Susceptibility of Ponderosa Pine to *Endocronartium harknessii* and Other Causes of Mortality in Pennsylvania

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ABSTRACT

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The effects of *Endocronartium harknessii* on provenances of *Pinus ponderosa* planted in 1969 on a coal strip-mine spoil bank in central Pennsylvania were reassessed. In 1982 infection levels among seed sources ranged from 4.9 to 52.5%. In 1991 infection levels ranged from 29 to 95%, and mortality due to rust infection ranged from 9 to 58% among these seed sources. Levels of infection, mortality due to rust infection, and mortality unrelated to rust infection differed significantly among seed sources ($P < 0.001$, < 0.001 , and $= 0.023$, respectively). Among geographic ecotypes, there were no significant differences among percentages of trees infected ($P = 0.094$), but there were significant differences among trees surviving outplanting ($P = 0.007$), mortality due to rust ($P = 0.004$), and mortality unrelated to rust ($P < 0.001$). Only one provenance incurred less than 40% infection, indicating that virtually none of these types of provenances are suitable for reforestation in areas of eastern North America where *E. harknessii* occurs.

In 1969 the U.S. Forest Service established a provenance study in central Pennsylvania to evaluate the suitability of 49 seed sources of *Pinus ponderosa* Laws. for reforestation of coal strip-mine spoil banks (2). The plantation was established on a spoil bank in Clearfield County, PA, consisting of black calcareous shale sloping gently to the south. The seedlings used were left over from a provenance study established in Michigan 1 year before (2,9), creating variation in number of replications among sources. The original planting consisted of randomized blocks containing 10 or 11 seedlings of each seed source, each replicated six times, except sources 862 (seven replications); 814, 837, and 843 (five replications); 720, 822, and 856 (four replications); and 823 and 832 (two replications). The seedlings had been grown at Bessey Nursery, Halsey, NE, and transplanted twice prior to outplanting. The elevation, latitude, longitude, and geographic ecotype of each provenance are listed by Davidson (2), and approximate source locations were mapped by Merrill et al. (5). Six years after outplanting, survival and height growth of seedlings were recorded, and based on these measurements, 11 seed sources were

recommended as "superior" for reforesting bituminous spoil banks (2). Rust infection that existed at the time either was not recognized or was ignored.

Some seedlings were infected in the seedbed or transplant bed by the autoecious fungus *Endocronartium harknessii* (J.P. Moore) Y. Hiratsuka, which causes pine-pine gall rust, and were outplanted (4,5). By 1982 the pathogen had become well established throughout the plantation, and the susceptibility of the various seed sources to the pathogen was evaluated (5). Since 1982 rust incidence has increased dramatically and caused substantial mortality in some seed sources. Mortality of uninfected trees also has occurred. Therefore, during the fall of 1991 the effects of this pathogen on these ponderosa pine provenances were re-evaluated.

MATERIALS AND METHODS

Each tree was examined and placed in one of eight categories: 1 = alive and non-infected; 2 = alive and infected, <25 galls; 3 = alive and infected, 25 to 50 galls; 4 = alive and infected, >50 galls; 5 = dead due to rust infection; 6 = dead, cause indeterminate; 7 = dead, uninfected; and 8 = missing. Some categories were later combined to facilitate analyses. The Kruskal-Wallis chi-square multiple comparison nonparametric test was used to detect differences among the average frequencies in each category in relation to seed source, geographic ecotypes, and blocks.

When lateral shoots are infected, shoot growth the following year frequently is stunted, probably due to disrupted translocation. During the second year after infec-

tion, most of these stunted shoots die. Thus, a high incidence of infection in susceptible trees causes progressive crown deterioration and eventual mortality (4). If more than half the branches on a dead tree bore terminal branch galls or girdling galls on the main stem, mortality was considered to be caused by rust infection. Trees classified as indeterminate were infected but bore no main stem galls and less than half of the branches had terminal galls. Based on 25 years of research on *E. harknessii* in the northeastern United States, such trees died from some factor(s) other than rust infection.

RESULTS AND DISCUSSION

Provenance effects. In 1982 4.9 to 52.5% of the trees from the various seed sources were infected (5). By 1991 the proportion of rust-infected trees, both living and dead, ranged from 29 to 95% (Table 1, column 7), and differences among seed sources were significant ($P < 0.001$). Ten of eleven provenances recommended by Davidson (2) as superior for reforesting spoil banks contained more than 63% infected trees (Table 1, column 7). Based on these results, although some of these provenances undoubtedly might be useful in selection or breeding trials, none is superior for reforestation plantings in any eastern area where *E. harknessii* is known to occur. However, because the pathogen appears to spread via wind only limited distances from infected trees (6), many of these provenances might be useful if the plantation could be established from rust-free seedlings in an area free of the pathogen.

Tree mortality due to pine-pine gall rust ranged from 9 to 58% and varied significantly ($P < 0.001$) among the seed sources (Table 1, column 2). Two provenances, 833 and 861, showed no evidence of mortality due to agents other than *E. harknessii* (Table 1, columns 3 and 4).

The percentages of dead uninfected trees differed significantly ($P = 0.023$) among provenances (Table 1, column 3). We were unable to ascertain the cause(s) of this mortality. There was no evidence of root rots, and although some trees bore evidence of attack by one or more of the pine shoot moths or the pitch nodule maker, *Petrova albicapitana*, their incidence was insufficient to cause the observed mortality. Adjacent plantings of *Larix decidua* and *Pinus resinosa* did not incur mortality.

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The percentages of trees per provenance that survived outplanting and were still living in 1991 ranged from 29 to 88% and differed significantly ($P < 0.001$) among seed sources (Table 1, column 8). Four of the five seed sources with the best survival rates, 839, 838, 827, and 837, originated in the Black Hills-high plains area. These five seed sources also had 17% or less mortality due to pine-pine gall rust (Table 1, column 2).

The high incidence of rust infection is consistent with Merrill and Wenner's (4) finding that gall incidence in *P. sylvestris* Christmas trees increased logistically for several years after infection. They reported more than 17,000 galls on a single 2.5-m Scots pine. Baxter (1) similarly reported more than 18,000 galls on a 3-m Scots pine in Oneida County, NY. The development of this disease in forest plantations bears no

resemblance to development of diseases caused by the heteroecious *Cronartium* spp. As in any autoecious rust, once the pathogen begins to sporulate on an infected plant many of the spores reinfect the same plant, causing massive galling, almost exclusively on the lateral branches, and leading to extensive crown mortality (4). As crown mortality progresses up the stem, height and diameter growth of the infected tree is re-

Table 1. The number of trees in the original planting of ponderosa pine trees in central Pennsylvania, by provenance and ecotype, that survived outplanting and the percentages of those trees that in 1991 were alive, infected or uninfected, or dead due to infection by *Endocronartium harknessii* or other causes

Provenance	Ecotype ^a	Number surviving outplanting (Col. 1)	% Dead in 1991 ^b			% Alive in 1991 ^b		% Dead and living trees infected ^c (Col. 7)	% Trees surviving outplanting living in 1991 (Col. 8)
			Due to rust (Col. 2)	Uninfected (Col. 3)	Indeterminate (Col. 4)	Infected (Col. 5)	Uninfected (Col. 6)		
839	BH	33	9	0	3	58	30	70	88
838	BH	44	14	2	0	52	32	68	84
856	ELE	10	10	10	0	50	30	60	80
827 ^d	HP	42	10	10	2	17	62	29	79
837 ^d	BH	46	17	7	0	61	15	78	76
831	CR	38	16	6	0	54	24	70	78
704 ^d	HP	54	17	4	7	44	28	69	72
835 ^d	BH	39	26	0	3	49	23	77	72
760	CR	42	10	7	6	52	19	71	71
854	HP	27	22	7	0	33	37	56	70
824	HP	36	33	3	0	42	22	75	70
830	CR	30	30	0	3	60	7	95	67
860	CP	14	29	7	0	50	14	79	64
848	CR	40	30	5	2	45	18	78	62
814 ^d	CM	42	17	14	7	40	21	64	62
832 ^d	HP	16	25	14	0	44	18	69	62
853	HP	24	17	17	4	21	42	42	62
834 ^d	BH	44	30	7	2	55	7	86	61
701	HP	20	25	10	5	55	5	85	60
822	HP	22	27	0	14	45	14	86	59
833	BH	36	42	0	0	39	19	81	56
702	HP	39	33	8	5	49	5	87	54
724	CP	26	35	12	0	42	12	77	54
703	HP	43	30	7	7	26	30	63	53
825 ^d	HP	50	42	4	2	36	16	80	52
758	CP	29	45	3	0	41	10	86	52
862	SR	29	45	3	0	31	21	76	52
761	CR	49	29	10	10	41	10	80	51
722	HP	39	18	26	5	26	26	49	51
757 ^d	ELE	46	30	15	4	28	22	63	50
723	HP	32	34	6	9	44	6	88	50
815	CN	30	10	27	13	23	27	47	50
851	HP	18	39	6	8	39	11	83	50
829	CM	29	24	17	10	45	3	79	48
858	CP	29	45	3	3	34	14	83	48
852	HP	33	42	6	9	30	15	79	45
812	CM	50	40	10	6	38	6	84	44
754	T	34	38	6	12	32	12	82	44
836	BH	28	43	7	7	35	7	86	43
863 ^d	SR	36	39	11	8	28	14	75	42
845	CR	36	50	3	6	31	11	86	42
861	CP	43	58	0	0	35	7	93	42
763	CR	51	45	6	8	29	12	82	41
813	CM	48	23	25	12	38	2	73	40
759	CP	36	56	3	2	28	11	86	39
847	CR	36	58	3	0	25	14	83	39
720	ELE	21	48	14	0	29	10	76	38
765	SR	26	58	4	8	19	12	85	31
823 ^d	CM	17	29	18	24	29	0	82	29
Kruskal-Wallis chi-square ($\alpha = 0.05$)			92.06	69.45	64.29	68.15	86.76	83.06	92.54
P			<0.001	0.023	0.058	0.031	<0.001	<0.001	<0.001

^a CM = central Montana; ELE = east-low elevation; HP = high plains; BH = Black Hills; SR = southern Rockies; T = transition; CR = central Rockies; and CP = Colorado plains.

^b Because of rounding off, percents may not add up to 100.

^c Sum of columns 2, 4, and 5.

^d Considered "superior" by Davidson (2).

duced. Eventually the few living branches near the top can no longer support continued growth, and the tree dies.

P. sylvestris generally has been considered relatively susceptible to pine-pine gall rust (4), but in 25 years of research involving multiple provenances from the British Isles, France, Spain, Greece, and Turkey planted on sites ranging from former fertile farm lands to strip-mine spoil banks, incidence of infection rarely has exceeded 10%, and mortality usually ranges from 3 to 5% (4; W. Merrill, B. Kistler, L. Zang, and N. Wenner, unpublished data). In contrast, some *Pinus* spp. from the western United States are much more susceptible when planted in the East, including ponderosa (5,9) and Jeffrey pines (1). Indeed, between 1943 and 1964 this pine-pine gall rust killed nearly 100% of the *P. jeffreyi* plantations in the Stinchfield Forest in Michigan, and Baxter (1) stated that this fungus was "...more destructive to pines than has been observed for any rust on any host for over 60 years of plantation experiences..."

Such high incidence of infection and mortality has not been reported in the more arid western plains and mountains, probably due to lack of sufficient moisture during the infection period. Wave years of infection have been reported in the western United States (7) and Canada (8), and Peterson (7) related these to summer rains. Our studies showed that infection occurs during the early stages of shoot elongation, beginning as needles emerge from the fascicle sheath, and can be prevented by a single application of fungicide at that time (3). In the eastern United States, the normal spring weather during this period is characterized by frequent rains. In the mid-Atlantic states, high levels of infection have occurred every year from 1965 to 1996, except during the severe drought of 1991, when no rains occurred from prior to budbreak during late May until early October (W. Merrill, B.

Kistler, L. Zang, and N. Wenner, unpublished data). Because the southern and southeastern United States have virtually the same spring weather patterns, we believe that the same levels of infection would occur there should this pathogen be introduced.

To identify the best ponderosa pine seed sources for reforestation plantings under conditions similar to those existing in central Pennsylvania, the relationship between tree survival after outplanting and incidence of infection was investigated for each provenance (Fig. 1). Seed sources in the upper right quadrant of Figure 1 had high rates of survival and low percentages of infection. Thus, the 1991 data suggest provenances 827, 854, 839, 704, and 838 were the most

successful seed sources included in this study. Of these, only source 827 had less than 40% infected trees. Thus, none of these sources is suitable for reforestation use in any area of the eastern United States where this pathogen occurs.

Geographic ecotypes. There were no significant differences among ecotypes in the percentages of trees infected ($P = 0.094$) (Table 2, column 7). There were some similarities between this study and those of Merrill et al. (5) and Thomas et al. (9). All three studies showed a general trend of increasing infection among ecotypes from north to south, although the means of evaluating infection levels in the field varied from study to study. We found the percent-

Fig. 1. Relationship between the percentages of the seedlings of 49 provenances of *Pinus ponderosa* that survived outplanting in central Pennsylvania and the percentage of those survivors that remain uninfected by *Endocronartium harknessii*. Data points enclosed in circles indicate provenances designated by Davidson (2) as "superior" for reforestation of strip-mine spoil banks in Pennsylvania.

Table 2. Percentages of the original 1969 planting of ponderosa pine trees in central Pennsylvania, by ecotype, that were missing in 1991, trees that survived outplanting and in 1991 were dead due to various causes, and trees that survived outplanting and in 1991 were alive, infected or uninfected by *Endocronartium harknessii*

Ecotype	% Original planting missing in 1991 (Col. 1)	% Dead in 1991 ^a			% Alive in 1991 ^a		% Surviving trees	
		Due to rust (Col. 2)	Uninfected (Col. 3)	Indeterminate (Col. 4)	Infected (Col. 5)	Uninfected (Col. 6)	Infected in 1991 ^b (Col. 7)	Alive in 1991 ^c (Col. 8)
Central Rockies	32	33	5	5	43	14	81	50
Central Montana	31	24	11	10	38	12	71	50
East-low elevation	45	39	12	2	31	18	71	48
Transition	43	38	9	10	32	11	79	43
Black Hills	35	26	5	2	48	20	75	67
High plains	42	31	6	5	36	21	73	57
Colorado plains	51	46	4	1	38	12	84	49
Southern Rockies	51	46	7	6	27	14	79	41
Kruskal-Wallis chi square	19.25	20.65	31.53	16.81	16.07	12.29	12.20	22.77
P	0.007	0.004	<0.001	<0.001	0.024	0.091	0.094	0.002

^a Because of rounding off, percents in columns 2 through 6 may not add up to 100.

^b Sum of columns 2, 4, and 5.

^c Sum of columns 5 and 6.

age of infected trees in central Montana = east-low elevation < high plains < Black Hills < southern Rockies = transition < central Rockies < Colorado plains. The Kruskal-Wallis multiple comparison test indicated a significant difference ($\alpha = 0.05$) in average percentages of infected trees between sources in the Colorado plains and four other areas: central Montana, east-low elevation, Black Hills, and high plains. There were no significant differences among ecotypes in the percentages of trees that were alive and uninfected ($P = 0.091$) (Table 2, column 6).

Forty percent of the original seedlings in the plantation were missing. This agrees closely with Davidson's (2) estimated survival of 61% of original seedlings in 1971, 2 years after planting. Seedlings described by Davidson (2) as not surviving outplanting were categorized in 1991 as missing trees. All other trees were accounted for in one of the other seven categories. The percentages of missing trees varied among the eight ecotypes, but no geographic trend was apparent.

There were significant differences among the eight ecotypes, both in mortality due to rust ($P = 0.004$) and mortality unrelated to rust ($P < 0.001$) (Table 2, columns 2 and 3, respectively). The Colorado plains and southern Rockies sources had the highest average percentage of trees dead due to rust (46%) (Table 2, column 2). Of the seedlings from provenances originating in east-low elevation and central Montana, 12 and 11%, respectively, succumbed to environmental factors and pathogens other than *E. harknessii* (Table 2, column 3). However, the central Montana ecotype ranked low both in the percentages of trees infected with rust (71%) and trees succumbing to rust (24%) (Table 2, columns 7 and 2, respectively). There may have been more seedlings from this region available to be killed by other pathogens, or trees from central Montana sources may have higher resistance to pine-pine gall rust but lower resistance to other as yet unidentified disease agent(s) or pest(s).

The percentages of trees that were alive in 1991 differed significantly ($P = 0.002$)

(Table 2, column 8). Trees from the Black Hills (67%) and high plains (50%) had more living trees in 1991 than did other ecotypes. In terms of percentage of trees infected with pine-pine gall rust, these ecotypes were about average (Table 2, column 7). Provenances from the southern Rockies had the lowest percentage of living trees (41%) (Table 2, column 8).

Block effects. Six experimental blocks were arranged from west (block 1) to east (block 6) to investigate the possible effect of prevailing westerly winds on the spread of gall rust inoculum through the plantation. To facilitate analysis, data were combined for blocks 1 and 2, 3 and 4, and 5 and 6. Analysis of the proportion of rust-infected trees per paired blocks indicated a block effect of borderline significance ($P = 0.055$). The Kruskal-Wallis chi-square test indicated a difference ($P = 0.04$) between block pairings 1 and 2 (74% infected) and 5 and 6 (80% infected). This agrees with Merrill et al. (5) who reported increasing levels of infection from west to east.

Concluding comments. Although no provenance was free of infection by *E. harknessii*, some seed sources may be cautiously recommended over others. In so doing, more than one variable must be considered. For example, provenance 839 had the highest survival rate (88%) among all seed sources. However, 70% of trees from this seed source were infected with pine-pine gall rust. The smallest percentage of pine-pine gall rust infection 22 years after planting (29%) was in provenance 827. Further, a relatively high percentage (79%) of trees from this seed source were still alive and a relatively small percentage had died from rust infection (10%). Any recommendations as to seed source for reforestation purposes should be framed by this type of information.

Conversely, most seed sources contained trees that remained uninfected even when their branches were entwined with branches of galled trees. We have noted the same phenomenon within numerous provenances of *P. sylvestris* (4). Thus, there are trees in all provenances that could be used in breed-

ing trials.

It is apparent that *P. ponderosa* seedlings from sources in the high plains and Black Hills have the greatest chances of surviving on reclamation sites and under conditions similar to those investigated here. Although they were below average in terms of mortality due to rust, they ranked near average in terms of percentage of trees infected.

The results of this study indicate that the initial predictions about the performance of seedlings in this outplanting (2) were extremely tenuous. The dangers in recommending seed sources for reforestation projects based only on height and survival 6 years after outplanting are obvious. If reforestation is to be considered successful, the evaluation of disease and pest resistance and long-term tree survival within the ecosystem are essential.

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