Journal of the Torrey Botanical Society 135(3), 2008, pp. 423–437

Distribution of *Ribes*, an alternate host of white pine blister rust, in Colorado and Wyoming[1]

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Kearns, H. S. J., W. R. Jacobi (Department of Bioagricultural Sciences and Pest Management, Colorado State University, Fort Collins, CO 80523-1177), K. S. Burns (USDA Forest Service, Forest Health Management, Golden, CO 80401-4720), and B. W. Geils (USDA Forest Service, Rocky Mountain Research Station, Flagstaff, AZ 86001). Distribution of *Ribes*, an alternate host of white pine blister rust, in Colorado and Wyoming. J. Torrey Bot. Soc. 135: 423–437. 2008.—*Ribes* (currants and gooseberries) are alternate hosts for *Cronartium ribicola*, the invasive fungus that causes blister rust of white pines (*Pinus*, subgenus *Strobus*) in the Rocky Mountain region of Colorado and Wyoming. The location, species, and density of *Ribes* can affect the spread and impact of this potentially serious forest disease. We assessed the distribution and density of *Ribes* growing near white pine stands for 15 study areas in Colorado and Wyoming with 1258 survey plots of two types, an intensive white pine/*Ribes* survey and an extensive *Ribes* survey. Species present, total numbers of stems and bushes, average number of stems per bush, and average stem length were recorded. Various *Ribes* species were present in all study areas across a range of elevations. The most frequent and common species were *R. cereum*, *R. inerme*, *R. lacustre*, and *R. montigenum*. Densities and probabilities of occurrence were related to site variables and varied by *Ribes* species. The most common predictive variables included type of dominant overstory, elevation, and general plot classification such as riparian area. The predictive information provided can be utilized by tree health specialists for risk rating of forests and in planning white pine blister rust mitigation projects. We expect that other areas in Colorado and Wyoming with similar site characteristics will have similar distributions and densities of *Ribes* and thus have similar risks to white pine blister rust.

Key words: *Cronartium ribicola*, currants, gooseberries, invasive species, predictive models.

Species of the genus *Ribes*, commonly known as gooseberries and currants, act as the primary alternate host for the exotic, invasive forest pathogen *Cronartium ribicola* (J.C. Fisch.), the causal agent of white pine blister rust (Mielke 1943). In western North America, the impact of *C. ribicola* on infected *Ribes* is minimal, typically causing only late-season defoliation under severe infestations; while it can cause lethal stem cankers on white pines (many species of genus *Pinus*, subgenus *Strobus*). In order for the rust to complete its life cycle, three spore stages are produced on the *Ribes* host. *Ribes* are infected by aeciospores that are produced on white pines in the spring. Aeciospores germinate and the hyphae usually enter *Ribes* leaves through stomata. After two to three weeks, urediniospores that serve to intensify the rust by re-infecting *Ribes* are produced in uredinia on the lower side of *Ribes* leaves or other young tissues. The next spore stage, teliospores, form in long columns, remain attached to the bottom of leaves, and

[1] Funding and support for this project was provided by the USDA Forest Service Special Development and Technology Program, USDA Forest Service Rocky Mountain Research Station, and the Colorado Agricultural Experiment Station.

[2] We recognize the contributions of Brian Bromelow, Robert Flynn, Betsy Goodrich, Kelly Mogab, Melodie Moss, Celeste Park, Jason Watkins, Robin Reich, Bill Romme, Jim zumBrunnen (Franklin A. Graybill Statistical Laboratory) at Colorado State University and Jeri Lyn Harris, Jim Hoffman, Meg Halford, John Lundquist, Anna Schoettle, and John Schwandt of the USDA Forest Service. In addition, USDA Forest Service personnel from the Medicine Bow, Roosevelt, and Shoshone National Forests; William Mack and Don Whyde (Bureau of Land Management); and Eric Rhodenbaugh (Wind River Reservation, Bureau of Indian Affairs), provided assistance. Helpful reviews of previous versions of the manuscript were provided by Michael Marsden, David Steingraeber, and two anonymous reviewers.

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Received for publication December 9, 2007, and in revised form May 7, 2008.

may be produced throughout the growing season. The pine-infecting spores, basidiospores, form on the telia during periods of high humidity and are wind dispersed to living pine needles that upon infection complete the pathogen's life cycle.

Species of *Ribes* vary greatly in their susceptibly to infection by *Cronartium ribicola* and ability to support production of rust basidiospores (Kimmey 1938). Several species of *Ribes* are reported to occur in Colorado and Wyoming based on plant check lists, but their distribution and spatial location in relation to white pines is not known. The species reported to occur in Colorado and Wyoming include *Ribes americanum* Mill., *R. aureum* Pursh, *R. cereum* Dougl., *R. hudsonianum* Richards., *R. inerme* Rydb., *R. lacustre* (Pers.) Poir., *R. laxiflorum* Pursh, *R. leptanthum* A. Gray, *R. montigenum* McClat., *R. oxyacanthoides* L. var. *oxyacanthoides*, *R. oxyacanthoides* L. var. *setosum* (Lindl.) Dom., *R. viscosissimum* Pursh, and *R. wolfii* Rothrock, (Nelson and Hartman 1994, Hartman and Nelson 2001, Van Arsdel and Geils 2004). The relative importance of individual *Ribes* species and even plants to the spread and intensification of the rust depends on the genetics of both the host and pathogen; microclimate conditions affecting spore dispersal, germination, and development; and host physiology and morphology. For example, in studies of the relative susceptibility of western North American *Ribes* species to *C. ribicola*, the partial-shade and shade forms of *Ribes* species are reported to be more susceptible to *C. ribicola* and produce more telia than do full-sun, or open-grown, forms of the same species (Mielke 1943, Mielke et al. 1937). Van Arsdel and Geils (2004) compiled the results of several studies on the susceptibility and inoculum production of various *Ribes* species and developed their own rating system (Table 1). For this paper, the taxonomy of Van Arsdel and Geils (2004) was employed.

White pine blister rust (WPBR) was first reported on limber pine (*Pinus flexilis* James) in northern Colorado in 1998 (Johnson and Jacobi 2000). In 2003, isolated WPBR infestations were discovered in the Wet and Sangre de Cristo Mountains of southern Colorado, more than 280 km from other known infections (Burns 2006). Infections were found primarily on limber pine, but Rocky Mountain (RM) bristlecone pines (*Pinus aristata* Engelm.) were also observed for the first time as infected in their native range (Blodgett and Sullivan 2004). It is likely that WPBR will spread naturally or be introduced throughout the range of white pines in Colorado and southeastern Wyoming. Recent surveys in Wyoming have already documented areas of high incidence of WPBR and detrimental impacts on limber pine ecosystems (Kearns and Jacobi 2007).

Table 1. Relative importance of Colorado and Wyoming *Ribes* to the spread and intensification of white pine blister rust. Table modified from Van Arsdel and Geils (2004).

Species	Relative importance[a]
Ribes americanum	low
Ribes aureum	low
Ribes cereum	very low
Ribes hudsonianum	high
Ribes inerme	moderate
Ribes lacustre	moderate
Ribes laxiflorum	moderate
Ribes leptanthum	very low
Ribes montigenum	moderate
Ribes viscosissimum	moderate
Ribes wolfii	low

[a] Relative importance is based on the species relative susceptibility and potential inoculum production.

We did not know at the time of this study which, if any, species of *Ribes* grow within or in the vicinity of native white pine stands in Colorado and Wyoming. Because species of *Ribes* differ in their potentials for production of pine-infecting basidiospores, it is important for understanding the epidemiology of this disease to know the distribution and density of *Ribes* by species. We hypothesized that *Ribes* would be present throughout the range of white pines in Wyoming and Colorado, but that specific species distribution and density would vary by location. Information on *Ribes* distribution by site condition could help predict where rust-caused damage may be most likely and severe. We, therefore, conducted *Ribes* surveys in selected areas of Wyoming and Colorado with high populations of limber and RM bristlecone pines. The objectives of these surveys were: 1) to describe the distribution and abundance of *Ribes* species growing within and in the vicinity of native white pine stands in Colorado and Wyoming, and 2) to identify site-related variables for predicting *Ribes* presence and density.

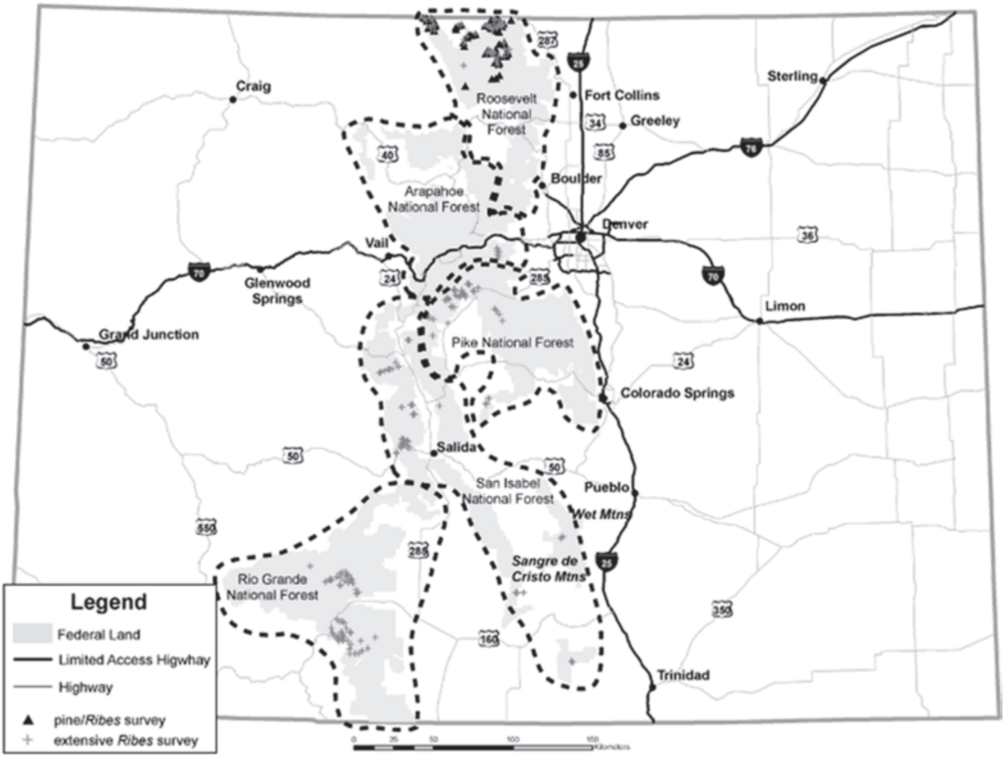

FIG. 1. Location of study areas and *Ribes* survey plots in Colorado.

Materials and Methods. STUDY AREAS. Surveys occurred on 15 study areas in Colorado and Wyoming. Study areas in Colorado (Fig. 1) were defined by National Forest (NF) boundaries and included the Arapaho, Pike, Rio Grande, Roosevelt, and San Isabel NFs. Wyoming study areas (Fig. 2) were defined by government management units and geographic features and included the Horse Creek area of the Shoshone NF; Wind River Indian Reservation, on lands managed by the Bureau of Indian Affairs; Green Mountain, Shirley Mountains, and Muddy Mountain, on lands managed by the Bureau of Land Management; and the Laramie Peak, Sierra Madre, northern and southern areas of the Medicine Bow Mountains, and Pole Mountain areas of the Medicine Bow NF.

PLOT SELECTION. Two surveys, an intensive pine/*Ribes* survey and an extensive *Ribes* survey, were conducted to determine *Ribes* occurrence and density on 11 of the study areas. On the remaining four study areas (Arapaho, Pike, Rio Grande, and San Isabel NFs), only the extensive survey was conducted. The 504 pine/*Ribes* survey plots assessed *Ribes* occurrence and density within limber pine stands, which were also examined to characterize WPBR incidence and severity (Kearns and Jacobi 2007). The 754 extensive *Ribes* survey plots were located near limber pine in habitats typically occupied by various *Ribes* species but were not within limber pine stands. The extent and location of all *Ribes* populations within Wyoming and Colorado were unknown, so our sample did not attempt to represent the entire population but only some typical areas where white pines were expected based on existing databases and expert knowledge. The surveys were located and carried out to provide maximum efficiency with a limited amount of time and resources.

PINE/*RIBES* SURVEY. Stand level data on the occurrence of limber pine in the Roosevelt and Medicine Bow NFs were obtained from the USDA Forest Service Rocky Mountain Resource Inventory System (RMRIS) database. Post-stratification was employed based on site characteristics to capture the variability of site

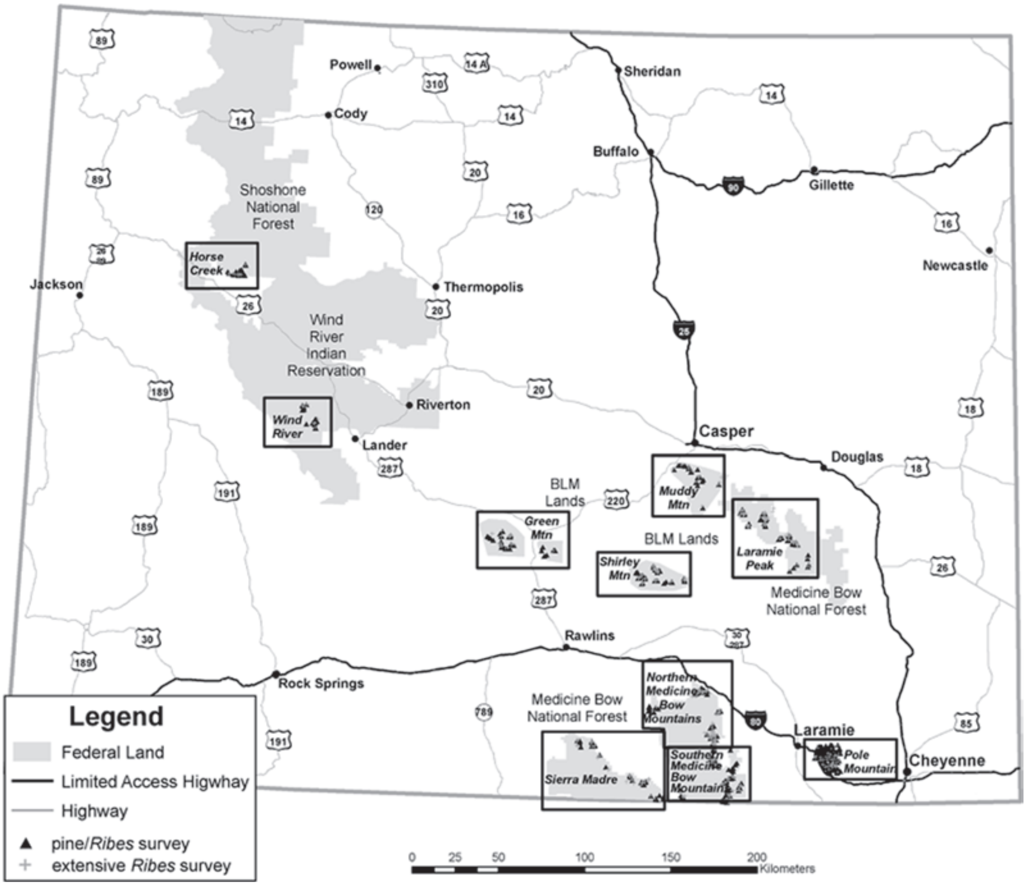

FIG. 2. Location of study areas and *Ribes* survey plots in Wyoming.

conditions under which limber pine grows without regard to WPBR. Selected stands provided a representation of the elevation range of limber pine, on all aspects, topographic positions, and forest composition types available for sampling. Selected stands were further limited to those within 3 km of a road (to minimize travel time and maximize plot number). Paper maps with vegetation and site information were obtained for areas managed by Bureau of Land Management and Bureau of Indian Affairs. Sample locations for areas not included in the RMRIS database were selected on the basis of identification as having significant populations of limber pine.

EXTENSIVE SURVEY. In study areas also surveyed for WPBR, extensive survey plots were located within two km of white pine plots and three km of a road. In Colorado study areas not surveyed for WPBR; extensive survey plots were located along random elevation transects from lower tree line to upper tree line. These plots represented the range of *Ribes* habitats within two km of stands of limber and RM bristlecone pines. Transect locations (latitude and longitude) were determined with a GPS receiver.

SURVEY METHODS. *Pine/*Ribes *Survey.* Two or three belt transects (30.5 × 4.6 m) were established to examine the *Ribes* growing within limber pine stands at the same location of 504 WPBR survey plots (Kearns and Jacobi 2007). The *Ribes* species present, total number of stems and bushes, average number of stems per bush, and average stem length were recorded. The variability in the number of stems per bush required a count of stems present rather than number of bushes alone. Data for all transects at a plot were aggregated

Table 2. Dominant overstory tree species and understory cover types used in *Ribes* survey plots in Colorado and Wyoming. RM = Rocky Mountain.

Dominant overstory tree species	Dominant understory cover types
Ponderosa pine (*Pinus ponderosa*)	Big sagebrush (*Artemisia tridentata*)
Lodgepole pine (*Pinus contorta* var. *latifolia*)	Mountain mahogany (*Cercocarpus montanus*)
Limber pine (*Pinus flexilis*)	Snowberry (*Symphoricarpos* spp.)
RM Bristlecone pine (*Pinus aristata*)	Antelope bitterbrush (*Purshia tridentata*)
Aspen (*Populus tremuloides*)	Common juniper (*Juniperus communis)*
Douglas-fir (*Pseudotsuga menziesii*)	Heart-leaved arnica (*Arnica cordifolia*)
Subalpine fir (*Abies bifolia*)	Willow (*Salix* spp.)
RM juniper (*Juniperus scopulorum*)	Horsetail (*Equisetum* spp.)
Alder (*Alnus* spp.)	Grasses
Engelmann spruce (*Picea engelmannii*)	Soil
Colorado blue spruce (*Picea pungens*)	Rock
Cottonwood (*Populus* spp.)	Leaf litter
Birch (*Betula* spp.)	
Maple (*Acer* spp.)	
No overstory trees present	

and statistics for densities of *Ribes* by species in linear meters of live stem per hectare (m ha^{-1}) were calculated. At each plot, elevation, percent slope, slope aspect, slope position (ridge/summit, shoulder, mid-slope, slope base, valley bottom), slope configuration (broken, concave, convex, linear, undulating), canopy structure (closed canopy, open canopy, mosaic of open and closed canopy, or none if no overstory trees were present), and plot type (riparian, meadow, limber pine forest, other forested/wooded, wetland) were recorded. In addition, the three most common overstory tree species and the three most dominant understory cover types (including both individual plant species and broad cover type classifications such as rock or litter) were recorded (Table 2). Using these methods 504 pine/*Ribes* plots were established from mid-May through September of 2002, 2003, and 2004 (Figs. 1 and 2)

Extensive Survey. Plots were located as described above and sampled by a single 61 by 6.1 m belt transect which constituted the sample plot. The same data items were collected as described in the pine/Ribes survey. During mid-May through September of 2002, 2003, and 2004, 754 extensive survey plots were established in Wyoming and Colorado (Figs. 1 and 2).

DATA ANALYSES. All statistical analyses were performed utilizing the SAS (version 9.1, SAS Institute Inc., Cary, NC, USA) statistical program. To normalize skewed data, *Ribes* densities were transformed to a $\log_{10}$ scale. A one-way analysis of variance with Tukey's honest significant difference (HSD) was used for multiple comparisons of $\log_{10}$ density means by study areas. A three, plot-level variable (plot type, slope position, stand canopy structure), main effects model using Proc Mixed, with study area as a random effect and plots as subsamples, was used to determine differences among densities by plot-level variables. Pearson correlations were used to determine relationships between *Ribes* density and continuous plot-level variables (elevation, latitude, percent slope). Comparisons of *Ribes* densities in plots with and without one of 15 dominant overstory tree species or one of 12 understory cover types were made using a 15 or 12 main effects model. The critical level of significance was set as $P = 0.05$ for LSD and Tukey's HSD analyses and $P < 0.0001$ for Pearson correlation coefficients.

Using the plot-level variables described above, logistic regressions were run for each *Ribes* species to predict the types of sites on which those species were likely to occur. Proc Logistic using stepwise model selection was used to find a reduced model to predict the presence or absence of individual *Ribes* species. Plot variables were only considered for logistic regression if they exhibited significant differences in $\log_{10}$ densities for the *Ribes* species under consideration. All first order interactions between selected variables were also tested for inclusion in the models. Final model selection was determined by maximum values for the Kappa statistic (K), which provides a measure of prediction accuracy while incorporating a correction for chance-

Table 3. Distribution and density of *Ribes cereum* in Colorado and Wyoming.

Study area[a]	Mean density m ha^{-1}	SE[b]	Mean $\log_{10}$ Density[c]	SE[b]	Occurrence[d]	Elevation[e]
Pole Mountain, WY	995.6	117.9	1.88 a	0.09	0.68 (154/226)	2307–2834
Wind River Indian Res., WY	1155.4	597.1	1.27 ab	0.33	0.42 (10/24)	2295–2888
Roosevelt NF, CO	736.9	170.7	1.19 ab	0.12	0.44 (59/134)	2347–2819
Arapahoe NF, CO	1477.4	1352	0.87 bc	0.58	0.25 (2/8)	3018–3231
Southern Medicine Bow Mtns, WY	572.9	188.4	0.86 bc	0.11	0.31 (44/142)	2316–2907
San Isabel NF, CO	1897.6	817.4	0.81 bc	0.19	0.25 (15/60)	2560–3068
Shirley Mountains, WY	196.3	60.4	0.81 bc	0.15	0.32 (21/66)	2256–2667
Sierra Madre, WY	271.3	109.1	0.71 bc	0.15	0.26 (18/68)	2480–2929
Rio Grande NF, CO	934.4	400.2	0.59 bc	0.17	0.18 (11/62)	2679–3414
Pike NF, CO	559.3	216.5	0.55 bc	0.14	0.17 (13/76)	2861–3231
Green Mountain, WY	98.2	40.1	0.50 bc	0.14	0.20 (10/51)	2160–2655
Laramie Peak, WY	68.1	18.8	0.45 bc	0.08	0.19 (25/130)	2112–2597
Muddy Mountain, WY	237.7	150.8	0.43 bc	0.19	0.16 (5/32)	1884–2467
Northern Medicine Bow Mtns, WY	191.8	85.6	0.42 bc	0.08	0.17 (26/151)	2399–2979
Horse Creek, WY	64.1	59.3	0.24 c	0.14	0.11 (3/28)	2354–2679

[a] Study areas were within these government ownership units and do not represent the entire unit.
[b] Standard error of the mean.
[c] Mean $\log_{10}$ m of live stem per $\log_{10}$ ha, means followed by different letters are significantly different at $P = 0.05$ based on Tukey's HSD.
[d] Proportion of plots occupied (plots occupied/plots examined).
[e] Elevation range of occupied plots in m (lowest–highest).

expected agreement. Kappa statistic values < 0.4 were considered as indicating poor agreement, $0.4 \leq K < 0.75$ good agreement, or $K \geq 0.75$ excellent agreement (Fielding and Bell 1997). The reduced models were then fit using Proc Glimmix (generalized linear mixed models), with study areas as a random effect. Plots with no occurrence of a particular *Ribes* species were weighted such that they would be equal to plots with that *Ribes* species. The weighting primarily moved the y-intercept on each model. Due to the categorical nature of the data, no meaningful fit of the data would have been possible without having all categories represented. As such, all the available data were used to build the presence/absence models, and the developed models would need testing against new data to obtain an unbiased estimate of their predictive ability.

Results. Distribution and Density of *Ribes* Species. Ribes cereum. The wax currant was the most commonly encountered *Ribes* species and was present on 33% of all plots (26% of the extensive survey plots and 44% pine/*Ribes* plots). *Ribes cereum* was present in all 15 study areas. Densities of *R. cereum* ranged from 0 to 37,401 m ha^{-1} (0 to 4.57 on $\log_{10}$ scale). Mean density for 1258 plots was 590 m ha^{-1} (standard error of the mean (SE) 62) (0.91 $\log_{10}$, SE 0.04). Densities ($\log_{10}$) differed significantly among some areas (Table 3); the highest density was at Pole Mountain and the lowest density on the Horse Creek study area. The proportion of plots occupied by wax currant within individual study areas ranged from 68% at Pole Mountain to 11% at Horse Creek. This species ranged in elevation from 1884 to 3414 m (Table 3). Of the 416 plots with wax currant, 64% occurred in stands with limber pine as a dominant overstory species, 48% with aspen (*Populus tremuloides* Michx.), 30% with ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), 30% with lodgepole pine (*P. contorta* var. *latifolia* Dougl. ex Loud.), 20% with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and 7% with subalpine fir (*Abies bifolia* A. Murr.). Mean density ($\log_{10}$) differed between the pine/*Ribes* plots (1.15, SE 0.06) and the extensive survey plots (0.74, SE 0.05). This suggested that densities were greater in limber pine stands than elsewhere on the landscape. The density ($\log_{10}$) of *R. cereum* was not different between the Wyoming plots (0.92, SE 0.04, $N = 918$) and the Colorado plots (0.86, SE 0.07, $N = 340$).

Ribes inerme. The whitestem gooseberry was found in 15 study areas on 29% of plots. Whitestem gooseberry was recorded more

Table 4. Distribution and density of *Ribes inerme* in Colorado and Wyoming.

Study area[a]	Mean density		Mean $\log_{10}$		Occurrence[d]	Elevation[e]
	m/ha	SE[b]	Density[c]	SE[b]		
Pole Mountain, WY	3627.5	1004.9	1.57 a	0.12	0.47 (106/226)	2307–2661
San Isabel NF, CO	4658.5	3285.9	1.39 a	0.22	0.43 (26/60)	2560–3506
Pike NF, CO	2702.3	871.4	1.24 ab	0.20	0.36 (27/76)	2857–3597
Wind River Indian Res., WY	7259.9	5557.4	1.20 abc	0.37	0.33 (8/24)	2295–2888
Green Mountain, WY	1632.6	481.0	1.20 abc	0.23	0.35 (13/51)	2160–2655
Shirley Mountains, WY	2360.1	712.9	1.15 abc	0.21	0.33 (22/66)	2256–2508
Roosevelt NF, CO	714.5	133.9	1.00 abc	0.13	0.32 (43/134)	2256–2745
Rio Grande NF, CO	2234.5	1101.2	0.91 abc	0.20	0.27 (17/62)	2642–3414
Southern Medicine Bow Mtns, WY	3519.7	1481.8	0.89 abc	0.13	0.25 (36/142)	2316–2699
Laramie Peak, WY	270.5	72.0	0.67 abc	0.11	0.25 (33/130)	2102–2569
Horse Creek, WY	199.2	112.5	0.50 abc	0.21	0.18 (5/28)	2370–2679
Northern Medicine Bow Mtns, WY	142.7	55.7	0.28 bc	0.07	0.10 (15/151)	2399–2900
Muddy Mountain, WY	224.1	189.4	0.26 bc	0.15	0.25 (3/32)	1747–1966
Sierra Madre, WY	412.4	289.4	0.19 bc	0.10	0.06 (4/68)	2450–2644
Arapahoe NF, CO	1.5	1.5	0.14 c	0.14	0.13 (1/8)	2882

[a] Study areas were within government ownership units and do not represent the entire unit.
[b] Standard error of the mean.
[c] Mean $\log_{10}$ m of live stem per $\log_{10}$ ha, means followed by different letters are significantly different at $p = 0.05$ based on Tukey's HSD.
[d] Proportion of plots occupied (plots occupied/plots examined).
[e] Elevation range of occupied plots in m (lowest–highest).

commonly in the extensive survey plots with 329 of 754 occupied than in the pine/*Ribes* plots with 36 of 504 occupied. *Ribes inerme* densities were extremely variable, ranging from 0 to 209,973 m ha^{-1} (0 to 5.32 $\log_{10}$) and averaging 2027 m ha^{-1} (SE 325) (0.94 $\log_{10}$, SE 0.04) across the 1258 plots. Mean $\log_{10}$ density was highest in the Pole Mountain study area at 1.57 (SE 0.12) and lowest on the Arapaho NF plots at 0.14 (SE 0.14) (Table 4). The proportion of plots occupied by whitestem gooseberry within areas ranged from 47% at Pole Mountain to 6% at the Sierra Madre. The species occurred at elevations from 1747 m to 3597 m (Table 4). Whitestem gooseberry occurred in stands with aspen in 55% of the plots, willow (*Salix* spp.) in 50%, limber pine in 30%, lodgepole pine in 25%, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in 21%, subalpine fir in 12%, ponderosa pine in 11%, and Douglas-fir in 10% of plots. Mean density ($\log_{10}$) differed between the extensive survey plots (1.43, SE 0.06) and the pine/*Ribes* plots (0.20, SE 0.03). This suggested that densities were lower in limber pine stands than elsewhere on the landscape. Mean density was greater in the 340 Colorado plots (1.08, SE 0.08) than in the 918 Wyoming plots (0.89, SE 0.05).

Ribes lacustre. The prickly currant was present on only 8% of plots—13% of extensive survey plots and 1% of pine/*Ribes* plots established in seven of the 15 study areas (Table 5). Densities of *Ribes lacustre* ranged from 0 to 23,786 m ha^{-1} (0 to 4.38 $\log_{10}$). Mean density ($\log_{10}$) was significantly higher within the Northern Medicine Bow Mountains study area (1.02, SE 0.13) than in all other study areas except the Sierra Madre (Table 5). The Northern Medicine Bow Mountains study area also had the highest proportion of plots occupied by prickly currant. *Ribes lacustre* was found on plots ranging in elevation from 2321 to 3101 m. Tree species listed among the three most common in the 99 plots with *R. lacustre* were subalpine fir in 70% of plots, Engelmann spruce in 64%, lodgepole pine in 45%, alder (*Alnus* spp.) in 31%, aspen in 30%, and limber pine in 10% of plots. Densities of *R. lacustre* were greater in the Wyoming plots (0.32, SE 0.03) compared to the Colorado plots (0.06, SE 0.05).

Ribes montigenum. The gooseberry currant was present on 6% of plots: 10% of the extensive survey plots and only 1% of pine/*Ribes* plots. Plots with record of *Ribes montigenum* were present in 6 of the 15 study areas (Table 6). Densities of *R. montigenum* ranged from 0 to 51,050 m ha^{-1} (0 to 4.71 $\log_{10}$). Mean $\log_{10}$ densities of gooseberry currant were higher within the Rio Grande and Pike NFs of Colorado (1.73 and 1.22,

Table 5. Distribution and density of *Ribes lacustre* in Colorado and Wyoming.

Study area[a]	Mean density m/ha	Mean density SE[b]	Mean $\log_{10}$ Density[c]	Mean $\log_{10}$ SE[b]	Occurrence[d]	Elevation[e]
Northern Medicine Bow Mtns, WY	1332.7	291.9	1.02 a	0.13	0.30 (46/151)	2580–3101
Sierra Madre, WY	321.8	111.1	0.68 ab	0.15	0.24 (16/68)	2479–2893
Southern Medicine Bow Mtns, WY	351.0	157.7	0.35 bc	0.08	0.11 (16/142)	2576–3077
Wind River Indian Res., WY	245.8	231.5	0.26 bc	0.18	0.08 (2/24)	2824–2888
Laramie Peak, WY	320.4	201.8	0.20 bc	0.07	0.07 (9/130)	2321–2558
Shirley Mountains, WY	26.2	16.2	0.15 bc	0.07	0.06 (4/66)	2398–2592
Roosevelt NF, CO	94.6	54.4	0.14 bc	0.06	0.04 (6/134)	2603–2862

[a] *Ribes lacustre* was not observed in study areas not listed. Study areas were located within government ownership units and do not represent the entire unit.
[b] Standard error of the mean.
[c] Mean $\log_{10}$ m of live stem per $\log_{10}$ ha, means followed by different letters are significantly different at $p = 0.05$ based on Tukey's HSD.
[d] Proportion of plots occupied (plots occupied/plots examined).
[e] Elevation range of occupied plots in m (lowest–highest).

respectively) than in any other study areas (Table 6). Elevations of plots on which *R. montigenum* occurred ranged from 2670 m to 3658 m. Presence of *R. montigenum* was most commonly associated with the following species: Engelmann spruce in 88%, subalpine fir in 36%, RM bristlecone pine in 17%, lodgepole pine in 13%, and limber pine in 10% of plots. There were significant differences between Colorado and Wyoming with regard to the density of gooseberry currant, 0.69 (SE 0.04) and 0.03 (SE 0.03), respectively.

OTHER *RIBES* SPECIES. Three other species of *Ribes* were found only rarely. *Ribes laxiflorum*, trailing black currant, was present in only three areas in Colorado (Pike, San Isabel, and Rio Grande NFs). *Ribes laxiflorum* was found on five of the 754 extensive survey plots with densities that ranged from 0 to 6631.4 m ha^{-1} (0 to 3.66 $\log_{10}$). *Ribes laxiflorum* was not recorded in any of the 504 pines/*Ribes* plots. Elevations of plots with *R. laxiflorum* ranged from 2966 to 3330 m. *Ribes laxiflorum* was found growing in stands with Engelmann spruce, subalpine fir, aspen, lodgepole pine, and RM bristlecone pine among the three dominant tree species. *Ribes hudsonianum*, northern black currant, was present on only four of the 754 extensive survey plots (all on Wind River Indian Reservation, WY) and was not recorded in any of the 504 pine/*Ribes* plots. Mean $\log_{10}$ density of *R. hudsonianum* within the nine extensive survey plots on the Wind River Indian Reservation was 1.29 (SE 0.08). *Ribes hudsonianum* was found from 2475 to 2681 m. Dominant tree species in plots with *R. hudsonianum* were aspen, Douglas-fir, lodgepole pine, limber pine, and alder. *Ribes viscosissimum*, sticky currant, was recorded on

Table 6. Distribution and density of *Ribes montigenum* in Colorado and Wyoming.

Study area[a]	Mean density m/ha	Mean density SE[b]	Mean $\log_{10}$ Density[c]	Mean $\log_{10}$ SE[b]	Occurrence[d]	Elevation[e]
Rio Grande NF, CO	5048.7	1427.7	1.73 a	0.24	0.48 (30/62)	2966–3609
Pike NF, CO	2292.0	824.2	1.22 a	0.19	0.37 (28/76)	3048–3658
San Isabel NF, CO	764.5	294.1	0.56 b	0.17	0.17 (10/60)	3008–3597
Horse Creek, WY	168.1	155.3	0.22 bc	0.16	0.07 (2/28)	2670–2731
Wind River Indian Res., WY	141.8	141.8	0.15 bc	0.15	0.04 (1/24)	2824
Northern Medicine Bow Mtns, WY	166.0	133.8	0.13 bc	0.05	0.04 (6/151)	2899–3155

[a] *Ribes montigenum* was not observed in study areas not listed. Study areas were located within government ownership units and do not represent the entire unit.
[b] Standard error of the mean.
[c] Mean $\log_{10}$ m of live stem per $\log_{10}$ ha, means followed by different letters are significantly different at $p = 0.05$ based on Tukey's HSD.
[d] Proportion of plots occupied (plots occupied/plots examined).
[e] Elevation range of occupied plots in m (lowest–highest).

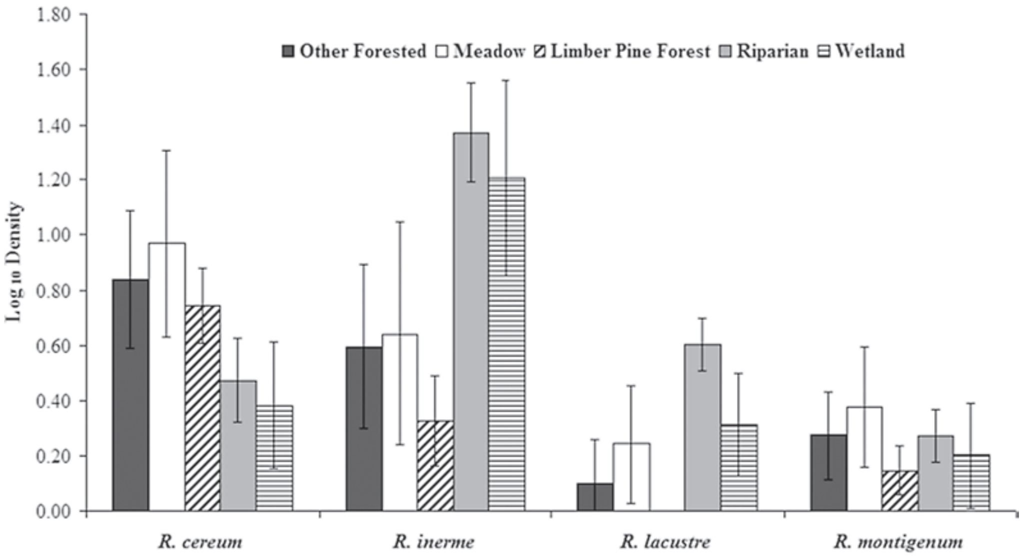

FIG. 3. Mean $\log_{10}$ density of four *Ribes* species by plot type in Colorado and Wyoming.

only one of the 754 extensive survey plots (Laramie Peak study area, Medicine Bow NF) and in none of the 504 pine/*Ribes* plots. That plot was located at 2393 m elevation, and the density of *R. viscosissimum* was 98.4 m ha^{-1} (2.0 $\log_{10}$). Engelmann spruce, subalpine fir, lodgepole pine, and *R. lacustre* were growing in association with *R. viscosissimum.*

RELATIONSHIPS BETWEEN DENSITY AND PLOT VARIABLES. Relationships between plot variables and *Ribes* densities were explored for *Ribes cereum*, *R. inerme*, *R. lacustre*, and *R. montigenum*; the other species were found too rarely for quantification.

Ribes cereum. Wax currant $\log_{10}$ densities were weakly, negatively correlated with elevation ($r = -0.22$) and positively correlated with percent slope ($r = 0.19$). Densities of *R. cereum* were greater in meadow plots compared to wetland and riparian plots (Fig. 3) based on Tukey's HSD. Plots located in closed canopy stands had lower stem densities (0.40) than did stands with either open canopies (1.04) or a mosaic of both open and closed canopies (0.83). *Ribes cereum* densities did not differ by slope position, configuration or aspect. Wax currant densities were greater when ponderosa pine and Douglas-fir were among the three dominant tree species on the plot. Densities were lower on plots with lodgepole pine and subalpine fir among the three dominant tree species. Dominant ground cover types affected densities with greater densities associated with big sage (*Artemisia tridentata* Nutt.), common juniper (*Juniperus communis* L.), and rock; significantly lower wax currant densities were associated with willow and leaf litter. These data suggest that *R. cereum* densities would be higher in lower elevation, dry, open areas than in moist, densely forested areas.

Ribes inerme. Whitestem gooseberry $\log_{10}$ densities were significantly, though weakly, negatively correlated with elevation ($r = -0.21$) and percent slope ($r = -0.24$). Plant densities varied by plot type (Fig. 3); higher mean densities occurred on plots described as riparian (1.37) than limber pine forest (0.33), other forested (0.60), or meadow (0.64) plots. Whitestem gooseberry densities were also greater within wetland plots (1.21) compared to limber pine forest plots. Plots in valley bottoms had greater average densities (1.25) than did plots in ridge/summit (0.52), shoulder (0.58), or mid-slope (0.76) positions. Neither stand canopy structure nor slope configuration were related to density. Higher densities were associated with plots on eastern and northeastern aspects (1.32 and 1.25, respectively) than plots located on western, northwestern, or northern aspects (0.61, 0.61, 0.69, respectively). Higher densities were found on plots with aspen as a dominant component,

Table 7. Results of logistic regression on the odds of *Ribes cereum* occurrence in Colorado and Wyoming.

Parameter	DF	Estimate	SE	p^a	Odds ratios[b] Unit	Estimate	95% C.I.	
Intercept	14	10.209	1.335	< 0.0001				
Elevation (m)	1226	−0.004	0.000	< 0.0001	100	0.65	0.59	0.71
Slope (%)	1226	0.058	0.006	< 0.0001	1	1.06	1.05	1.07
Ponderosa pine (Present)	1226	1.479	0.248	< 0.0001		4.39	2.70	7.15
Subalpine fir (Present)	1226	−1.025	0.216	< 0.0001		0.36	0.23	0.55

[a] *P*-value based on *F*-test. Kappa statistic = 0.47.

[b] Likelihood adjusted odds ratios indicate the change in odds that *Ribes cereum* will occur on a plot if the parameter increases by one or 100 m for elevation or if that parameter is present as one of the three dominant tree species on the plot.

and lower densities were associated with plots dominated by lodgepole pine, limber pine, Engelmann spruce, subalpine fir, ponderosa pine, or Douglas-fir. Higher densities were found on plots with willow dominating the understory and lower densities were associated with plots dominated by common juniper, big sage, and leaf litter. These data indicate that whitestem gooseberry densities are likely to be highest on lower elevation, riparian and wetlands areas with gentle slopes and components of aspen and willow.

Ribes lacustre. The density of prickly currant did not differ by elevation or percent slope, but greater $\log_{10}$ densities were found on plots described as riparian (0.60) than on any other plot type (Fig. 3). Prickly currant densities did not vary by slope position, but plots located on northeastern aspects had higher densities than those located on southern, southwestern, western, and northwestern aspects. Prickly currant densities were greatest in closed canopy stands (0.41), which were significantly greater than the average densities found in open canopy stands (0.17) and those with no overstory present (0.01). Greater densities of *Ribes lacustre* were associated with the presence of subalpine fir, alder, and Engelmann spruce when compared to plots without those species as dominant overstory cover types. Plant densities were also higher in plots with leaf litter listed as a dominant understory cover type, which likely corresponds with the significantly higher densities found in closed canopy stands. These data suggest that the highest densities of *R. lacustre* are likely to be associated with riparian areas and closed canopy forests with components of Engelmann spruce, subalpine fir, and alder.

Ribes montigenum. Gooseberry currant $\log_{10}$ densities were correlated with elevation (r = 0.55); elevation alone explained 27% of the variance in densities. Densities also were negatively correlated with latitude (r = −0.43) indicating that densities were higher in more southern (Colorado) plots. No relationships between gooseberry currant and the plot variables plot type, slope position, canopy structure, slope configuration or slope aspect were significant. Greater densities were associated with Engelmann spruce as a dominant overstory tree. No comparisons between presence and absence of understory cover types were considered significant due to small sample sizes (i.e., less than 30). These data indicate that the highest densities of gooseberry currant would be found in more southerly locations, in high elevation stands of Engelmann spruce.

PREDICTING THE PRESENCE OF *RIBES* BY SPECIES. Ribes cereum. The generalized linear mixed model for predicting the presence/absence of *Ribes cereum* included four variables (Table 7). The odds of a plot having *R. cereum* increased with percent slope and the presence of ponderosa pine as a dominant in the overstory. The probability of a plot having *R. cereum* decreased with elevation and the presence of subalpine fir as dominant overstory components. The Kappa statistic of 0.47 was low relative to the other species modeled and indicated fair agreement between predicted and actual presence of *R. cereum*. The model accurately predicted the presence of *R. cereum* in 75.0% of cases and accurately predicted the absence of *R. cereum* in 75.1% of cases. The model suggests that low elevation, xeric sites with an overstory dominated by ponderosa pine are likely habitats for *R.*

Table 8. Results of logistic regression on the odds of *Ribes inerme* occurrence in Colorado and Wyoming.

					Odds Ratios[b]			
Parameter	DF	Estimate	SE	p^a	Unit	Estimate	95% C.I.	
Intercept	14	12.879	1.550	< 0.0001				
Elevation (m)	1231	−0.006	0.001	< 0.0001	100	0.56	0.50	0.62
Plot type: riparian	1231	2.706	0.274	< 0.0001		14.97	8.74	25.62
Plot type: meadow	1231	1.915	0.333	< 0.0001		6.78	3.53	13.05
Plot type: forested	1231	2.146	0.324	< 0.0001		8.55	4.52	16.15
Plot type: wetland	1231	2.603	0.309	< 0.0001		13.50	7.36	24.77
Plot type: limber pine		0						
Lodgepole pine (present)	1231	−0.836	0.189	< 0.0001		0.43	0.30	0.63
Subalpine fir (present)	1231	−0.761	0.223	0.0007		0.47	0.30	0.72
Overstory trees (present)	1231	1.022	0.321	0.0015		2.78	1.48	5.22
Big sage (present)	1231	−0.923	0.241	0.0001		0.40	0.25	0.64
Willow (present)	1231	0.885	0.240	0.0002		2.42	1.51	3.88

[a] *P*-value based on *F*-test. Kappa statistic = 0.56.
[b] Likelihood adjusted odds ratios indicate the change in odds that *Ribes inerme* will occur on a plot if the parameter increases by one unit or 100 m for elevation, or when compared to plots with limber pine, or if that parameter is present as one of the three dominant overstory or understory cover types on the plot.

cereum in central and southeastern Wyoming and Colorado.

Ribes inerme. The selected model for predicting the presence of *Ribes inerme* (Table 8) included seven variables. The probability of *R. inerme* on a plot increased with the presence of an overstory composed of willow. The odds of finding *R. inerme* on a plot was nearly 15 times greater in riparian areas, 13.5 times greater in wetland areas, and 8.5 times greater in forested areas other than limber pine stands, than in limber pine forests. Odds of occurrence decreased with elevation, with the presence of lodgepole pine and subalpine fir as dominant overstory components, and with the presence of big sage as dominant understory cover. The Kappa statistic for the selected model was 0.56 and indicated good agreement. The model accurately predicted the presence of *R. inerme* in 80.8% of cases and accurately predicted the absence of *R. inerme* in 80.3% of cases. The model suggests that lower elevation, mesic sites with a component of willow are likely habitats for *R. inerme* in central and southeastern Wyoming and Colorado.

Ribes lacustre. The generalized linear mixed model for predicting the presence of *Ribes lacustre* included five variables (Table 9). The model indicated that probability of *R. lacustre* occurrence increased with the presence of subalpine fir, alder, and Engelmann spruce as dominant overstory components. Plot type also influenced the odds of finding *R. lacustre* with higher odds associated with riparian (23 times) and wetland plots (seven times) as compared to the odds of finding *R. lacustre* in limber pine forested plots. Leaf litter as a dominant understory cover type was associated with greater odds of *R. lacustre* occurrence. In most cases, leaf litter is a dominant cover type in densely forested areas and where growing conditions are inadequate to support shrub and herbaceous cover. The Kappa statistic was 0.52 and indicated moderate agreement between predicted and actual occurrence of *R. lacustre*. The model accurately predicted the presence of *R. lacustre* in 93.9% of cases and accurately predicted the absence of *R. lacustre* in 88.5% of cases. Overall, the model correctly classified 90.0% of the 1258 plots used to develop and test the model. The model suggests that wetter sites, riparian and wetland areas, with subalpine fir, Engelmann spruce, and alder comprising a dense overstory are likely habitats for *R. lacustre* in Colorado and central and southeastern Wyoming.

Ribes montigenum. The selected model for predicting the odds of occurrence of *Ribes montigenum* utilized two variables: elevation and the presence or absence of Engelmann spruce (Table 10 and Fig. 4). The odds of a plot containing *R. montigenum* increased by 2.6 with every 100 m increase in elevation and increased by a factor of 2.5 with Engelmann spruce as a dominant overstory component compared to plots without Engelmann spruce. The Kappa statistic (0.56) indicated the model provides good agreement between actual and

Table 9. Results of logistic regression on the odds of *Ribes lacustre* occurrence in Colorado and Wyoming.

Parameter	DF	Estimate	SE	P^a	Odds Ratios[b] Estimate	95% C.I.	
Intercept	14	−5.783	0.906	< 0.0001			
Plot type: riparian	1235	3.132	0.329	< 0.0001	22.92	12.01	43.73
Plot type: meadow	1235	1.010	0.768	0.1888	2.75	0.61	12.40
Plot type: forested	1235	0.936	0.476	0.0494	2.55	1.00	6.48
Plot type: wetland	1235	1.968	0.421	< 0.0001	7.16	3.14	16.34
Plot type: limber pine		0					
Subalpine fir (present)	1235	1.136	0.221	< 0.0001	3.11	2.02	4.80
Alder (present)	1235	1.316	0.328	< 0.0001	3.73	1.96	7.10
Engelmann spruce (present)	1235	1.464	0.252	0.0005	4.32	2.64	7.08
Leaf litter (present)	1235	1.380	0.290	< 0.0001	3.97	2.25	7.02

[a] *P*-value based on *F*-test. Kappa statistic = 0.52.
[b] Likelihood adjusted odds ratios indicate the change in odds that *Ribes lacustre* will occur on a plot compared to limber pine forest plot or if that parameter is present as one of the three dominant overstory or understory cover types on the plot.

predicted occurrence of *R. montigenum*. The model accurately predicted the presence of *R. montigenum* in 96.1% of cases and accurately predicted the absence of *R. montigenum* in 91.9% of cases. Overall, the model correctly classified 92.1% of the 1256 plots used to develop and test the model. The model suggests that high elevation sites with Engelmann spruce are likely habitats for *R. montigenum*.

Discussion. In this first extensive survey of *Ribes* in the mountains of Colorado and Wyoming, we found species susceptible to WPBR in all study areas indicating a potential risk of infection for many areas not already infested with WPBR. *Ribes* were found growing across a wide elevation range, 1750 to 3650 m, which encompasses much of the range of white pines in central and southeastern Wyoming and Colorado. Although *Ribes* were present in all of the study areas, the species present and the density of each varied greatly among the plots. *Ribes inerme*, a species thought to be of moderate importance in the spread and intensification of WPBR, and *R. cereum*, a species of low relative importance to the spread and intensification of WPBR, were present in all of the study areas; *R. lacustre* and *R. montigenum* (both moderate in relative importance) were locally prevalent in some study areas and absent from others; and *R. laxiflorum*, *R. hudsonianum*, and *R. viscosissimum* were not common in any of the study areas.

Site Factors and *Ribes* Species Occurrence and Densities. Our attempts to predict which specific types of sites *Ribes cereum* occur were not all that promising ($K = 0.47$). Nonetheless, our model indicated that the odds of *R. cereum* occurrence increase with slope steepness and the presence of ponderosa pine and decrease with increasing elevation and the presence of subalpine fir. Although *Ribes cereum* is generally considered among

Table 10. Results of logistic regression on the odds of *Ribes montigenum* occurrence in Colorado and Wyoming.

Parameter	DF	Estimate	SE	P^a	Odds Ratios[b] Unit	Estimate	95% C.I.	
Intercept	14	−30.444	2.764	< 0.0001				
Elevation (m)	1239	0.010	0.001	< 0.0001	100	2.62	2.19	3.13
Engelmann spruce (present)	1239	0.907	0.281	0.0013		2.48	1.43	4.30

[a] *P*-value based on *F*-test. Kappa statistic = 0.56.
[b] Likelihood adjusted odds ratios indicate the change in odds that *R. montigenum* will occur on a plot if the parameter increases by the unit (100 m) or if that parameter is present as one of the three dominant overstory tree species on the plot.

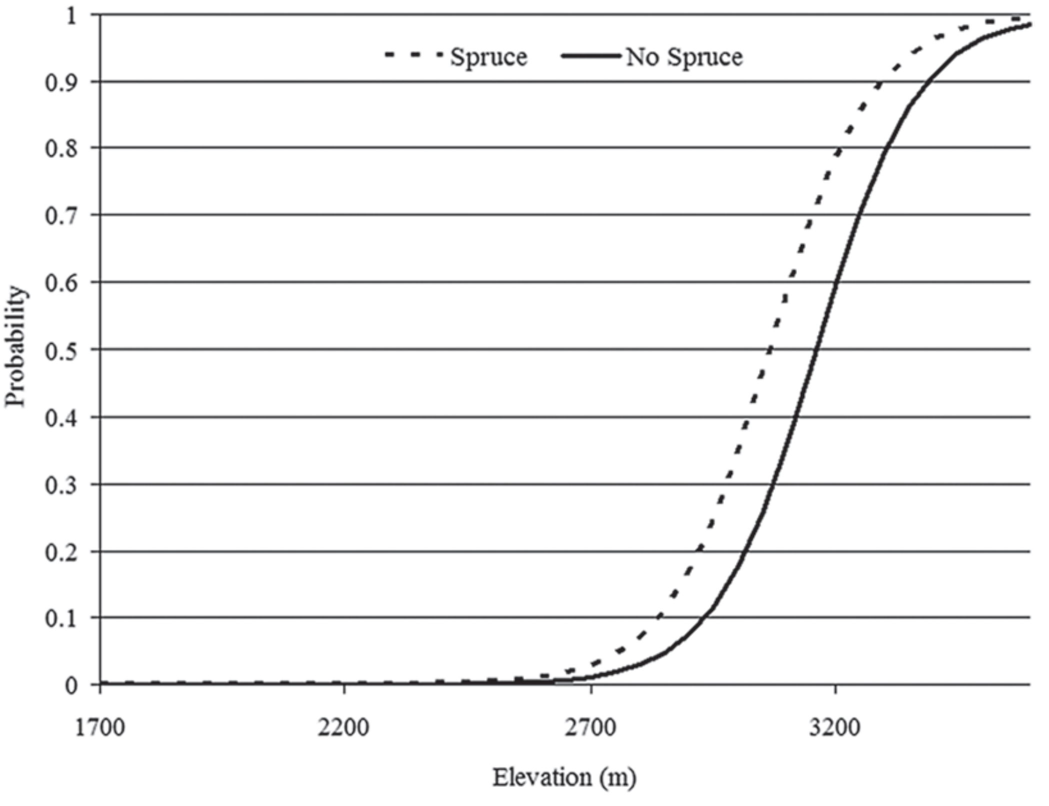

FIG. 4. Cumulative probability curve for the occurrence of *Ribes montigenum* illustrating increasing probability of *R. montigenum* with increasing elevation and the presence of Engelmann spruce.

the least susceptible of western North American *Ribes* species to *Cronartium ribicola* and the lowest producer of telia when infected (Kimmey 1938), some forms are reported to produce significant inocula under conducive infection conditions (Kimmey and Mielke 1944). The observation of a heavily infected *R. cereum* in the Pole Mountain area leads us to speculate that this species may be more important than previously reported in the epidemiology of the rust. In Colorado and central and southeastern Wyoming, *R. cereum* densities appear to be highest in lower elevation, meadow and open sites, which supports an earlier study of limited geographic range at Rocky Mountain National Park and anecdotal observations (Peet 1981, Van Arsdel and Geils 2004). These are usually drier sites, but under conducive meteorological conditions these plants may be important inoculum sources.

We found densities of *Ribes inerme* were significantly higher in riparian and wetland areas. Although *R. inerme* was found on slopes of all aspects, northeastern facing slopes appeared to have the highest densities, followed closely by eastern, southeastern, and southwestern facing slopes. Our field data support the reports of Peet (1981) and Van Arsdel and Geils (2004). The odds of *R. inerme* growing on a plot increased at lower elevations on plots with willow, indicating more mesic environments. *Ribes inerme* has a relatively high susceptibility to *Cronartium ribicola* and a high capacity for telial production (Mielke et al. 1937, Mielke 1943). The higher occurrence and density of *R. inerme* in riparian and wetland areas, sites that are likely to have favorable conditions for infection and intensification of the rust fungus (Mielke 1937), indicates that *R. inerme* is or has the potential to become important in the spread and intensification of *C. ribicola* in Colorado and central and southeastern Wyoming. For example, at the isolated WPBR outbreak on Gallinas Peak (Cibola NF, New Mexico), *R.*

inerme is the only *Ribes* species present (Van Arsdel and Geils 2004).

We found densities of *Ribes lacustre* highest in riparian areas, in valley bottoms, and in forested areas with closed canopies, which agrees with general anecdotal observations (Peet 1981, Van Arsdel and Geils 2004). The odds of finding *R. lacustre* on a plot increased for mesic plots with subalpine fir, Engelmann spruce, and alder in a denser overstory. Several studies indicate that *R. lacustre* is moderately susceptible to *Cronartium ribicola* and that telial production on *R. lacustre* is relatively low (Kimmey 1938, Mielke et al. 1937). However, in one area of British Columbia a rapid increase in WPBR could be attributed solely to *R. lacustre* (Mielke 1937). Considering that *R. lacustre* appears to occupy sites likely to have favorable conditions for infection and spore production (i.e., shaded, cool, riparian areas), this species should be considered a potentially important component the white pine blister rust pathosystem.

In subalpine and alpine communities, *Ribes montigenum* is frequently a dominant shrub of open slopes and spruce-fir forests (Peet 1981, Van Arsdel and Geils 2004). We found greatest *R. montigenum* densities in Engelmann spruce forests at higher elevations. Kimmey and Mielke (1944) reported that *R. montigenum* is moderately susceptible to infection by *Cronartium ribicola* and intermediate in telial production. As such, it must also be deemed a potential substrate for inoculum production at higher elevations.

IMPLICATIONS ON THE OCCURRENCE OF WHITE PINE BLISTER RUST. Our survey indicates that various species of *Ribes* grow throughout the range of native white pines in Colorado and central and southeastern Wyoming. Although the species that are commonly found throughout these study areas vary in their susceptibility and ability to produce inocula, all can contribute to the completion of the life cycle of *Cronartium ribicola*. The ability to predict *Ribes* species presence and stem density can be used by forest managers and tree health specialists in developing landscape-scale hazard ratings and WPBR mitigation plans. This study did not investigate synergistic interactions within the WPBR pathosystem where multiple species of *Ribes* are present on a site or in the surrounding landscape. The ecology and genetics of individual *Ribes* populations and species communities should be considered in assessing the potential impacts of *C. ribicola* on white pines. It is evident from this study, however, that the white pines of Colorado and central and southeastern Wyoming are not likely to escape infection by *C. ribicola* solely due to the absence of the *Ribes* host.

Even though the presence of *Ribes* is known as a major factor in the incidence and severity of WPBR there are limited models that utilize this relationship since *Ribes* populations are not easy to quantify. For managed western white pine stands in northern Idaho, eastern Washington, and western Montana, a preliminary expert hazard rating system was developed based on habitat type and potential *Ribes* density based on site preparation method, slope aspect, and the amount of disturbance to the duff layer (Rust 1988). Rust hazard could also be estimated by measuring within stand *Ribes* populations, but this method was not considered as effective as a rust index based on previous canker incidence (Hagle et al. 1989). Smith and Hoffman (2001) created a series of logistic regression models to predict incidence of WPBR in southern Idaho and western Wyoming. Higher incidence was related to greater average pine stem diameter, lower elevation, greater mean summer precipitation, the presence of *Ribes* species within the stand, lower stand densities, gentle slopes, topographic position, and habitat type.

In a related risk rating modeling effort we found that the presence of *Ribes inerme* was the first variable in a classification and regression tree (CART) analysis used to as the first splitting point for probabilities of finding the rust (Kearns 2005). The classification tree based on plot variables contained five terminal nodes and included *Ribes inerme* density within 1 km radius of the plot, stream density within 1 km radius of the plot, and the presence/absence of ponderosa pine as predictor variables. Stream density was a good surrogate for *Ribes* species that grow in wet sites such as *R. inerme* and *R. lacustre*

Recently, two species in the family Orobanchaceae (*Pedicularis racemosa* Dougl. and *Castilleja miniata* Dougl.) were reported to be naturally infected with *Cronartium ribicola* in northern Idaho (McDonald et al. 2006). These species occur throughout much of the limber pine and RM bristlecone pine habitats of Wyoming and Colorado. Their role in the WPBR pathosystem of the central Rocky Mountains is currently unknown and will require further investigation.

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