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Frequency of Comandra Blister Rust Infection Episodes on Lodgepole Pine

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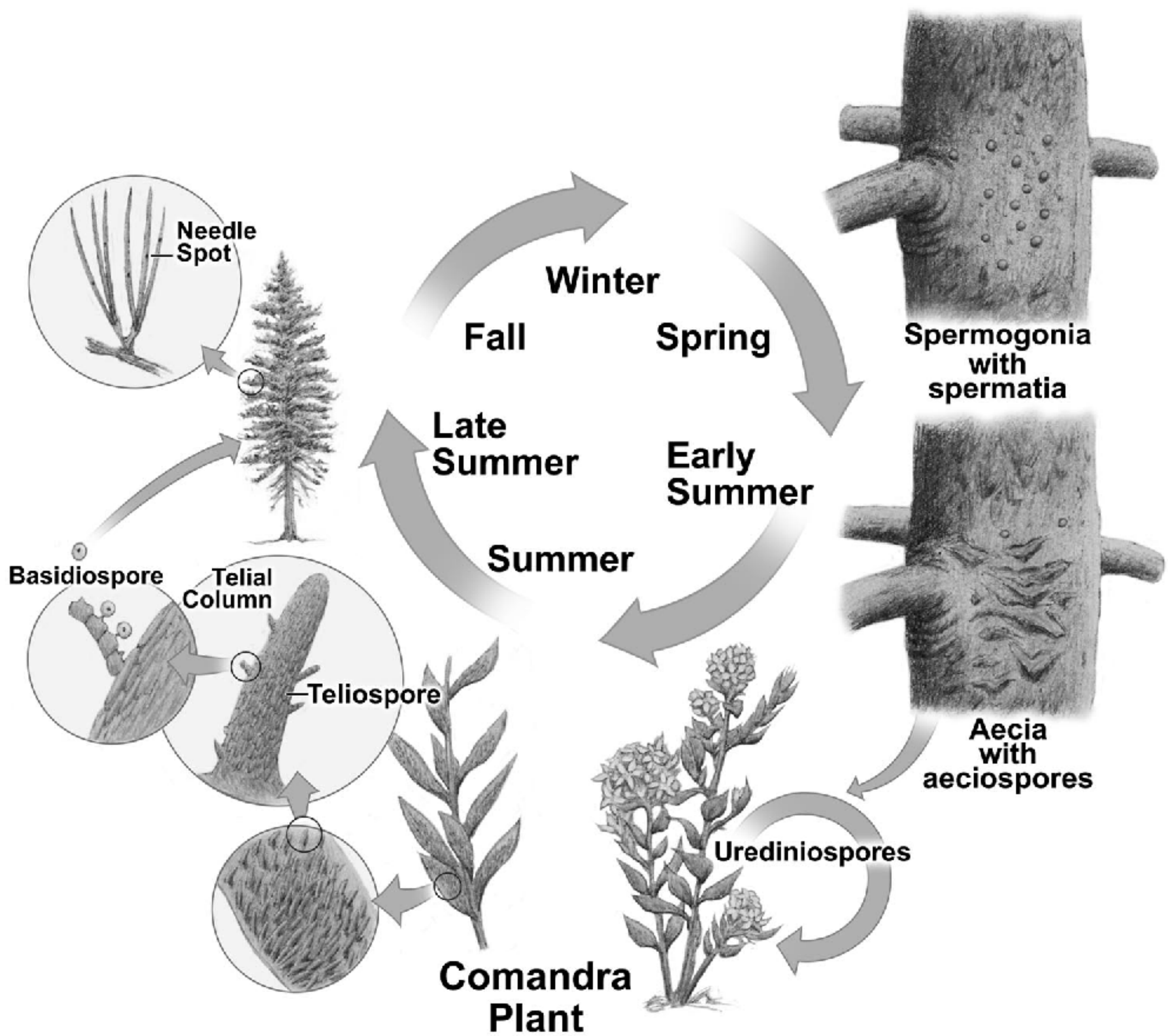

Abstract

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Comandra blister rust is a damaging canker disease of lodgepole pine in the Central Rocky Mountains. Our knowledge of previous blister rust outbreaks and the effects of weather and climate on rust epidemiology has not been sufficient to explain the frequency and severity of disease outbreaks. Thus, we sought to describe the seasonal and annual frequency and duration of meteorological conditions favorable for infection of lodgepole pine, to relate infection episodes to various weather phenomena, to observe new canker appearances on young trees, and to age existing cankers on mature trees. We examined comandra blister rust outbreaks for three areas in the Central Rockies—Beaverhead in southwestern Montana, Shoshone in western Wyoming, and Medicine Bow in south-central Wyoming. We defined periods suitable for comandra blister rust infection of lodgepole pine (potential infection episodes), based on published criteria, and identified as continuous periods longer than 6 hours during the months of July, August, and September when temperature ranged between 10 and 20 °C and the air was nearly saturated. Synoptic daily weather maps were examined to classify weather systems associated with potential infection episodes. We also observed canker establishment on young and mature lodgepole pine trees to determine canker age distributions. Meteorological records indicated that weather conditions considered suitable for infection of lodgepole pine occurred at least every few (~3) years. The frequency, but not the duration of potential infection episodes, were related to the prevailing summer weather patterns within various regions of the Central Rocky Mountains. The pattern of infection observed in one young stand for 8 years was like that which would result from several, sequential wave years. We found no evidence in the age distribution of bole cankers for only one comandra blister rust outbreak in the three study areas. A consistent pattern between meteorological and canker age data indicates that infection occurs frequently enough across the Central Rocky Mountains that comandra blister rust can be considered a continuing threat where populations of comandra and lodgepole coexist.

Keywords: climate, weather, meteorology, risk rating, spore dispersal

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Introduction

Comandra blister rust is a damaging canker disease of pine caused by the native fungus *Cronartium comandrae* Peck (Johnson 1986). Although the pathogen is distributed across North America, the disease is most prevalent in the Western United States and Canada (Powell 1970), particularly in the Rocky Mountain region (Krebill 1965; Mielke 1957; Peterson 1962). The pine species in Western North America that are most often cankered are lodgepole pine (*Pinus contorta* Dougl. ex Loud. subsp. *latifolia* (Engelm. ex S. Wats.) Critchf.) and ponderosa pine (*P. ponderosa* Laws.). Several years after infection, a rust canker girdles the host stem and kills individual branches ("flagging"), a portion of the crown ("topkill"), or the entire tree ("mortality") (Geils and Jacobi 1990). The resulting damage to the pine host is growth loss, deformity, cull, and reduced cone and seed production (Geils and Jacobi 1993; Schaffer and others 1983). Like all blister rust fungi, this pathogen is an obligate parasite, but on a living pine it can persist for years and continue spreading and intensifying the infestation. Outbreaks occur and persist when and where the pathogen encounters susceptible hosts under favorable environment conditions. Evidence of the resulting damage endures as cankers for decades in mature trees but only a few years in seedlings because these trees are girdled quickly and die.

The life cycle of comandra blister rust (fig. 1) requires a complex alternation of spore stages on different plant genera (Bergdahl and French 1976; Krebill 1968). Aeciospores are produced from spring to early summer on perennial cankers of the pine host and wind blown for kilometers to infect herbaceous comandra plants. In the Central Rocky Mountains, the common alternate host is the pale comandra (*Comandra umbellata* (L.) Nutt. subsp. *pallida* (DC.) Piehl); in northern Montana and Canada, the usual host is northern comandra (*Geocaulon lividum* (Richards.) Fern.) (Krebill 1991). Germinating aeciospores infect comandra leaves, and the repeating spore stage (urediniospores) spreads and intensifies the fungus in the comandra population (fig. 1). Several weeks later, the fungus produces telia and basidiospores on the comandra plants (Tainter 1973). These delicate basidiospores are wind dispersed during periods of high humidity and infect pine needles or young shoots. Over the next couple of years, the fungus grows into the branch and begins producing aeciospores 2 or 3 years after infection. The occurrence and severity of rust outbreaks are usually limited by the requirements for spatial proximity and abundance of the two different host species, and occasional periods during the summer when the air remains humid long enough for an infection episode, when basidiospores form, disperse, germinate, and infect pines (Krebill 1968).

The impacts of comandra blister rust on management of lodgepole pine can be mitigated by planning for expected mortality and growth loss (Geils and Jacobi 1991; Navratil and Bella 1988). We have developed functions to describe the spatial relationship between comandra and the incidence of the rust on pine (Jacobi and others 1993), the development of rust on pine (Geils and Jacobi 1990), and the effects of topkill on growth and survival of lodgepole pine trees (Geils and Jacobi 1993). Our knowledge of previous blister rust outbreaks and the effects of weather and climate on rust epidemiology, however, has not been sufficient to explain the frequency and severity of disease outbreaks (Krebill 1991). An understanding of the historic changes in host distribution, abundance, and age-class structure, the spatial and temporal variations in weather patterns, and the extent and duration of comandra blister rust outbreaks would benefit our ecological understanding and management of lodgepole pine forests. Understanding these comandra blister rust outbreaks would also be instructive for assessing the potential impacts of the introduced white pine blister rust (*Cronartium ribicola* Fisch.) in the Central Rockies. Knowledge of the past is needed to manage for the future (Swetnam and others 1999).

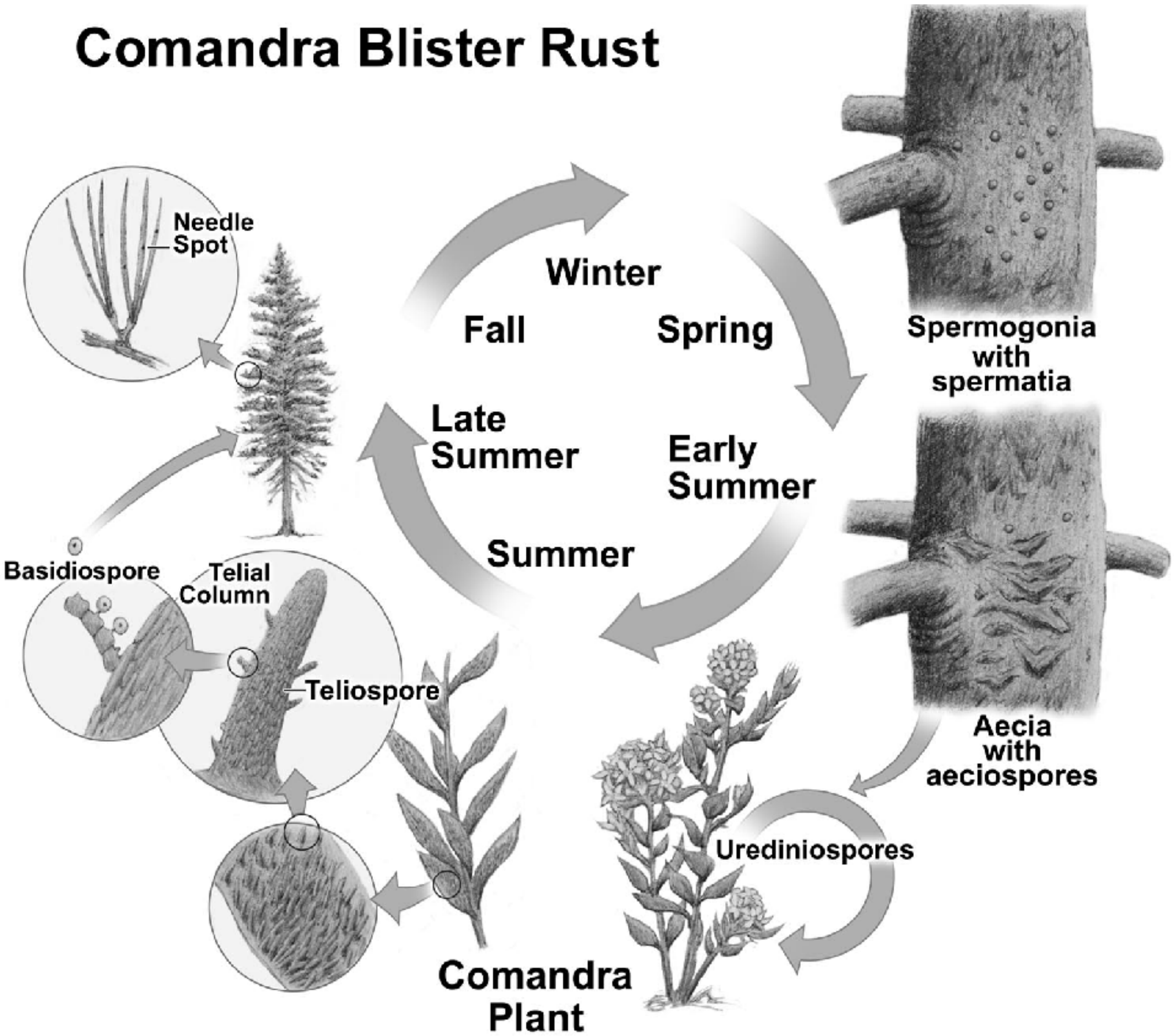

Figure 1—Life cycle of the comandra blister rust fungus (*Cronartium comandrae*) on lodgepole pine (Greg Nelson and Loretta Mannix artists).

Concepts developed for hazard rating various blister rusts are useful for investigating and describing comandra blister rust outbreaks, especially infection frequency. In general, hazard rating systems (as criteria or maps) attempt to describe the influences of landform and climate on the probability of the rust infecting pines. Examples of hazard rating systems are available for white pine blister rust (Charlton 1963; Geils and others 1999; Hagle and others 1989; Hunt 1983; Kimmey and Wagener 1961; Van Arsdel and others 1961), fusiform rust (Anderson and others 1988; Froelich and Snow 1986), and comandra blister rust (Geils and Jacobi 1991; Jacobi and others 1993). These systems describe expected incidence at a region-synoptic scale, landscape-mesoclimatic scale, or site-microclimatic scale. They characterize hazard as "high" where infection could be expected nearly every year, as "moderate" where infection is about as likely as not, and "low" where infection is infrequent. Areas hazard mapped as uniform at a larger scale, however, are often recognized as composed of patches of differing hazard at a smaller scale. Various rating systems may or may not consider whether the alternate host species are present ("potential" hazard). Most are based on the idea that outbreaks are limited by infection of the pine, and that infection is limited by the occurrence of storms or fronts at the right time and duration. Potential infection episodes can therefore be determined from meteorological data. The year infection occurred can be approximated from observation of initial aeciospore production or age of the shoot on which the canker appeared (canker age) (Bergdahl and French 1976;

Miller and Blomstrom 1968). Years (or periods) in which many infections occurred or the weather was favorable are described as wave years (or periods). In the Central Rockies, however, reconstructing infection history many years after the fact is difficult because old cankers are lost to tree mortality, and useful meteorology data are scarce. Other sources of information are a series of disease incidence reports that conclude a widespread comandra blister rust outbreak began in the Central Rocky Mountains about 1935 (Mielke 1957), 1920 (Peterson 1962), or 1910 (Krebill 1965), and terminated about 1940.

The question remains whether comandra blister rust is a continuing disease threat in the Central Rocky Mountains or whether outbreaks are the result of unusual meteorological conditions that occur only once a century or so (Krebill 1965; Peterson 1962). To address this question, we conducted a series of studies beginning in 1981 on several National Forests in Wyoming and southwestern Montana. We tested the hypothesis that meteorological conditions suitable for infection are rare and that most existing cankers resulted from a single wave period. Because lodgepole stands develop on 100-year or more rotations (due to fire, bark beetles, or harvest), the meaning of "unusual" in this case would be, at most, several wave periods per century, not several wave years per decade. We sought to describe the seasonal and annual frequency and duration of meteorological conditions favorable for infection of pine, to relate infection episodes to various weather phenomena, to observe new canker appearance on young trees, and to age existing cankers on mature trees.

Materials and Methods

Study Areas

We examined comandra blister rust outbreaks for three areas in the Central Rockies. The Beaverhead area included the Dillon and Wise River Ranger Districts of the Beaverhead National Forest in southwestern Montana. The Shoshone area was on the Wind River Ranger District, Shoshone National Forest in western Wyoming. The Medicine Bow area was on the Laramie Ranger District, Medicine Bow National Forest in south-central Wyoming. Previous studies provided information on lodgepole pine age distribution, rust incidence, and spatial relationships of hosts and other factors (Geils and Jacobi 1984, 1991, 1993; Jacobi and others 1993). Mature lodgepole pine stands (origin 1980 to 1910) were common in the Beaverhead area; young stands were extremely uncommon. The Shoshone area included both old, multiaged stands (origin 1860 to 1910) and young stands that originated from harvest cuts after the 1950s. Most stands in the Medicine Bow area originated from 1860 to 1950. Differences in disease incidence were associated with differences in age-class distributions of trees. On the Beaverhead area, 15 percent of trees in each 10-year age class were cankered (disregarding trees originating before 1870 or after 1910). For the older age classes on the Shoshone area (origin before 1950), 50 percent of trees were cankered; among younger age classes (origin after 1950), only 12 percent of trees were cankered. On the Medicine Bow area, the density (trees per unit area) of older, cankered trees was similar to that on the Shoshone area, but disease incidence was lower as a percentage of trees.

Meteorological Data

Long-term, meteorology data for each study area was obtained from base stations maintained by several agencies (table 1). The National Weather Service (NWS) provided temperature, precipitation, and synoptic data from 1948 to 1987. The USDA Forest Service, Fire Weather Data Library (USFSFW) provided records of temperature, precipitation, relative humidity, windspeed and direction from 1965 to 1987. The Wyoming Water Research Center (WWRC) provided information of 6-hour recordings of temperature, precipitation, and relative humidity.

To supplement meteorological data from the long-term base stations, we (Colorado State University, CSU) maintained three meteorological stations (Campbell Scientific, Ogden, UT) at each study area from 1985 to 1987 (table 1). A station consisted of a CR-21 data logger, tipping rain bucket, temperature sensor at 2 m, and wind direction and speed sensors at 3.5 m. Each station was located in an open area where comandra was present and within 0.5 km of rust-infested stands of lodgepole pine. These onsite stations were at an elevation 300 to 700 m higher than the base stations. Data were collected hourly for maximum and minimum temperatures, total rainfall, and windspeed and direction. In the course of maintaining these stations and other research in the study areas, we observed whether comandra showed signs of rust infection.

Potential Infection Episodes

We defined and classified periods suitable for comandra blister rust infection of lodgepole pine (potential infection episodes) using epidemiological

Table 1—Meteorological data sources.

Study area	Agency	Station	Operation dates	Data type
Beaverhead	National Weather Service	Dillon, MT	1948–1987	Daily maximum and minimum temperature Daily total precipitation
			1950–1987	Hourly relative humidity
	USDA Forest Service	Wise River, MT	1961–1987	Daily maximum and minimum temperature Relative humidity at 1300 hours Wind direction at 1300 hours Windspeed at 1300 hours
	Colorado State University	Polaris, MT	1985–1987	Hourly maximum and minimum temperature Hourly total precipitation Hourly average wind direction Hourly average windspeed
Shoshone	National Weather Service	Dubois, WY	1948–1987	Daily maximum and minimum temperature Daily total precipitation
		Burris, WY	1964–1987	Daily maximum and minimum temperature Daily total precipitation
		Lander, WY	1953–1987	Daily maximum and minimum temperature Daily total precipitation
	USDA Forest Service	Dubois, WY	1967–1987	Daily maximum and minimum temperature Relative humidity at 1300 hours Wind direction at 1300 hours Windspeed at 1300 hours
	Colorado State University	Dubois, WY	1985–1987	Hourly maximum and minimum temperature Hourly total precipitation Hourly average wind direction Hourly average windspeed
Medicine Bow	National Weather Service	Fox Park, WY	1948–1976	Daily maximum and minimum temperature Daily total precipitation
		Centennial, WY	1948–1987	Daily maximum and minimum temperature Daily total precipitation
	USDA Forest Service	Fox Park, WY	1965–1987	Daily maximum and minimum temperature Relative humidity at 1300 hours Wind direction at 1300 hours Windspeed at 1300 hours
	Wyoming Water Research Center	Centennial, WY	1981–1987	6-hour temperature 6-hour relative humidity 6-hour precipitation
	Colorado State University	Wood's Landing, WY	1985–1987	Hourly maximum and minimum temperature Hourly total precipitation Hourly average wind direction Hourly average windspeed

criteria based on observations in Utah by Krebill (1968). Because we had observed that comandra plants were heavily infected with telia at all three sites in 6 out of 7 years during our studies, we assumed that spread of comandra blister rust was not typically limited by the weather necessary for infection of comandra (aecial and uredinial stages). Infection of pine was assumed, however, to be usually limited by the occurrence of moist periods of sufficient duration during the season when mature telia were present on comandra. We defined potential infection episodes as continuous periods longer than 6 hours during the months of July, August, and September when temperature ranged between 10 and 20 °C and the air was nearly saturated. We classified episodes for duration as "short" (6 to 12 hours), "moderate" (12 to 24 hours), or "long" (more than 24 hours).

Several criteria were used to identify and classify potential infection episodes in the long-term meteorological records from base stations. Because air tends to be drier at lower elevations (where the National Weather Service and other base stations were located), we accepted a recorded relative humidity of 90 percent or greater as indicating sufficiently moist air for infection at higher elevations. Because relative humidity data were seldom available in the records, we also identified potential infection episodes when rainfall exceeded 0.1 cm in a 24-hour period. When neither humidity nor rainfall data were available, we accepted the persistence of heavy cloud cover, indicated by reduced temperature range (Whiteman 2000), as indicating a potential infection episode. A preliminary comparison of temperature and humidity data (appendix A) was used to establish that a depression of diurnal temperature range less than 11.1 °C indicated a period of high humidity. We used diurnal temperature range to assign episodes to nominal duration-intensity classes, whereby a diurnal range less than 11.1 °C corresponded to a short (6- to 12-hour) duration, a diurnal range 11.1 to 8.3 °C corresponded to a moderate (12- to 24-hour) duration, and a range less than 8.3 °C corresponded to a long (more than 24-hour) duration.

Patterns of seasonal and annual frequency of infection episodes were tested by nonparametric one-way ANOVA (SAS, procedure “npar1way”). More information on these meteorological methods can be found in the thesis by Jane Taylor (Boyd 1989).

Weather Systems

Synoptic daily weather maps (U.S. Department of Commerce 1968–1987; U.S. Government Printing Office 1945–1968), including surface weather, atmospheric pressure at 500 mb, maximum and minimum temperature, and daily precipitation, were examined to classify weather systems associated with potential infection episodes. Weather systems were classified as synoptic or mesoscale, and each front was classified as warm or cold. Synoptic systems were large (1,000- to 2,500-km front), with a well-defined 500-mb low pressure, strong upper air flows, well-established moist air masses, and widespread, frontal precipitation. Mesoscale systems were small (less than 1,000 km), with precipitation from convection of a high humidity air mass (Whiteman 2000). Synoptic daily weather maps were available for 78 percent of the potential infection episodes. The relationships of weather systems with episode occurrence and duration were tested with contingency tables; concordance was compared to the gamma statistic (Agresti 1990).

Canker Initiations and Ages

To determine whether infections occurred in single years (wave years) or multiple years (wave periods), we monitored a select population of lodgepole pine trees. These trees originated from natural seeding after fire and were on a 25- by 30-m plot at Crystal Park in the Beaverhead study area (Geils and Jacobi 1990). From 1982 (stand age 22 years) to 1989, we closely inspected each branch of live trees and recorded the location of every canker and when it first produced aeciospores. Corresponding information on potential infection episodes was obtained from meteorological data collected for the Beaverhead study area. Inoculation studies and other observations (Bergdahl and French 1976; Miller and Blomstrom 1968) suggest that initial aeciospore production usually follows the second or third year after infection (although some may appear in the first or fourth year after infection). Data for canker numbers were therefore transformed with a 2-year moving window (for example, the sum of cankers appearing in 1981 and 1982) and a 2-year lag (for example, 1981 to 1982 cankers matched to episodes occurring in 1979).

We observed long-term infection patterns by determining age of bole cankers on mature trees from a series of temporary plots established on the three study areas (Geils and Jacobi 1990; Jacobi and others 1993). We felled trees containing 302 cankers, collected bole disks, and used stem analysis to determine the year the canker first killed tissue on the bole (year of canker establishment). Data for each study area were plotted as a histogram.

Results

Potential Infection Episodes

We identified 200 potential infection episodes of comandra blister rust from 1948 to 1987 in the meteorological records for three study areas in the Central Rocky Mountains. Years without any potential infection episodes (table 2) were infrequent (20 to 28 percent by study area); at least one potential infection episode occurred in most years (72 to 80 percent). Seasonally, potential infection episodes were well dispersed from July 4 to September 19 in a similar manner on each study area (fig. 2).

The only year when telia failed to develop during this season was 1988 (year of the Yellowstone fires). On an annual basis, potential infection episodes were recorded throughout the 40-year period examined for the three study areas (fig. 3). There was an average of 1.8, 1.9, and 1.4 episodes per year on the Beaverhead, Shoshone, and Medicine Bow study areas. Episode occurrence was well distributed throughout the period examined. There were only several periods of 2- or 3-year duration when no episodes occurred (and these were not coincident across the region). Excluding the numerous episodes of short duration, there was still an average of 0.5, 0.7, and 0.3 episodes (more than

Table 2—Frequency of episodes favorable for infection of lodgepole pine by comandra blister rust as percentage of years from 1948 to 1987 with episodes of different lengths.

	Percentage of years with favorable episodes [a]			
Study area	None	Short, moderate, or long	Moderate long	Long
Beaverhead	20	80	35	8
Shoshone	20	80	45	10
Medicine Bow	28	72	28	10

[a] Favorable episodes are periods of sufficient duration and humidity to allow basidiospores to mature, disperse, and germinate. Potential infection episodes are identified from historic records as periods from July to September when high humidity persisted for 6 to 12 hours (short), 12 to 24 hours (moderate), or more than 24 hours (long).

12-hour duration) per year on the Beaverhead, Shoshone, and Medicine Bow study areas. The meteorological records we examined indicated that weather conditions considered suitable for infection of lodgepole pine by comandra blister rust do not occur every year, but these conditions do occur at least every few years.

Weather Systems Associated With Potential Infection Episodes

Potential infection episodes corresponded in 72 percent cases examined with synoptic weather systems and 28 percent of cases with mesoscale systems (table 3). There was no significant concordance (gamma = 0.08) between the episode duration (short, moderate, or long) and the weather system scale (synoptic or mesoscale). Frontal types associated with episodes were: stationary (32 percent), weak cold (29 percent), strong cold (15 percent), and no discernible front activity (24 percent); no warm fronts were associated with infection episodes. Differences among study areas were associated with prevailing system tracks. On the Beaverhead (northernmost area), 91 percent of episodes were associated with synoptic systems. On the Shoshone (further south), 67 percent of episodes were associated with synoptic systems; and on the Medicine Bow (southernmost area), only 39 percent of episodes were associated with synoptic systems.

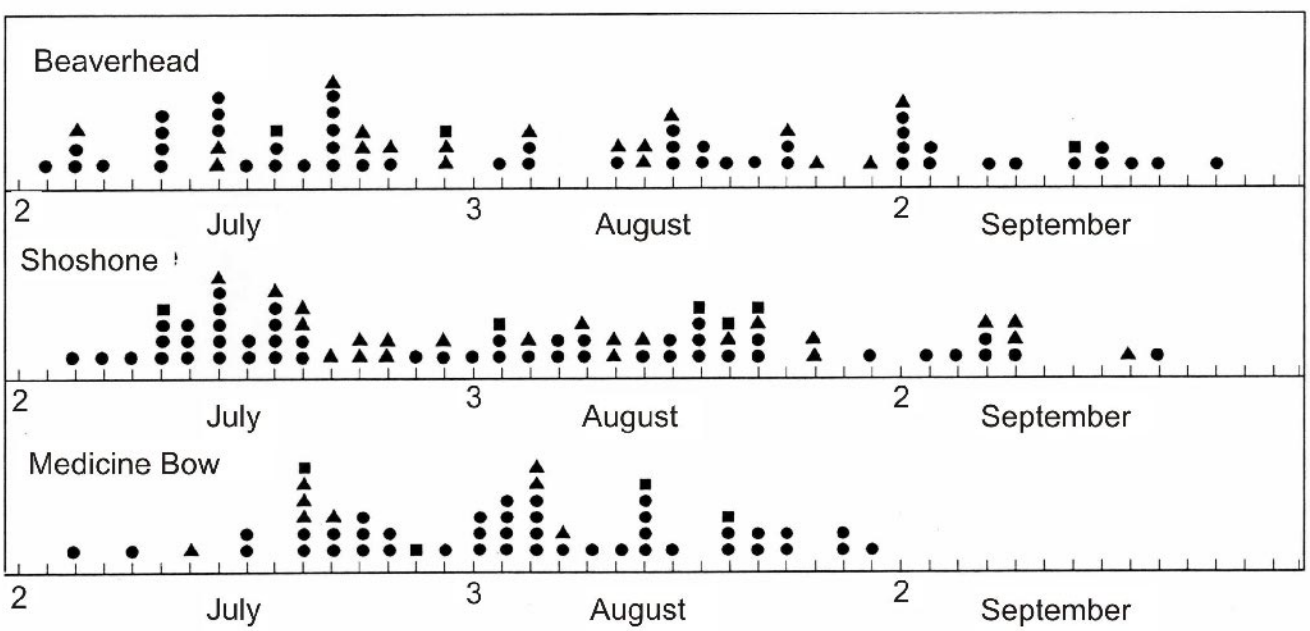

Figure 2—Distribution of potential infection episodes for comandra blister rust (*Cronartium comandrae*) by 2-day intervals summed over years 1948 to 1987 for three study areas. Episodes are periods from July to September when high humidity persisted for 6 to 12 hours (short, ●), 12 to 24 hours (moderate, ▲), or more than 24 hours (long, ■).

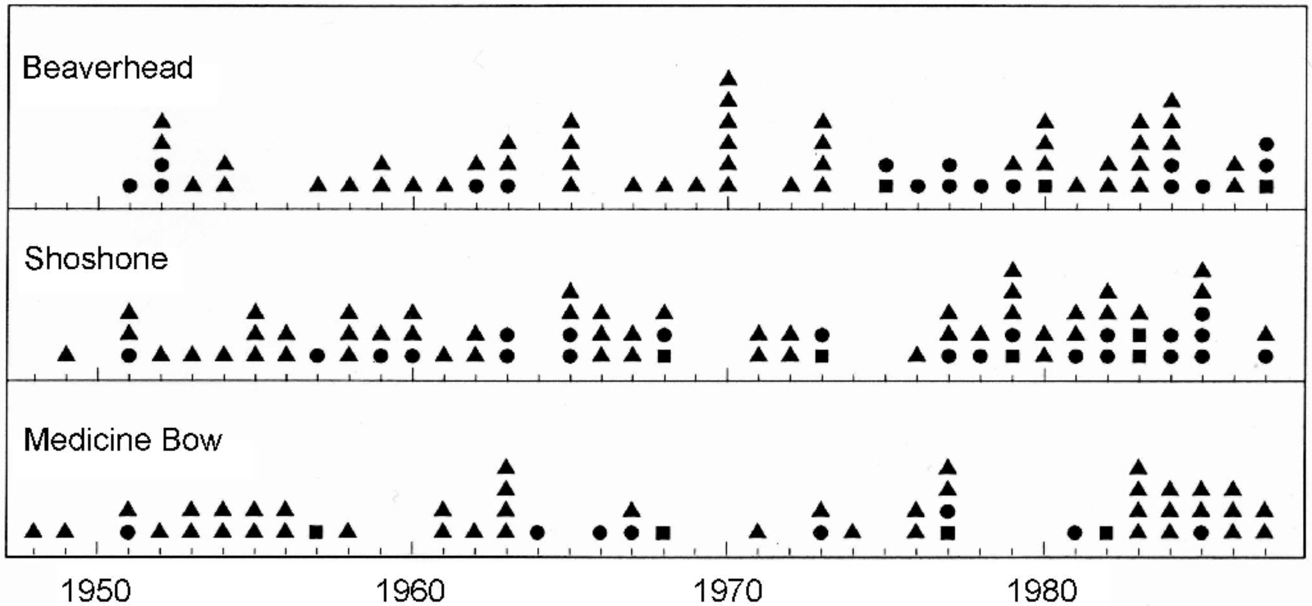

Figure 3—Distribution of potential infection episodes for comandra blister rust (*Cronartium comandrae*) by years 1948 to 1987. Episodes are periods from July to September when high humidity persisted for 6 to 12 hours (short, ●), 12 to 24 hours (moderate, ▲), or more than 24 hours (long, ■).

Only 3 percent of systems tracked across all three study areas, 19 percent occurred at two study areas, and 78 percent at a single area. The frequency, but not the duration, of potential infection episodes was related to the prevailing summer weather patterns within various regions of the Central Rocky Mountains.

Infection Episodes and Canker Initiations

The appearance of new cankers and frequency of potential infection episodes at Crystal Park (Beaverhead study area) indicated that numerous infections had occurred over a period identified as favorable by our meteorological criteria (fig. 4). From 1982 to 1989, we recorded the appearance of 344 rust infections on 72 infested young lodgepole pine trees. These trees increased in total height on average from 5 to over 8 m; the corresponding height to the lowest branches increased from 0.9 to 1.4 m. The number of new cankers per year ranged from 3 in 1989 to 76 in 1985. The distribution of cankers (grouped into 2-year cohorts) illustrated a distinct wave period resulting from several, sequential years in which infection was successive (fig. 4). Nearly all cankers began as branch infections, and because of flagging and crown recession, most were naturally shed and did not develop into bole cankers (see Geils and Jacobi 1990). From 1979 to 1986, we identified one to four potential infection

Table 3—Weather systems associated with potential infection episodes of comandra blister rust on lodgepole pine.

	Favorable episodes [a]			
	Number	Percentage		
System type	Short, moderate, or long	Short	Moderate	Long
Synoptic	136	71	23	6
Mesoscale	52	67	27	6

[a] Favorable episodes are periods of sufficient duration and humidity to allow basidiospores to mature, disperse, and germinate. Potential infection episodes are identified from historic records as 188 periods from July to September when high humidity persisted for 6 to 12 hours (short), 12 to 24 hours (moderate), or more than 24 hours (long).

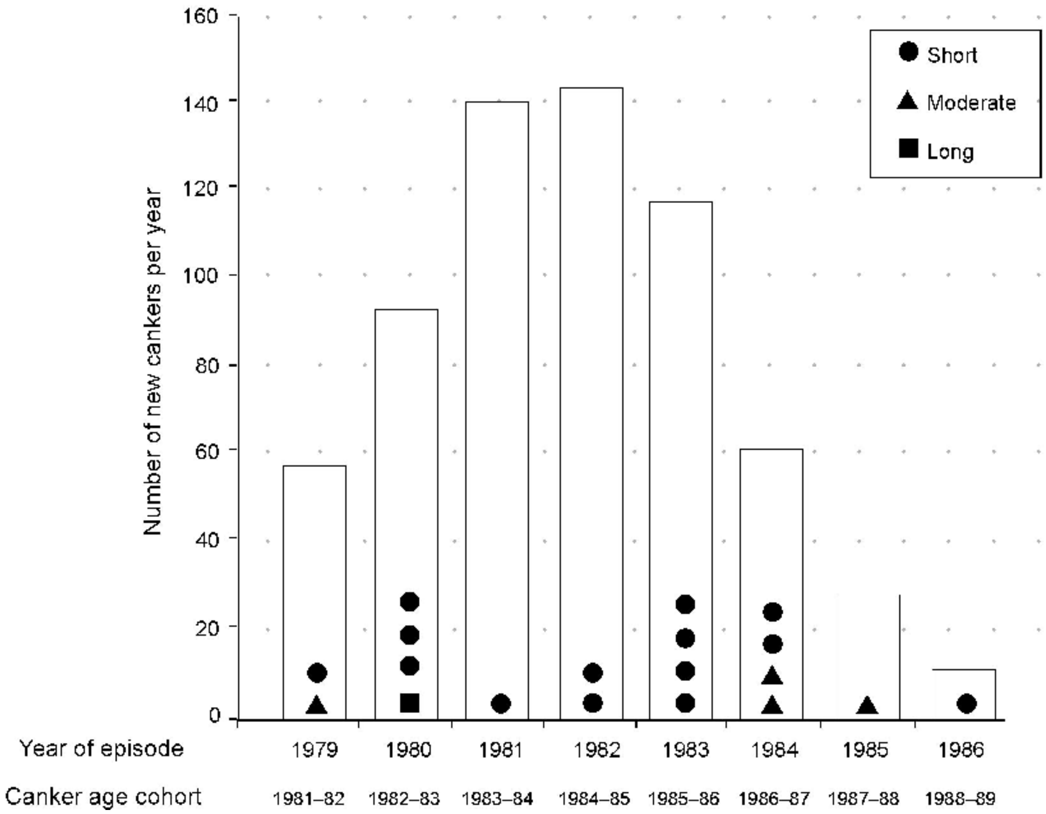

Figure 4—Occurrences of potential infection episodes and new comandra blister rust (*Cronartium comandrae*) branch cankers on lodgepole pine at Crystal Park, Beaverhead National Forest, MT. Episodes are periods from July to September when high humidity persisted for 6 to 12 hours (short, ●), 12 to 24 hours (moderate, ▲), or more than 24 hours (long, ■). Cankers are grouped into 2-year cohorts by the year of initial aeciospore production (for example, 1981–1982 cohort includes cankers first producing aeciospores in either 1981, 36 cankers, or 1982, 21 cankers). Frequencies of episodes and cankers are offset by a 2-year lag to reflect an incubation (for example, infections from episodes in 1979 are not expected to appear as cankers until 1981 or 1982).

episodes of various durations per year; there were 14 episodes of short duration, four of moderate duration, and one of long duration (fig. 4). Potential infection episodes were distributed throughout the period in a pattern that suggests episodes of even short duration, as we have defined them, may result in rust infection and branch cankers.

Bole Canker Ages

The age distributions of 302 comandra blister rust cankers from three study areas in the Central Rocky Mountains included a few bole cankers that date to 1815 and many cankers that date throughout a period up to several years before the sample was taken (fig. 5). Among all cankers, 76 percent were dated as bole cankers established after 1948. The few cankers collected in the Beaverhead area were established during the 1950s to 1970s. Cankers from the Shoshone and Medicine Bow areas included some that date from 1900 to 1950. A greater number of cankers, however, were sampled that date to the period after 1950, during which year-to-year variation in establishment ranged from 0 to 8 cankers per year. There was no evidence of a single comandra blister rust outbreak that had ended before 1950 on the three study areas.

Discussion

Comandra blister rust impact on a forest is evident as the cumulative increase in cankers over time from multiple infection episodes and the loss of cankers through shedding of branches and falling of dead trees. For an area as large as the Central Rocky Mountains and a timeframe as long as a stand rotation (100-plus years), the frequency and severity of infection wave periods can only be approximated indirectly. Meteorological records and canker age distributions describe

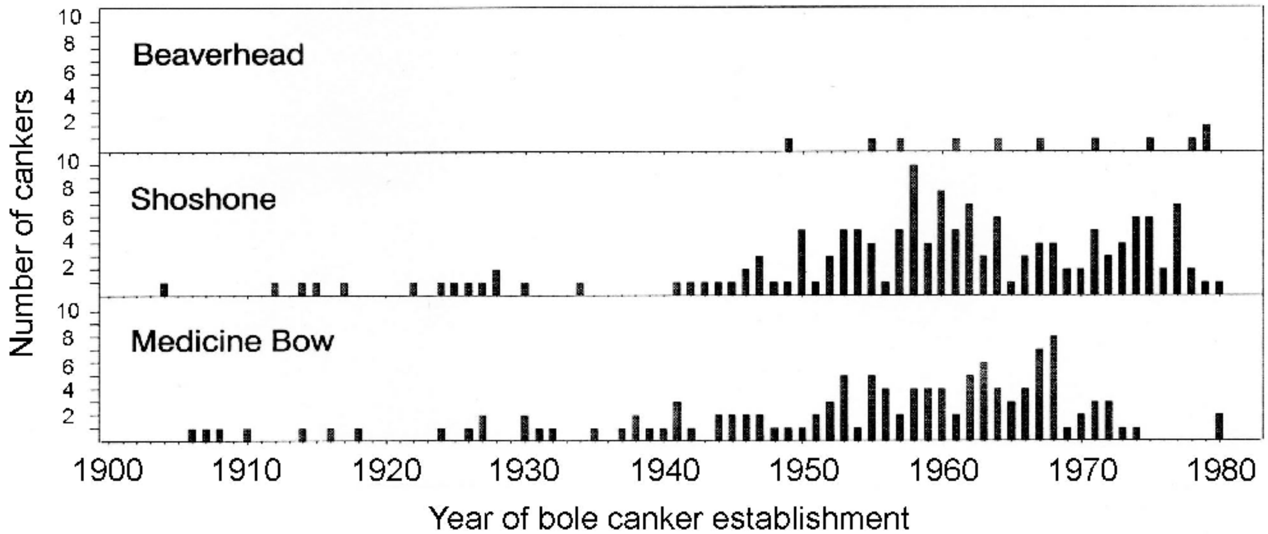

Figure 5—Age distributions of comandra blister rust (Cronartium comandrae) bole cankers in the Central Rocky Mountains for three study areas. Canker age is indicated by the calendar year a canker first became evident in the bole (even though infection may have occurred one to several years before in the branch at the center of the bole canker). Typically, cankered trees were sampled on plots distributed throughout study areas.

when infection may have occurred and when existing cankers had developed. Because of confounding factors in the meteorology and epidemiology, lag periods from infection to canker establishment, and loss of cankers, it is not possible to determine annual infection rates or identify wave years more than 20 years old. A consistent pattern, however, emerges that indicates infection is associated with common weather patterns, and has occurred frequently enough across the region to be considered a continuing threat where populations of comandra and lodgepole coexist.

Potential Infection Episodes

Although damage-incidence reports by Mielke (1957), Peterson (1962), and Krebill (1965) contain valuable observations, there are other sources of historic information, such as weather records that are especially useful for understanding rust outbreaks over long time spans and large areas. In using standard meteorological data, however, one must deal with two difficulties: (1) Weather stations in the Rocky Mountain region are widely dispersed, seldom located in the forest, of relatively recent origin, and have many data gaps. (2) Mesoscale atmospheric conditions documented in standard meteorological records are related to but do not measure the microscale phenomena (at the leaf and spore level) that control the dispersal and germination processes. Given that other factors (physiological, ecological, and so forth) also affect infection and our capability of estimating past infection rates in an unbiased manner, one must accept that historic weather records cannot identify each and only actual infection episodes (Bourke 1965). Nevertheless, we believe our efforts at validation and cross-referencing with canker ages are sufficient to justify interpreting the potential infection episodes determined in this study as reflecting the long-term, regional hazard of comandra blister rust. Our validation specifically considers the issues of season for rust dispersal, duration of episode, temperature range, humidity level, and correspondence between distant and onsite measurements. Our criteria for defining potential infection episodes are based on specific epidemiological studies of this fungus in this region (Krebill 1968), and are supported by studies with other blister rust fungi or regions (Bega 1960; Bergdahl and French 1976; Charlton 1963; Dolezal and Tainter 1979; Froelich and Snow 1986; Mielke 1943; Snow and Froelich 1968; Van Arsdel and others 1961). Our cross-referencing of meteorology and canker data includes examination of both cankers resulting from recent infections and cankers from long-past infections that persisted until later damage-incidence surveys. Our observations of canker initiation at Crystal Park soon after infection suggest that infection there had occurred when distant, low-elevation stations had recorded only 6- to-12-hour periods of relative humidity greater than 90 percent. Finally, the pattern of frequent potential infection episodes distributed throughout a 40-year period is consistent with the observed distribution of bole canker ages throughout the same period.

We found potential infection episodes were more common and consistent on a decadal basis than we expected from previous damage-incidence reports. Even if micrometeorological conditions are suitable for rust spread to the pine, infection may not occur because of numerous other requirements, especially proximity to comandra-bearing mature telia and effective dispersal to susceptible pine tissue. On the other hand, there are likely to be favorable microsites within any area where infections are more frequent than suggested by regional climate. Our identification of potential infection episodes suggests that at least the micrometeorology is favorable at least once from 1 to 7 years each decade. Although some may consider this as infrequent, it would appear sufficient to establish outbreaks in some stands where the incidence of rust exceeds 50 percent of live trees (most with topkill) and contributes to a high mortality rate (Brown 1977; Geils and Jacobi 1984; Krebill 1965; Mielke 1957; Peterson 1962).

Previous studies examined the effects of size and proximity of comandra populations on comandra blister rust outbreaks (Jacobi and others 1993; Krebill 1991). For fusiform rust, Davis and Snow (1968) indicated how synoptic and prognostic weather charts could be used to assess where conditions for infection are most likely. Although our work in this area is only preliminary, the observations of the relative importance of synoptic systems in the northern Beaverhead area and of mesoscale systems on the southern Medicine Bow area suggest an opportunity for using information on air-mass dynamics (Whiteman 2000) for hazard rating blister rusts in the Central Rocky Mountains.

Canker Initiation on Young Trees

Johnson (1979), Geils and Jacobi (1990), and this paper (fig. 4) describe comandra blister rust outbreaks in young lodgepole pine stands in the Rocky Mountains. At Crystal Park, comandra blister rust infected trees at an annual rate of one new canker per tree per year before 1985, and at a declining rate thereafter. Although favorable conditions for telial development, basidiospore dispersal, and infection are necessary for rust spread, these are not the only requirements for canker establishment. The amount of inoculum on comandra varies as a result of differences in infection from the pine and intensification in the uredinial stage. Severe drought or early hard frost may render later favorable episodes irrelevant. A population of mature telia may be exhausted in one episode, and another may not develop before the next episode occurs. Therefore, on a year-to-year basis with a constant target pine population, more or longer episodes may not result in the establishment of more cankers. Stand development over the course of several years can also reduce infection rate. As a tree grows in height, the base of the crown lifts, fewer branches are exposed to the humid environment close to the ground, and fewer spores reach suitable sites for germination and infection (van der Kamp 1994). The decline of infection rate after 1985 at Crystal Park may reflect a change in the target pine population and in the relation between the number and duration of potential infection episodes and the number of new cankers.

Bole Canker Ages

Although interpretation of age distributions for bole cankers has limitations, we find no support for the hypothesis that most existing cankers resulted from a single, long wave period that had ended by 1950 (Krebill 1965; Mielke 1957; Peterson 1962). The distribution of bole canker ages differs from a distribution of infection years because of variable lag periods and unequal loss. The time between infection and establishment of a canker in the bole (when an age can be determined) is composed of two variable-length phases—infection to initial sporulation (1 to 3 years) and growth of the fungus down the branch to the bole (1 to 10 years) (Geils and Jacobi 1990; Miller and Blomstrom 1968). The older cankers are lost (less likely to be sampled) when the host tree dies and falls; the younger cankers are not as easily detected because they are obscure. Therefore, a single infection episode generates cankers with a 1 to 10 year or more range of canker ages, the episode would be cryptic for several decades, and its existence would pass as cankers were lost. Even with uniform meteorological conditions suitable for infection over many decades, differences in infection rate and canker survival in trees of different age classes can generate different canker age distributions in forests of different age structures. In spite of these difficulties, several observations emerge from the canker age distributions. Infection by comandra blister rust has occurred throughout the past century. Infections before the 1950s are probably not rare, given the tendency to lose old cankers. Infections after 1950 were not sampled as cankers in the studies of the 1960s (Krebill 1965;

Peterson 1962), but infections from 1950 to 1970 were well represented in our studies in the 1980s (Geils and Jacobi 1990; Jacobi and others 1993). Although there are differences in canker age distributions by study area, they all support the same general conclusion that comandra blister rust infection has occurred commonly throughout the past century.

Management Implications

Weather conditions favorable for infection by comandra blister rust can be expected on numerous occasions during the 100-plus years duration of a typical lodgepole pine stand in the Central Rocky Mountains. Variations may affect annual infection rates, but not the long-term risk of infection (Froelich and Snow 1986). Disease incidence is influenced by numerous factors, especially abundance of inoculum from comandra plant populations, wind patterns and spore dispersal, microclimate, and the number, size, and susceptibility of host trees. Thus, despite year-to-year variations in number of weather episodes favorable for infection of lodgepole pine by comandra blister rust, forest managers in the Central Rocky Mountains should expect that stands near inoculum sources are at risk of infection through numerous infection episodes.

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Appendix A: Validation of Episodes

Dates of potential infection episodes identified by reduction in diurnal temperature range were validated against episode dates identified by periods of relative humidity greater than 90 percent. Dillon National Weather Service temperature-based episodes were checked with Dillon National Weather Service hourly, humidity-based episodes; Dubois National Weather Service temperature was checked with Dubois U.S. Forest Service Fire Weather Data Laboratory, 24-hour humidity; and Centennial National Weather Service temperature was checked with Centennial Wyoming Water Research Center, 6-hour humidity data. Only Wyoming Water Research Center and Dillon National Weather Service data could confirm the duration of potential episodes less than 24 hours. Episodes identified from distant National Weather Service, U.S. Forest Service Fire Weather Data Laboratory, and Wyoming Water Research Center stations also were compared for coincidence with episodes identified from onsite Colorado State University stations. Validation used contingency tables; the probability of concordance was tested against the gamma statistic (Agresti 1990).

We obtained significant concordance between episodes determined with relative humidity data and those determine by depression of diurnal temperature ranges. Relative humidity data were available for a total of 5,518 days distributed over 38 years at the Beaverhead, 13 years at the Shoshone, and 6 years at the Medicine Bow areas. Throughout these years, relative humidity greater than 90 percent was recorded at the three locations 76 times. Eighty-three percent of the episodes determined by relative humidity corresponded to reductions in diurnal temperature range. There was a significant concordance between episodes determined by relative humidity and reduction in diurnal temperature range (gamma ≥ 1.00). Coincident with the episodes, midday winds were light (2.4 to 3.2 m per second) and based on previous studies (Jacobi and others 1993), from the proper direction (28 to 68 percent of the time), to carry spores from comandra to pine (Jacobi and others 1993).

We found a significant concordance (gamma = 1.00) between episodes identified by temperature data from distant base stations and onsite stations. From 1985 to 1987, we recorded data for 457 days at three onsite stations and observed eight potential infection episodes; seven potential infection episodes were recorded at associated base stations. One episode recorded by the onsite Beaverhead station was not recorded at corresponding National Weather Service stations; one episode recorded by the onsite Shoshone station was noted the following day at the associated base stations; and the remaining seven episodes coincided day for day.

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