristics. Discrete BSRD mortality centers, delineated with GPS, had a mean area of 0.28 ha (range 0.07 to 0.63 ha) and a mean perimeter of 287.4 m (range 124.5 to 513.3 m). Mortality centers were irregularly shaped, having a mean ratio of perimeter to area 3.3 times larger (range 2.1 to 5.5 times larger) than the ratio of perimeter to area of a perfect circle, indicating that these mortality centers are not expanding evenly in all directions. Mortality centers were found on slopes ranging from 1% to 46% and on all aspects. The majority of mortality centers were located on topography generally described as even, but mortality centers were also found on topography characterized as concave or convex. Furthermore, plots were located in all possible slope position categories.

Overstory composition and structure

The trees that make up the overstory of BSRD mortality centers in southwestern Colorado are predominately piñon and two species of juniper, Utah juniper (*Juniperus osteosperma* (Torr.) Little) and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.). Piñon within mortality centers, including all live and dead piñon, had a mean height (standard error (SE)) of 3.7 m (0.05 SE) and a mean diameter at root crown (DRC) of 15.2 cm (0.28 SE). Utah juniper was present on 17 of 22 mortality centers at McPhee Reservoir and all 8 mortality centers near Ignacio, represented 76% of non-piñon tree species present on transects, and had a mean height of 3.8 m (0.17 SE) and a mean DRC of 18.6 cm (1.03 SE). Rocky Mountain juniper was present on 13 of 22 mortality centers at McPhee Reservoir and on 2 of 8 mortality centers near Ignacio, represented 21% of non-piñon tree species present on transects, and had a mean height of 3.7 m (0.22 SE) and a mean DRC of 15.7 cm (1.58 SE). Ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engel.) was present on only 3 of 22 mortality centers at McPhee Reservoir and none of the 8 mortality centers near Ignacio, represented 3% of non-piñon tree species present on transects, and had a mean height of 8.1 m (1.69 SE) and a mean DRC of 35.7 cm (7.93 SE).

BSRD significantly reduced the density of piñon within BSRD mortality centers and did not significantly alter the juniper population. All trees, living and dead, within mortality centers were examined to determine the composition of the area prior to occurrence of BSRD. Within mortality centers, piñon was the dominant tree species. Of 1235 trees measured within transects, 86% were piñon and 14% were Utah juniper, Rocky Mountain juniper, or ponderosa pine. Total tree densities, including all trees live and dead, within mortality centers were extremely variable, ranging from 223 to 2003 trees/ha with a mean density of 701 trees/ha. Total tree densities in the unaffected woodlands surrounding mortality centers ranged from 82 to 1318 trees/ha and averaged 555 trees/ha, which was not significantly different from the

Fig. 2. Interior view of black stain root disease mortality center near McPhee Reservoir, north of Cortez, Colorado.

mean total tree densities within BSRD mortality centers. The lack of a significant difference between the total tree densities of mortality centers and surrounding woodlands indicates that tree densities were similar in the two areas prior to infection by BSRD. Total piñon density within mortality centers, live and dead, ranged from 195 to 1963 trees/ha with a mean density of 598 trees/ha. Live piñon densities, including both healthy and symptomatic trees, within mortality centers ranged from 84 to 433 trees/ha with a mean of 221 trees/ha, while dead piñon densities ranged from 56 to 1538 trees/ha and averaged 377 trees/ha. Mean live piñon density for the 30 BSRD mortality centers has been reduced by 63% from mean density of all piñon, which at one time would have all been alive. Piñon densities in the surrounding woodlands ranged from 82 to 1153 trees/ha and averaged 458 trees/ha. The densities of live piñon are significantly lower ($p < 0.001$) within mortality centers than in the surrounding areas. The proportion of live piñon within the 30 mortality centers was not related to mortality center size. Densities of juniper, including both species, within mortality centers ranged from 0 to 477 trees/ha with a mean density of 101 trees/ha, and in surrounding areas densities of juniper ranged from 0 to 412 trees/ha with an average of 93 trees/ha. Juniper density in the surrounding, unaffected woodlands was not significantly different from that found within BSRD mortality centers.

BSRD mortality centers were composed primarily of piñon snags and logs (Fig. 2). Within mortality centers, 56% of all trees were dead; 68% of all piñon were dead, and 15% of trees in all other species were dead. Piñon status within mortality centers was as follows: 25% were apparently healthy, nonsymptomatic trees; 7% were chlorotic but living; 46% were snags (standing dead); 21% were logs (fallen dead); and 1% were cut stumps. For the other tree species combined, the distribution of tree-status classes was 84% healthy trees, 1% chlorotic, 2% snags, 5% logs, and 8% cut stumps.

Of 973 live and dead piñon in mortality centers, 110 (11%) had confirmed BSRD, 629 (65%) had suspected BSRD, and 234 (24%) had no indication of the presence of BSRD. The large proportion of piñon with suspected black stain infection highlights the difficulty in making definitive identification more than 1 year after death. Following death of the piñon, the characteristic dark stain confined by annual rings often becomes more diffuse, making conclusive identification difficult. Piñons suspected of black stain infection exhibited dark stain in the sapwood of the roots and (or) root crown, were located adjacent to piñons identified as infected by black stain, and had no evidence of other causes of mortality. Black stain infection, both suspected and confirmed, averaged 75% of all piñon within individual transects. Within BSRD mortality centers, live piñon with no evidence of black stain infection had a significantly ($p < 0.001$) smaller mean diameter at root crown (12.6 cm) than live piñon with suspected and confirmed black stain infection (20.7 cm). Live piñon with no evidence of black stain infection also had a significantly ($p < 0.001$) smaller mean height (3.8 m) than live piñon with suspected and confirmed black stain infection (5.2 m).

Damage agents

Insects and pathogens including bark beetles, *L. wageneri* var. *wageneri*, and decay fungi were active within mortality centers. At endemic levels, ips bark beetles often attack broken, fallen, and dying piñon affected by BSRD. The relationship between BSRD and ips bark beetles in declining and dead piñon was as follows: 8.5% of piñon had either suspected or confirmed BSRD but no evidence of ips bark beetles, only 0.5% of piñon had suspected or confirmed ips bark beetles but no evidence of BSRD, and 91.0% of piñon had suspected or confirmed presence of both BSRD and ips bark beetles. Ips bark beetles were considered secondary to BSRD when both were present owing to two sets of conditions. (1) Extensive staining of the xylem was present in the roots and root collars of piñon, indicating pervasive and long-term colonization by the pathogen. (2) The pattern of expanding mortality evident in all examined mortality centers indicated probable pathogen movement from one root system to adjacent root systems as opposed to clumps of piñon dying concurrently as is common in bark beetle attacks.

Of all dead piñon, 43% had decay in either the heartwood, sapwood, or both. Decay fungi (based on fruiting) included *Pycnoporus cinnabarinus* (Jacq. ex Fr.) Karst., *Gloeophyllum sepiarium* (Wulf. ex Fr.) Karst., *Trichaptum abietinum* (Fr.) Rhy., and *Stereum* sp. (personal communication, Dr. J.P. Lindsey, Fort Lewis College, Durango, Colorado). Wood borers, ants, and termites were also actively breaking down snags and coarse woody debris. The most commonly occurring agents aside from BSRD and ips bark beetles were non-ips bark beetles, wood borers, and fungi causing brown cubical rot that were found in 39%, 41%, and 5.3% of all trees, respectively. Non-ips bark beetles more commonly attacked shorter trees, wood borers were found on larger diameter trees, and both were more likely to be found on the piñons close to plot center that had been dead longer than those piñons farther from plot center. Brown cubical rot was also found more commonly on shorter, larger diameter trees that had been dead longer.

Shrub-level composition and structure

Fourteen shrub species were identified within BSRD centers (Table 2). The most commonly occurring shrubs within

Table 2. Occurrence and mean cover (%) with standard errors (SE) of shrub species inside and outside 30 black stain root disease mortality centers.

	Occurrence[a]					Mean cover[b]				
	Inside		Outside			Inside		Outside		
Species	%	SE	%	SE	p	% cover	SE	% cover	SE	p
Amelanchier species	55.6	5.8	47.8	6.1	0.229	2.6	0.5	2.8	0.7	0.769
Artemisia tridentata	38.9	6.8	40.0	6.1	0.856	1.6	0.5	2.0	0.5	0.585
Cercocarpus montanus	35.6	5.7	25.6	6.3	0.083	1.4	0.3	1.4	0.6	1.000
Chrysothamnus nauseosus	4.4	2.1	2.2	1.5	0.326	0.1	0.0	0.0	0.0	0.161
Fendlera rupicola	33.3	7.5	30.0	6.5	0.620	0.9	0.2	0.7	0.2	0.248
Peraphyllum ramosissimum	32.2	7.4	24.4	6.8	0.109	2.0	0.7	1.2	0.5	0.212
Prunus virginiana	0.0	0.0	2.2	1.5	0.161	0.0	0.0	0.2	0.2	0.281
Purshia tridentata	14.4	5.9	10.0	5.1	0.161	1.0	0.5	0.6	0.4	0.203
Quercus gambelii	52.2	6.7	55.6	5.4	0.712	10.4	2.3	14.2	2.5	0.224
Rhus trilobata var. *trilobata*	2.2	1.5	2.2	1.5	1.000	0.2	0.2	0.0	0.0	0.351
Ribes leptanthum	1.1	1.1	2.2	1.5	0.573	0.0	0.0	0.1	0.1	0.252
Symphoricarpos albus	1.1	1.1	0.0	0.0	0.326	0.5	0.2	0.3	0.2	0.202
Yucca baccata	13.3	5.0	12.2	4.9	0.573	0.02	0.02	0.01	0.01	0.326
All shrub species combined	2.2	1.5	1.1	1.1	0.326	20.8	2.2	23.5	2.6	0.357

[a] The percent occurrence averaged over three shrub plots either inside or outside the 30 mortality centers.

[b] Mean shrub cover of three shrub plots either inside or outside 30 mortality centers.

Table 3. Mean values and standard errors (SE) of diversity indices for shrub-layer vegetation inside and outside 30 black stain root disease mortality centers.

	Inside		Outside			
Index	Mean	SE	Mean	SE	Difference	p
Species richness	4.70	0.32	4.43	0.26	0.27	0.392
Simpson's index[a]	0.53	0.03	0.54	0.03	–0.01	0.920
Shannon's index[b]	0.46	0.10	0.39	0.10	0.07	0.306
Hill's evenness ratio[c]	0.68	0.07	0.73	0.07	–0.05	0.606

[a] $\lambda = \Sigma[\% \text{ cover}_i\ (\% \text{ cover}_i - 1)] / [\text{total } \% \text{ cover } (\text{total } \% \text{ cover} - 1)]$.

[b] $H' = -\Sigma(P_i \times \ln[P_i])$ where P_i is the percent cover of a given species divided by the total percent cover of all species.

[c] $E = [(1/\lambda) - 1] / (e^{H'} - 1)$.

mortality centers were serviceberry (*Amelanchier alnifolia* (Nutt.) and *Amelanchier utahensis* Koehne), which were present on 50 of the 90 shrub plots (55.6%) inside mortality centers. Outside mortality centers, the most commonly occurring shrub species was Gambel oak (*Quercus gambelii* Nutt.), which was present on 50 of the 90 shrub plots (55.6%) outside mortality centers. Mountain mahogany (*Cercocarpus montanus* Raf.) was the only shrub species that showed a marginally significantly (p = 0.083) greater occurrence inside than outside mortality centers. For all other species there were no significant differences in occurrence between mortality centers and surrounding areas.

Cover (%) by shrub species did not differ significantly between BSRD mortality centers and surrounding areas. Mean shrub cover within the shrub plots for all species combined inside mortality centers was 20.8%, while outside mortality centers mean shrub cover was slightly, but not significantly (p = 0.357), greater at 23.5% (Table 2). In comparisons of mean cover inside mortality centers and outside mortality centers, none of the differences between mean cover of any shrub species were statistically significant (α = 0.05). Gambel oak contributed the most cover both inside and outside mortality centers. Total shrub cover was not significantly related to size of mortality center, nor was there a significant relationship between mean shrub cover and number of tree seedlings present within mortality centers.

The number of shrub species present inside BSRD mortality centers was not significantly different (p = 0.392) from the number of shrub species outside mortality centers. Mean shrub species richness inside mortality centers was 4.7 and in surrounding areas was 4.4 (Table 3). Mortality center size had no effect on the number of shrub species present. The least square mean values derived for Simpson's index and Shannon's index indicate that the distribution of proportional abundances among species was essentially the same both inside and outside mortality centers. Hill's evenness ratio also indicates that there is no significant difference in the abundance of different shrub species between BSRD mortality centers and surrounding areas.

Herbaceous-level composition and structure

There were significant differences between mortality centers and surrounding areas in nonwoody plants and woody plants less than 30.5 cm tall. Seventy-eight types of herbaceous-level plant cover were identified within the study sites. Four herbaceous plant cover types were found more frequently

Table 4. Occurrence and mean cover with standard errors (SE) of common herbaceous-level plants inside and outside 30 black stain root disease mortality centers.

	Occurrence[a]					Mean cover[b]				
	Inside		Outside			Inside		Outside		
Herb-layer plants	%	SE	%	SE	p	% cover	SE	% cover	SE	p
Grasses	71.1	5.1	52.2	5.1	0.002	10.8	1.8	3.9	0.7	0.001
Achillea lanulosa	7.2	2.5	2.2	1.1	0.037	0.1	0.1	0.1	0.1	1.000
Alisma minus	8.9	4.4	4.4	2.5	0.103	0.7	0.4	0.2	0.1	0.154
Artemisia ludoviciana	7.2	2.4	6.1	2.0	0.702	0.4	0.2	0.1	0.0	0.184
Carduus nutans	7.2	3.1	0.6	0.6	0.021	0.7	0.3	0.0	0.0	0.044
Ceratocephala orthoceras	5.0	2.5	3.3	1.7	0.522	0.1	0.1	0.1	0.1	0.614
Collinsia parviflora	5.0	2.5	3.3	1.9	0.415	0.1	0.1	0.1	0.1	0.691
Comandra umbellata	3.3	1.5	5.6	2.8	0.459	0.1	0.0	0.2	0.1	0.416
Erigeron flagellaris	5.6	2.3	0.6	0.6	0.017	0.5	0.3	0.0	0.0	0.060
Lomatium triternatum	5.0	2.1	7.2	3.0	0.403	0.8	0.4	0.4	0.1	0.253
Mosses	4.4	1.9	6.1	1.9	0.448	0.3	0.2	0.4	0.2	0.479
Penstemon linarioides	5.0	2.3	6.1	2.3	0.625	0.3	0.1	0.2	0.1	0.540
Penstemon species	5.6	2.2	4.4	2.3	0.690	0.2	0.1	0.4	0.3	0.607
Quercus gambelii	3.3	1.2	5.6	2.2	0.380	0.3	0.2	0.7	0.4	0.268

[a] Frequencies of the 14 most common herbaceous-level plant types (found on 5% or more of herbaceous-layer plots) as the percent occurrence averaged over six herb subplots either inside or outside the 30 mortality centers.

[b] Mean cover of six herb subplots either inside or outside 30 mortality centers.

and exhibited statistically significant differences in occurrence inside than outside mortality centers (Table 4). Grasses were the most commonly occurring herbaceous plant type both inside and outside mortality centers, but had a significantly greater occurrence inside mortality centers. *Achillea lanulosa* Nutt. (yarrow), *Carduus nutans* L. (musk thistle), and *Erigeron flagellaris* Gray (trailing fleabane) were also found more frequently inside mortality centers.

Mean herbaceous cover was 20.2% inside BSRD mortality centers, which was significantly greater ($p < 0.001$) than the 9.4% herbaceous cover found outside mortality centers. Grasses, which were found within all mortality centers, had a mean cover of 10.8% inside mortality centers and a significantly lower ($p < 0.001$) mean cover of 3.9% outside mortality centers (Table 4). *Carduus nutans*, an introduced weed species associated with disturbed areas, was found more frequently inside mortality centers, and its cover was also significantly greater ($p = 0.044$) within mortality centers than in surrounding areas. Overall cover by nonherbaceous ground cover types, which were bare soil, litter, and rock combined, was significantly greater ($p < 0.001$) at 90.6% outside mortality centers than the 79.8% inside mortality centers. Ground covered by bare soil was significantly greater ($p = 0.043$) outside mortality centers at 21.0% than inside mortality centers at 14.7%, but coverage by litter and rock did not differ significantly ($p = 0.214$ and $p = 0.561$, respectively) inside and outside mortality centers.

Diversity indices could not be accurately applied to herbaceous-level vegetation. The indices are predicated on identification of each individual species, rather than on the identification of the mixture of broad cover types, such as grasses and mosses, and individual herbaceous species that were applied in this present study. Mean number of herbaceous cover types within the 0.1-m^2 herb subplots was 6.60 inside and 5.43 outside mortality centers. Though this measure is not an actual count of individual species present, since not all species (i.e., grasses and mosses) were identified, it does indicate that there were on average more types of herbaceous cover present inside mortality centers than in the unaffected surrounding forest. Of the 78 types of herbaceous cover identified, 45% were found both inside and outside mortality centers, 32% were unique to mortality centers, and 23% were found only outside BSRD mortality centers.

Tree regeneration

There was no significant difference ($p = 0.629$) in the density of piñon seedlings inside mortality centers, with a mean of 552 seedlings/ha (86 SE), compared with outside mortality centers, with a mean of 612 seedlings/ha (123 SE). Piñon seedlings were present on 74% (67 of 90) of the 40-m^2 plots inside mortality centers and on 63% (57 of 90) of the 40-m^2 plots outside mortality centers. Piñon seedlings were found in 29 of the 30 mortality centers and in 27 of the 30 areas outside mortality centers. There was no significant relationship ($p = 0.368$) between mortality center size and the density of piñon seedlings.

Mean seedling density of juniper species, *J. osteosperma* and *J. scopulorum* combined, was slightly significantly greater ($p = 0.085$) inside mortality centers, with 69 seedlings/ha (20 SE), compared with outside mortality centers with 33 seedlings/ha (11 SE). However, juniper seedlings were present on only 19 of the ninety 40-m^2 plots inside mortality centers and on 10 of the ninety 40-m^2 plots outside mortality centers. Thus, occurrence of juniper regeneration was much less than that of piñon regeneration (21% and 74% of seedling plots inside mortality centers, respectively). Juniper seedlings were found in 14 of the 30 mortality centers and in 8 of the 30 areas outside mortality centers.

Pathogen viability

Leptographium wageneri var. *wageneri* was successfully isolated from 64 samples obtained from 29 of the 30 mortality centers studied. The pathogen was regularly obtained from roots of piñons estimated to have died an average of 5 years prior to excavation (tree status 7) and occasionally

Table 5. Mean expansion rates (m/year) and standard errors (SE) of black stain root disease mortality centers in piñon–juniper woodlands.

	Tree-status classes 2–7		Tree-status classes 2–12	
Site	Mean	SE	Mean	SE
McPhee	1.12	0.39	1.15	0.17
Ignacio	1.24	0.32	0.93	0.15
All sites	1.16	0.18	1.10	0.07

from trees estimated to have died an average of 8 years before excavation (tree status 8). In one case, the pathogen was successfully isolated from the sound root of a piñon in tree-status class 12, which was estimated to have died 16 years prior to excavation.

Mortality center expansion rates

The rate of radial expansion of mortality was variable among the 30 BSRD mortality centers, but overall averaged 1.1 m/year. Rate of expansion of mortality was used as a surrogate for rate of disease spread; presumably, the rate of fungal growth within host roots is directly related to the rate of mortality. Apparently, the progression of mortality does not differ between declining to newly dead (2–7) piñon and all piñon classes combined (2–12). Trees in status classes 2–7 (declining to newly dead) had a mean rate of linear expansion of 1.16m/year (0.18 SE) (Table 5), as calculated from the 28 mortality centers having piñon in those status classes. When status classes 2–12 were examined, the mean rate of linear expansion was 1.10 m/year (0.07 SE). The maximum mean rate of expansion for an individual mortality center was 2.01 m/year. Status classes 13 and 14 were left out of the analysis because the age of mortality associated with them could not be determined and they are not a part of the snag and coarse woody debris continuum, respectively. Although there was an apparent difference in mean rate of expansion between the two study sites, the differences were not statistically significant. A mean expansion rate of 1.1 m/year and a mean transect length of 33 m, as well as the fact that the oldest dateable dead piñon had died 26 years prior to measurement, indicate that the mortality centers examined in this present study likely formed in the last 30 years.

Although there were significant differences in mean expansion rates between the 30 mortality centers ($p < 0.001$), none of the evaluated soil characteristics (including available water-holding capacity, percent organic matter, and pH), piñon density, or any other site data recorded were significantly correlated with rate of mortality expansion. Soil chemistry attributes were determined for 26 of the 30 BSRD mortality centers for which soil data were available. Expansion rates were positively correlated with soil percent organic matter, soil pH, and piñon density, but there were high leverage points (outliers) in each analysis, and the associated correlations were considered spurious. In stands with total piñon densities, live and dead, of less than 500 trees/ha, mean expansion rate was 0.44 m/year. When piñon density ranged from 500 to 750 trees/ha, mean expansion rates increased to 1.07 m/year. For stands with piñon densities greater than 750 trees/ha, expansion rates averaged 1.35 m/year. However, regression analysis indicated that there was no statistically significant relationship ($p = 0.249$) between piñon density and expansion rate. Plot attributes such as slope position, general topography, percent slope, tree density (all species), aspect direction, and mean age of piñon were not significantly related to expansion rate.

Discussion

Tree-, shrub-, and herbaceous-level impacts

At the time of the present study, ground surveys indicated that BSRD was affecting 2%–3% of the piñon population in the two study areas. The discrete BSRD mortality centers examined in this study were all relatively recently formed and still expanding. The presence of BSRD can significantly affect both the structure and composition of the piñon–juniper woodlands in southwestern Colorado, even in these young mortality centers, by reducing live piñon density an average of 63% and creating stands dominated by piñon snags and logs in which a mean of 75% of piñon are affected by *L. wageneri* var. *wageneri*. The two nonsusceptible juniper species composing the overstory of these woodlands were not affected by the changes in piñon density within BSRD mortality centers. Piñons infected by *L. wageneri* var. *wageneri* were significantly larger in both diameter at root crown and height than noninfected piñons, which may be related to more extensive root systems of larger trees and greater likelihood of coming into contact with or proximity to roots harboring the pathogen. Another possibility is that larger piñons provide a more conducive habitat for the pathogen and are more often successfully colonized, or that these larger trees are more likely to be stressed and, therefore, more attractive to insect vectors of BSRD. In any case, BSRD is affecting these woodlands by removing larger diameter piñon within disease centers.

In these recently formed, discrete mortality centers, shrub-layer vegetation was not significantly impacted in composition, frequency of occurrence, cover, or diversity by presence of BSRD or its removal of the piñon overstory. Nor was there any apparent association of the shrub-layer composition and structure with mortality center size or corresponding age. These results indicate that mortality of piñon caused by BSRD is not having a significant impact on associated shrub species, at least within the relatively short interval following mortality evident in our sampled mortality centers. Holah et al. (1993) examined the effects of *Phellinus weirii*, a native root pathogen, on Douglas-fir forest composition in western Oregon and found that shrub cover did not differ significantly between disease centers and the surrounding forest at most study sites. The authors concluded that shrub cover response was highly species and site specific, which resulted in a reorganization of existing shrub populations rather than significant shifts to new species. Long-term vegetation monitoring plots in Mesa Verde National Park found no difference in the number of shrubs present under open and dense piñon–juniper canopies (Floyd and Colyer 2003), indicating that the shrub species present within these woodlands do not respond to increasing resource availability by filling canopy gaps. As the discrete mortality centers examined in this present study likely originated more recently than 30 years prior to measurement, a shrub-level response may occur as more time passes.

Herbaceous cover was significantly greater inside mortality centers, and frequencies of individual species or cover types were significantly altered. The differences in occurrence of herbaceous-level plant cover types inside BSRD mortality centers compared with adjacent woodlands indicate that reduction of the overstory piñon population through BSRD-caused mortality is having an effect on the composition of the herbaceous-level community, although the response by herbaceous-level plants varies by species. Successional models for piñon–juniper woodlands indicate that this more immediate response of the herbaceous-level to the opening of the woodlands through piñon mortality relative to the lack of apparent response at the shrub level is not unexpected (West and Van Pelt 1987). The presence of tree roots extending laterally near the soil surface limits growth of other vegetation in intertree spaces because of competitive interactions for water and nutrients (West 1988; Pieper 1990). Litter accretion and decreased light intensity may also play a role in limiting understory vegetation under piñon–juniper canopies (Pieper 1990). Overstory removal experiments in piñon–juniper woodlands, including both chaining and fuelwood harvesting, have shown an increase in grasses following treatments (Brockway et al. 2002; Yorks et al. 1994; West 1988). Although these types of treatments result in more soil disturbance than piñon mortality related to BSRD, there appears to be a fairly consistent relationship between decreased overstory cover and increase in total understory cover, but this response is species specific (Pieper 1990; Everett et al. 1983). The greater herbaceous cover inside BSRD mortality centers in the present study is likely attributable to increased resource availability due to the removal of overstory cover through piñon mortality by BSRD and the decomposition of piñon snags and logs. Conversely, the greater cover by nonherbaceous ground cover types found outside mortality centers is presumably related to lower resource availability due to increased canopy cover and competition by piñon. The significantly greater herbaceous cover within BSRD mortality centers may be considered beneficial in terms of increasing forage for wildlife and cattle and decreasing soil erosion. However, the significantly greater frequency and cover by musk thistle within BSRD mortality centers suggests that BSRD may play a role in creating habitats conducive to the colonization and establishment of nonnative weedy plant species in piñon–juniper woodlands, which in turn may affect the ecological integrity of these ecosystems by displacing native species and altering natural ecosystem processes. The implications of this invasibility are unclear on a landscape scale, but BSRD mortality centers should be among the disturbed areas monitored for invasive species.

Tree regeneration

Piñon regeneration was not significantly different between mortality centers compared with the adjacent piñon–juniper woodlands. Whether these piñon seedlings will successfully occupy the sites remains to be seen. Regeneration of piñon typically takes place in the shade of piñon and juniper tree canopies, under shrubs, or beside fallen trees. Shade improves microclimate factors by reducing moisture and temperature stresses, but piñon is considered shade intolerant and seedlings that become established beneath mature trees and dense shrubs may have little chance of maturing (Ronco 1990). There may also be a risk of BSRD infection as roots of establishing piñon seedlings grow into contact or proximity with roots of infected trees. Although juniper regeneration was, on average, more abundant inside mortality centers than the nonaffected surrounding forest, it exhibited lower density and occurrence than piñon regeneration. These areas of BSRD-caused piñon mortality will likely continue to be dominated by piñon through both surviving and regenerating piñon. Long-term observations beginning in 1944 in one BSRD center at Mesa Verde National Park indicate that piñon regeneration is occurring, surviving, and not exhibiting disease symptoms (James and Lister 1978).

Pathogen viability

Although *L. wageneri* var. *wageneri* has been referred to as a poor saprobe (Cobb 1988; Wagener and Mielke 1961), the pathogen was regularly isolated from the roots of piñon dead for 5 to 8 years. In one instance, *L. wageneri* var. *wageneri* was isolated from the sound root of a piñon estimated to have died 16 years prior to excavation, demonstrating its ability to survive within dead material for long periods. These results suggest that the pathogen in roots of dead piñon may be capable of infecting regenerating piñon. However, the roots of piñon in the tree-status classes composed of dead trees are frequently too decayed to permit removal from the substrate and (or) isolation of the pathogen. Thus, the risk of infection to regenerating piñon is likely small, since root contact between piñon seedlings and older dead infected material is restricted by the rapid breakdown of buried woody material and the inability of the fungus to grow long distances through soil.

Mortality center expansion rates

Radial expansion rates of mortality centers averaged 1.1 m/year (0.07 SE) and were not predictable based on general plot or soil chemistry attributes. The mean expansion rate calculated in this present study is less than the 2 m/year radial rate reported by Wagener and Mielke (1961) in one BSRD center at Mesa Verde National Park, but corresponds to BSRD expansion rates reported in Douglas-fir by Hansen and Goheen (0.9 m/year) (1988) and in ponderosa pine by Cobb et al. (1982) (1.0 m/year). We had some plots with expansion rates equal to those found by Wagener and Mielke (1961), but the overall mean expansion rate of the 30 mortality centers was less. Insects may be involved in short distance spread of the pathogen and could impact calculated expansion rates; however, all mortality centers sampled in the present study showed a pattern of expanding mortality and a lack of individual dying or declining piñon outside the mortality centers. An understanding of the expected rate of expansion of mortality centers can provide land managers with a useful tool for evaluating the pattern and rate of mortality and improving prediction of the potential impact of the disease in existing disease centers.

Cobb et al. (1982), in 52 BSRD centers, found that ponderosa pine density was the only factor significantly related to rate of spread. Other researchers working in ponderosa pine report that wetter soils produced more infections in seedlings and that soil water potentials were significantly related to spread rates (Goheen et al. 1978; Wilks 1985). *Leptographium wageneri* has been shown to grow through soil, and a relationship between soil characteristics and expansion rate of mortality centers may be expected. However, in our study in piñon neither piñon density nor available water-holding capacity were significantly correlated with expansion rates.

Management considerations

The discrete mortality centers examined in this present study are representative of only recent mortality (i.e., within 30 years prior to measurement), and we cannot predict impacts of the disease or expansion of mortality on scattered individuals nor on larger, older, merged mortality centers. Approximately 25% of piñon within recently formed BSRD mortality centers survive. Piñon regeneration is occurring with a mean density of 552 seedlings/ha. The concern that the composition of these woodlands may be at risk of shifting to dominance by juniper species appears to be small based on our sample of recently formed mortality centers. *Leptographium wageneri* var. *wageneri* can remain viable within the roots of dead piñon for up to 16 years, but this evidently is rare. More often, the roots of dead piñon break down and are inhabited by decay fungi after being dead for 5 to 8 years. The ability of the pathogen to survive in dead material may present a risk to piñon establishment, though the potential of disease transmission is probably small because of the relatively fast breakdown of piñon in these ecosystems. Therefore, replanting piñon in high value areas such as campgrounds and recreation areas may be a management option although new infestations may arise with insect vectoring of the pathogen.

Fire is relatively rare in piñon–juniper woodlands partly because of the lack of continuity of fine fuels to carry fires across the landscape. In a study of fire regimes at Mesa Verde National Park, Floyd et al. (2003*b*) found that 90% of all fires burned less than 0.1 ha and that fire turnover time was approximately 400 years. Although piñon is very sensitive to fire, the presence of piñons more than 350 years old and the lack of evidence of fire indicate that fire has not been a recent factor in any of the study sites. There is concern that BSRD may increase the risk of fire by increasing fuel loads. This may be true in the short term, but, in general, dead piñons are devoid of fine fuels within 8 years of death. Larger piñon fuels also break down rapidly and essentially completely break down within 16 years (Kearns 2001). Typically, these piñon–juniper woodlands are open, and it is doubtful that the brief availability of piñon fuels through BSRD mortality will greatly increase the likelihood of major fire events.

The discrete BSRD mortality centers may not be as readily apparent today as they were when this present study was conducted. Southwestern Colorado is in the midst of a major piñon mortality event that has been related to both prolonged drought and piñon ips bark beetles. According to a report by USDA Forest Service Forest Health Protection (2004), piñon mortality was detected through aerial surveys conducted in 2003 on more than 3.0×10^5 ha in southern Colorado. In many stands, especially those near our study sites, mortality of mature piñon has reached 90% (USDA Forest Service Forest Health Protection 2004). This widespread mortality may mask the presence of BSRD mortality centers to the undiscerning eye, but the centers are still present on the landscape. The close association between ips beetles and BSRD found in the present study, prior to the current large-scale piñon mortality event, may indicate a role for BSRD in supporting endemic ips beetle populations.

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