Temporal and Spatial Variation in Infection of Lodgepole Pine by Western Gall Rust

B. J. VAN DER KAMP, Department of Forest Sciences, University of British Columbia, Vancouver, BC, Canada V6T 1W5

ABSTRACT

van der Kamp, B. J. 1988. Temporal and spatial variation in infection of lodgepole pine by western gall rust. Plant Disease 72: 787-790.

Variation in infection of lodgepole pine (Pinus contorta) by western gall rust (Endocronartium harknessii) over time was determined by back dating in a 20-yr-old natural stand in central British Columbia. The effect of height, branch order, and aspect within the crown and the influence of stand density on the amount of gall rust infection is described. The year of greatest infection (1976) accounted for 26% and the year of least infection (1982) for 2% of all infections on 370 trees over an 11-yr period. More than 80% of galls were alive 5 yr after infection, but less than 10% 3 yr later. Infection severity in nine heavily galled trees decreased with height aboveground from 1.4 galls per m of branch length at 1 and 2 m above the ground to less than 0.05 at 7 and 8 m. The number of stem infections decreased with height at a similar rate. Branch order and aspect had no significant influence on galls per meter of branch length. Infection did not vary significantly over the range of densities studied (640-2,200 stems per ha). The probability of damaging stem infections decreases rapidly with stand age, and few new stem infections are likely to occur following precommercial thinning.

Western gall rust, caused by Endocronartium harknessii (J. P. Moore) Hirat., occurs in Canada throughout the ranges of lodgepole pine (Pinus contorta Dougl.) and jack pine (P. banksiana Lamb.), except at their extreme northern limits (5). In addition, the rust is parasitic on several other hard pine species. In British Columbia, it is the most damaging stem rust of lodgepole pine

Accepted for publication 28 March 1988 (submitted for electronic processing).

(11). The rust is more common in the central than in the southern interior of British Columbia (8,10).

The rust infects stems and branches by direct penetration of the epidermis of elongating shoots in May and June. The resulting woody gall usually encircles the stem or branch on which it occurs. An infected branch can live for many years. Death usually occurs as a result of girdling by rodents feeding on infected bark or invasion of the gall by secondary organisms (3). Branch galls result in the eventual death of the distal part of the branch. Stem galls can arise from infection of the elongating leader. Such galls are usually located between whorls

and often encircle the stem. Stem galls also can arise from infections of the female flower (4) or from branch infections so close to the stem that they become embedded in the stem as it grows. Such galls rarely encircle the stem and eventually result in pronounced sunken areas on the tree bole called hip cankers (1). Stem galls usually lead to death of the tree by breakage at the gall, but often not until 20 or more years after infection. especially if the gall is located more than a meter above the ground.

In dense, natural stands the rust might be regarded as an inefficient natural thinning agent; inefficient because it kills trees of all sizes and at varying, but usually slow, rates of speed. In plantations, however, the loss of trees may create openings in the canopy and reduce productivity. The rust also can frustrate efficient precommercial thinning. Large, dominant trees are also the most heavily infected (2,10), and the removal of such trees may leave an insufficient number of stems with suitable crown development to form an acceptable stand.

If the rate of infection observed in young stands is extrapolated over the life of such stands, the projected damage is often severe. For stem rusts such as Cronartium ribicola J. C. Fisch, ex Rabh., however, infection often decreases rapidly as height aboveground increases (6,9). One purpose of this study was to

^{© 1988} The American Phytopathological Society

determine whether this also occurs with western gall rust.

The amount of infection by western gall rust typically varies from year to year. Peterson (7) has coined the term "wave year" to describe the phenomenon. Presumably, years of heavy infection occur when climatic conditions favor infection. If these conditions can be determined, it may be possible to predict more reliably where heavy infection is likely to occur. Infection might also be reduced by changing the microclimate through stand density manipulation. The second purpose of this study was to record the variation in amount of infection from year to year, and to determine the relationship between infection and stand density.

MATERIALS AND METHODS

Variation in amount of infection over time. Three plots (two at 1,250 and one at 1,800 m²) were established in 1984 in a stand of lodgepole pine on a south-facing slope near Buckhorn Lake, about 30 km southeast of Prince George, BC. The stand had regenerated naturally following a forest fire in 1961. Plot size was chosen to give approximately 120 trees per plot. The year of formation of each living, infected internode (here meaning a branch or stem segment formed in a single year) was determined by a combination of internode and ring counts. Many trees produced more than one whorl of branches per year, but the multinodal habit was restricted to the main stem. Counts of branch internodes always agreed with stem age, as determined by a ring count of the main bole directly above the branch in question. Initially, dead galls were not dated since such dating is much more laborious than dating living galls, and sometimes virtually impossible. When it became evident that many galls were dead, a subsample consisting of every twentieth tree was established in 1985, and the year of infection of all living and dead galls was recorded.

Amount of infection and position in crown. The variable of interest in this study was number of galls per meter of branch length. This method of expressing the amount of infection was chosen because infection at different locations in the crown is likely to be heavily dependent on the amount of tissue (elongating new shoots) available for infection at that location. Only internodes formed in 1978 and 1980 were inspected. These were the most recent years of substantial and nearly equal infection. Earlier years were ignored because their inclusion would have resulted in confounding the effect of height and variation in infection among years. Also, virtually all infections established since 1978 were still present on the tree at the time of observation. Some unknown proportion of older infections would have been lost, possibly depending on their location within the crown.

Six heavily infected trees with live crowns extending to the ground were selected in the natural stand at Buckhorn Lake and three more were chosen in a natural, 24-yr-old stand near Chilco Creek, 50 km west of Prince George. The trees were felled and their branches were removed and inspected. For each internode formed in 1978 and 1980 the following parameters were recorded: tree number and location; year of formation; branch height at the bole; branching order (internodes along the main branch axis were recorded as first order, branches arising from the main axis as second order, etc.); aspect of the branch within the crown (N, E, S, W); internode length; and number of galls. In subsequent analyses, internodes on the main bole and on branches of fourth or higher order were ignored because the total number of such internodes was very small compared with the other classes. The number of galls per meter of internode was calculated for each of the 192 cells (two locations [replicates] by eight height classes of 1 m each by 4 aspects by 3 branching orders). Analysis of variance (ANOVA) was then used to determine the effect of height, aspect, branch order, and their interactions on galls per meter of internode.

Amount of infection and stand density. Variation in amount of infection in relation to stand density was studied in a set of 14-yr-old plantations consisting of two 107-220 tree blocks at each of three planting densities (640, 1,080, and 2,200 stems per ha) replicated at three locations (Buckhorn Lake, Cluculz Lake, and Chilco Creek) all within 90 km of Prince George, BC. All the blocks were established from a single seed lot, and individual blocks were separated from each other by similar blocks of two other tree species. The overall level of infection in these blocks was much lower than that of the natural pine stands surrounding them, possibly because the blocks were much younger and the trees were still small during the years of heavy infection in 1975 and 1976.

Each tree in the 18 blocks was inspected and the total number of infections (live and dead, stem and branch) were recorded. The average number of infections per tree and the percent of trees infected was determined for each block. ANOVA was then used to determine the effect of stand density, location, and their interaction on the average number of infections per tree and the percent of trees infected.

RESULTS AND DISCUSSION

Variation in infection over time. The 370 trees observed in 1984 had an average of 8.6 living and 30.9 dead galls per tree. The 19-tree subsample taken in 1985 had 8.9 living and 27.3 dead galls per tree. The differences between the original survey and the later subsample were not statistically significant. Since the dating of dead galls occurred 1 yr later than that of living galls, there may be some double counting. Some galls recorded as living in

Table 1. Annual western gall rust infection on stems and branches of lodgepole pine on 370 trees in a 20-yr-old natural stand in central British Columbia

Date of infection	Branch galls		Stem galls		
	Per tree	Percent alive in 1984	Total	Percent of all galls in that year	
pre-1972	7.76	3	41	1.4	
1972	1.36	4	16	3.1	
1973	1.89	5	11	1.6	
1974	2.35	8	21	2.4	
1975	5.17	5	19	1.0	
1976	7.25	9	23	0.9	
1977	2.18	33	10	1.2	
1978	2.59	56	12	1.2	
1979	1.30	88	2	0.4	
1980	2.28	93	4	0.5	
1981	1.15	96	4	0.9	
1982	0.60	92	1	0.5	

Table 2. The effect of height class on branch infections per meter of branch internode and average branch internode length

Height class (m)	Average internode length (cm)	Number of internodes observed	Number of infections per meter of branch	
0-1.0	12.9 ab ^z	137	1.41 a	
1.1 - 2.0	13.2 ab	336	1.41 a	
2.1 - 3.0	12.4 a	546	0.86 ab	
3.1-4.0	12.4 a	534	0.41 b	
4.1 - 5.0	12.5 a	451	0.44 b	
5.1-6.0	13.8 bc	286	0.22 b	
6.1 - 7.0	12.8 ab	165	0.04 b	
7.1-8.0	15.1 c	34	0.00 b	

^z Values within columns followed by the same letter are not significantly different from each other at P = 0.05, according to Duncan's multiple range test.

1984 may have been counted again as dead in 1985.

The 2 years of heaviest infection, 1975 and 1976, together accounted for 44.2% of the total number of infections established between 1972 and 1982. Apart from these 2 years, the average number of infections per tree for the period 1972 to 1982 was 1.74, with relatively little variation from year to year (Table 1).

These results rank among the least pronounced examples of wave years as described by Peterson (7), who found that in 20 of 24 plots established in five western U.S. states more than half the infections occurred in 1 or 2 years of a 10-to 14-year observation period. At Prince George, conditions suitable for the establishment of at least some infections, presumable periods of moist weather during the spring, occur every year. This may also explain the high level of infection encountered in the central interior relative to the drier southern interior of British Columbia (8).

For the first 5 yr after infection, almost all branch galls remained alive (Table 1). After that survival dropped rapidly, so that 8 yr after infection less than 10% of the branch galls survived. Causes of gall death included branch mortality by shading, rodent feeding on gall bark, and invasion by secondary fungi. These data show that whereas some branch galls remain alive for many years, most galls are relatively short-lived. Stem galls survive much longer. All the stem galls recorded in Table 1 were alive in 1984. A number of trees in the plots had been killed by gall rust, but in all cases, the lethal infection occurred before 1972.

The percentage of all stem galls occurring during each year of the 11-yr period was significantly different from that of branch galls (chi-square = 38.97, df = 9, P < 0.01). Stem galls became less common with time; branch galls varied from year to year but did not show an overall decline with time. The percentage of galls established on the main bole declined from about 2% during the period 1972-1975 to about 0.6% during 1979-1982. These observations suggest a decline of stem infection with age and/or

Table 3. Effect of branch order on the number of galls per meter of branch internode

Branch order	Inter	Galls per	
	Number	Length (cm)	meter of
1	800	16.6 a²	0.701 a
2	1,476	11.1 b	0.639 a
3	252	9.4 c	0.723 a

^z Values within columns followed by the same letter are not significantly different from each other at P=0.05, according to Duncan's multiple range test.

height

Infection severity and crown position. Height aboveground had a significant effect on number of galls per meter of internode (ANOVA, P = 0.002). The effects of aspect, branch order, and all the interactions were not significant (P ranged from 0.221 to 0.935). The number of galls per meter decreased from 1.4 at 1 and 2 m to 0.04 and 0 at 7 and 8 m above the ground, respectively (Table 2). Such a pattern has been described for other Cronartium stem rusts (6,9) but neither of these studies has considered the variation in the amount of susceptible tissue with height. At least two interpretations are possible. The rate of infection may drop rapidly with absolute height above the ground, so that as the lower branches die and the canopy lifts, the rate of infection in the lower living crown decreases. Such a pattern would result if juvenile tissue were more susceptible than mature tissue, or if there were a more favorable microclimate near the ground. A second explanation is that the amount of infection increases with distance below the leader, so that the rate of infection in the lower canopy remains high and is independent of canopy height or stand age. Such an effect might be expected because of the higher relative humidity, shade, and moderate temperatures in the middle and lower canopy of older stands. Also, in the case of gall rust, spores are produced in the living crown. Basidiospores of most Cronartium sp. are produced on shrubs or herbs.

Table 1 allows a distinction between these two explanations. If the latter were correct, one would expect the proportion of galls on the main bole to remain constant over time because all bole infections occur in the top of the canopy. Table 1, however, shows that the percentage of galls on the main stem decreases with age and height, and at a rate that is very similar to the rate at which branch galls decrease with height (Table 2). Hence the amount of infection, expressed as galls per meter of susceptible tissue (both stem and branch), decreases rapidly with height aboveground.

Table 3 shows the effect of branch order on infection. It supports the view that galls per meter of branch internode is a useful measure of disease severity.

Internode length varied significantly between branch orders, but galls per meter of internode remained constant. Thus, the number of infections per internode was directly proportional to internode length. The simplest explanation is that the number of spores landing on an internode is a function of the length of that internode, but apart from that effect, the resistance of the various branching orders is the same.

Amount of infection and stand density. Neither the percentage of trees infected nor the average number of infections per tree varied significantly with stand density, location, or their interaction (ANOVA, P > 0.10 in all cases) (Table 4). These findings confirm our previous results (10) that the rate of gall rust infection in precommercially thinned stands of lodgepole pine does not differ from that in unthinned controls. The range of densities tested in this trial was much smaller than that encountered in natural stands. Such stands can vary from a few scattered trees to over 50,000 stems per hectare. Nevertheless, the range from 640 to 2,200 stems per hectare represents the range of densities that are silviculturally acceptable in lodgepole pine stands of this age in central British Columbia. Thus, gall rust apparently cannot be significantly reduced by manipulation of stand density within the limits set by other considerations.

In conclusion, this study indicates that gall rust infection decreases markedly with height aboveground, but is not significantly affected by branch order, aspect within the crown, or stand density. Furthermore, in central British Columbia at least some gall rust infection occurs every year. These findings have important practical consequences. They show that in stands like the ones examined, most stem infections will be visible before the optimum time for precommercial thinning.

While the experimental plots were located in young lodgepole pine stands typical of the region, they do not represent all the varied conditions in which the species occurs. The phenomena described in this study, namely the occurrence of some infection every year and the rapid decrease of infection with height, probably do not occur everywhere. They, therefore, become important

Table 4. The effect of lodgepole pine stand density on the average number of infections per tree and the percent of trees infected by western gall rust

Stems per hectare	Location					
	Buckhorn Lake		Cluculz Lake		Chilco Creek	
	Infection/ tree	Infection (%)	Infection/ tree	Infection (%)	Infection/ tree	Infection (%)
2,200 1,080 640	2.01 ^z 2.83 2.56	44.2 44.5 45.2	1.29 0.96 0.62	37.6 37.1 27.4	1.59 1.30 0.91	32.6 33.1 28.2

²Each value is the average of two blocks.

aspects of the disease that should be considered in the assessment of potential damage and the delineation of high-risk areas.

ACKNOWLEDGMENTS

This work was supported in part by the British Columbia Ministry of Forests and NSERC of Canada Grant No. F0003.

LITERATURE CITED

- Bega, R. V. 1978. Diseases of Pacific Coast Conifers. USDA Agric. Handb. 521. 206 pp.
- Bella, I. E. 1985. Western gall rust and insect leader damage in relation to tree size in young lodgepole pine in Alberta. Can. J. For. Res. 15:1008-1010.
- Byler, J. W., Cobb, F. W., Jr., and Parmeter, J. R., Jr. 1972. Effects of secondary fungi on the epidemiology of western gall rust. Can. J. Bot. 50:1061-1066.
- Byler, I. E., and Platt, W. D. 1972. Cone infection by *Peridermium harknessii*. Can. J. Bot. 50:1429-1430.
- Hiratsuka, Y., and Powell, J. M. 1976. Pine stem rusts of Canada. Environ. Can., Can. For. Serv., North. For. Res. Cent. Edmonton, Alberta. For. Tech. Rep. 4. 103 pp.
- Tech. Rep. 4. 103 pp.
 Hunt, R. S. 1982. White pine blister rust in British Columbia. I. The possibilities of control by branch removal. For. Chron. 58:136-138.
- Peterson, R. S. 1971. Wave years of infection by western gall rust on pines. Plant Dis. Rep. 55:163-167.

- Tripp, H. A., Ross, D. A., and Van Sickle, G. A. 1976. Pages 82-83 in: Annual Report of the Forest Insect and Disease Survey, 1975. Pac. Reg. Can. For. Serv.
- Van Arsdel, E. P., Riker, A. J., Kouba, T. F., Suomi, V. E., and Bryson, R. A. 1961. The climatic distribution of blister rust on white pine in Wisconsin. USFS, Lake States Stat. Pap. 87. 34 pp.
- van der Kamp, B. J., and Spence, M. 1987. Stem diseases of lodgepole pine in the British Columbia interior following juvenile spacing. For. Chron. 64:334-339.
- Ziller, W. G. 1974. The tree rusts of western Canada. Environ. Can., Can. For. Serv., Pac. For. Res. Cent. Victoria, B. C. Publ. 1392. 272 pp.