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This study concerns factors affecting production and survival of ascospores of Elytroderma deformans (Weir) Darker, a needle cast of ponderosa pine (Pinus ponderosa Laws.).

The results show that summer cooling and a reduction in host vigor delays and diminishes the number of fertile hysterothecia produced. Evidence is offered for classification of Elytroderma as an obligate parasite. It was demonstrated that completion of the perfect stage requires a living host and that the rate and amount of fungal activity is directly related to host vigor.

Results of additional experiments revealed that secondary fungi entering infected needles via pycnidial scars play a definite role in reducing the number of hysteothecia attaining maturity, and that the casting of needles is independent of the stage of development of the hysterothecia on the needle.

In controlled humidity and temperature experiments, testing

the ability of ascospores to survive in the hysterothecium after attaining maturity, it was found that survival occurred only under very low humidities at cool temperatures.

Ascospore germination studies in the presence of natural pine needle microflora revealed that best germination takes place between 5° and 20° C and that germ tube elongation was maximum at 5° C.

From the results of these experiments the prerequisites of an Elytroderma induced epiphytotic are hypothesized.

Factors Influencing the Production and Survival of Inoculum of *Elytroderma deformans*

by

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Sincere appreciation is offered to my major professor for his guidance and assistance during the study, to Mr. David Adams for his assistance with field work and time given to discussion. Also acknowledged is the valuable assistance of Mrs. Bertha Wade with laboratory preparations.

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FACTORS INFLUENCING THE PRODUCTION AND SURVIVAL OF INOCULUM OF *ELYTHRODERMA DEFORMANS*

INTRODUCTION

Needle blight of ponderosa pine (*Pinus ponderosa* Laws), incited by *Elytroderma deformans* (Weir) Darker, is an endemic disease of localized areas in the ponderosa pine forests of Oregon, Washington, Idaho, Montana and California. The disease has been reported to reach epiphytotic levels only infrequently.

The precise factors that influence the development of the epiphytotics are unknown. Wagener, Childs and Kimmey (1949) related increased disease incidence with mild, humid springs and autumns. They further reasoned that weather of this type could increase the level of disease by creating favorable conditions for the ascosporic infection of the hosts. Although it is generally agreed upon that wet weather favors ascosporic infections there appears to be more important phenomena involved in creation of the periodic outbreaks of the disease.

The study undertaken here describes factors related to the phenomena of survival and production of ascosporic inoculum. All of the plant material in the study was collected on Pringle Butte on the Deschutes National Forest in Central Oregon during the summer and fall of 1966.

In this particular area needle blight has never been reported at epiphytotic levels The disease is presently evident in widely scattered patches of saplings. Only occasional overstory trees show symptoms of the disease. Incidence of the disease on the saplings varies from trees having one blighted tip to trees near death.

LITERATURE REVIEW

Elytroderma deformans (Weir) Darker is a Discomycete commonly classified in the family Hypodermataceae of the Hysteriales (Darker, 1932) or the family Phacidiaceae of the Helotiales (Alexopoulus, 1962) or Pezizales (Bessey, 1951). Elytroderma deformans was originally described by Weir (1916) as Hypoderma deformans. On the basis of ascospore characteristics Darker (1932) proposed erection of a new genus, Elytroderma, for Hypoderma deformans, the elongate two-celled spores of Hypoderma deformans differing significantly from the shorter one celled spores characteristic of the genus Hypoderma and from spores of any other member of the Hypodermataceae.

Elytroderma deformans, by far the most destructive of the needle cast fungi, is severely parasitic on ponderosa (Pinus ponderosa Laws) and Jeffrey pine (Pinus jeffrei Grev. and Balf.) (Boyce, 1961). Darker (1932) lists jack pine (Pinus banksiana Lamb.), shortleaf pine (Pinus echinata Mill.), pinyon pine (Pinus edulis Engelm.) and lodgepole pine (Pinus contorta Dougl.) as additional hosts.

Reports of needle blight epiphytotics are rare in the literature. Wagener, Childs and Kimmey (1949) reported epiphytotic conditions in various localities east of the Cascades in Oregon from 1946 through 1948. Mortality reached 90 percent in certain areas of the Ochocho National Forest. They reported that mild, rainy weather was

recorded immediately prior to and during the years of outbreak.

Lightle (1954) reported that adjacent areas in Idaho and California were similarly affected in 1947-48. He stated that pine foliage (except for the current year's growth) of entire basins turned straw yellow to deep red in color. Heavy salvage cuts were made in these areas between 1946 and 1952 to utilize dead and dying trees and to reduce the likelihood of significant increase in bark beetle activity.

According to Childs (1959), infection in stands where the pathogen is present in an endemic nature is almost invariably most severe in partly shaded thickets of reproduction, in the interior of groups of pole sized trees and on the lower crowns of north to northwest sides of pole sized and larger trees. Childs logically reasons that these relationships are indicative of the dependence of Elytroderma deformans on moist shaded conditions for infection of the hosts foliage.

Symptoms and signs of the disease and the time of the year of their appearance are discussed by Weir (1916), Lightle (1954), Waters (1957 and 1962), Roth (1959) and Childs (1955 and 1959). General foliage symptoms on trees of all sizes included fading, turning red then brown and finally a premature casting of the needles. Stunted, malformed branches are characteristic of saplings diseased over a period of years. Large branches of poles and sawtimber that have been infected over a period of years develop characteristic large,

compact, globose witches-brooms. The signs of the disease are the small (one mm. in diameter), concolorous blister-like pycnidia that appear soon after the foliage has turned red, and the long (average 10 mm. in length), shiny, black hysterothecia that appear a short time later. Both occur on the dorsal surface of the discolored needles.

Reports found in the literature on the seasonal appearance of signs and symptoms are not in agreement. Weir (1916) reported needle discoloration and hysterothecial initiation normally to occur in the fall of the year on the current season's growth with fruiting bodies maturing the following spring. These findings are at variance with observations with recent workers.

Lightle (1954), Childs (1955 and 1959) and Roth (1959) report that only a slight needle fading and tip discoloration is observed on needles of the current year in the fall. General discoloration of the needle and hysterothecial initiation is delayed until the following spring. During late May or early June the pycnidial stage is formed (Lightle, 1954), (Waters, 1957). In the presence of high humidity the pycnidiospores are exuded in tendrils. Upon the return of drier conditions the dried tendrils resemble sugar crystals on the needle surface. Concurrently with or slightly later than pycnidial formation the faint lines of the hysterothecia begin to appear on the outer convex surface of the needle (Lightle, 1954), (Childs 1955 and 1959), (Gordon

and Laurent, 1966). Reported times for hysterothecial maturity vary from early July to November (Lightle, 1954), (Waters, 1957), (Roth, 1959), (Childs, 1955 and 1959), (Sikorowski, 1960) and (Gordon and Laurent, 1966). Lightle (1954) and Sikorowski (1960) have shown experimentally that the majority of ascospores are disseminated during rainy periods in autumn.

The casting of blighted needles also occurs in the fall (Childs, 1955 and 1959), (Roth, 1959) and (Gordon and Laurent, 1966). Gordon and Laurent (1966) report from field observations in Montana that Elytroderma causes a casting of infected needles only after maturation of the hysterothecia and the liberation of ascospores.

Recent work by Roth (1959), Sikorowski and Roth (1960 and 1961) and Waters (1962) has proven the systemic nature of Elytroderma deformans first proposed in Weir's original paper in 1916 but later discounted by Lightle (1954) and Waters (1957). Gordon and Laurent (1966) have performed extensive studies on the systemic nature and morphogy of the fungus from the time it enters the newly formed needle in the infected bud until the needle is cast.

Reports in the literature on ascospore germination also are quite varied. Weir (1916), working with hysterothecia that had lain in the laboratory for two months, reported ascospores were still capable of forcible discharge from the asci when exposed to moisture at 35° C but not at 5° C. He reported successful germination after

four days incubation in two percent sucrose at 35° C. Lightle (1954) had extreme difficulty in obtaining ascospore germination under any conditions. However Mielke (as cited by Lightle, 1954) obtained abundant germination of ascospores at temperatures between 10° and 15° C, indicating that the temperature requirement for germination is rather low. Mielke's experimental methods, date of collection of material and dates of observed germinations were not reported. Waters (1957) also reported ascospore germination at 10° C, but again no details were given.

Successful artificial inoculation of ponderosa pine by Elytroderma deformans has been reported by Weir (1916) and Gordon and Laurent (1966). Weir obtained successful inoculation on the 20th of May. Gordon and Laurent obtained successful infection between the first day to third week after bud break, but failed in all attempts of inoculation after the third week of bud break. They conclude that tender young leaf tissue is required for infection of ponderosa pine foliage by Elytroderma. In view of the fact that this requirement does not correlate with the time of normal ascospore dispersal Gordon and Laurent (1966, p. 11) postulate that, "When hysterothecial development and maturation are delayed by environmental conditions until spring of the following year then there is potential for mass infection."

Three reports exist in the literature on attempts to culture

Elytroderma deformans. Weir (1916) obtained abundant white mycelium by placing ascospores on culture media. Lightle (1954) using nine different culture media and ten different sources of the fungus (i. e. ascospores, pycnidiospores, small pieces of hysterothecia, etc.) was unable to culture the fungus. Gordon and Laurent (1966) obtained the fungus in culture by application of sterile isolation technique from 12 month old needles. They noted the development of two hyphal forms; one being thick, aliform to undulate, multinucleate and septate and the other thin, bunucleate and septate. They also reported that they obtained formation of pycnidia in culture. These hyphal types found in culture correspond to the undulate multinucleate hyphae in the phloem (Sikorowski, 1960 and 1962), (Waters, 1962), (Gordon and Laurent, 1966) and the thin binucleate hyphae in the xylem rays, xylem, transfusion tissue and mesophyll (Gordon and Laurent, 1966) of the intact needle.

THE EFFECT OF COOLING BLIGHTED TREES DURING THE SUMMER AND FALL ON HYSTEROTHECIAL DEVELOPMENT

As mentioned previously the fruiting bodies of Elytroderma deformans normally mature and disperse their spores sometime between mid-July and early December. However, recent infection studies of Gordon and Laurent, (1966) reveal that successful inoculation of the host occurs only during the period of rapid growth in the spring. They postulate that when hysterothecial development is delayed by certain unknown conditions until spring of the following year the potential of a mass infection arises.

It was noted from a review of the weather data (U. S. Weather Bureau, 1943-48) that the last serious disease outbreak (1946-48) was preceded by two cool summers (1943-44) followed by a mild spring. The purpose of this experiment was to test the hypothesis that cool summers and falls may delay hysterothecial development causing ascospores to mature the following spring instead of the fall of the year of hysterothecial initiation.

Materials and Methods

Cooling of blighted trees was accomplished by moving blighted saplings to high elevations. The hysterothecial development on these trees was then compared with the hysterothecial development on

transplanted and natural growing trees on Pringle Butte which serve as the standard.

During the last two weeks of May and the first week of June 32 trees were transplanted from their natural sites at 4, 500 to 4, 700 ft on the north and west slopes of Pringle Butte (Deschutes Co., Oregon) into five gallon cans. The transplanted trees were well watered and were held on the northwest slope of Pringle Butte until June 16th. At which time 15 were moved to the summit of Davis Mountain, elevation 6, 665 feet, approximately 11 miles to the southwest of Pringle Butte. The other 17 trees remained on the northwest slope of Pringle Butte. Trees located at both sites were placed in areas that were quite shaded much of the day.

In addition to the transplanted trees 24 naturally growing trees located on the west and northwest slopes of Pringle Butte were included in the experiment as a control to test the effects of transplanting.

All trees selected for the experiment were blighted saplings ranging in height from four to 11 feet. Trees of the smaller size were easily placed in five gallon cans and transported via a covered pickup truck.

Temperature data at Davis Mountain was recorded on a recording thermometer whose accuracy had been previously checked using a mercury bulb thermometer. Weather recordings at the United States Weather Bureau Station at Wickiup Reservoir half way between

Pringle Butte and Davis Mountain at 4,200 feet were taken as indicative of the general conditions at Pringle Butte.

For the comparison of data on hysterothecial development between the groups of trees, needles blighted by the fungus were collected at intervals from June through October. Care was taken so that the most advanced stage of development on the tree was selected in each sample. Needles once removed from the tree were placed in paper envelopes numbered the same as the trees from which the needles were taken. The stage of hysterothecial development on these needles was then determined by microscopic examination into one of the following categories; asci not formed, asci formed, spores evident, septate spores formed, slit band of hysterothecium evident. The most advanced stage of hysterothecial development for each tree at the time of the sample was then recorded on the final data sheet. Each of the five stages respectively is designated in subsequent tables and figures by a Roman numeral. It should be emphasized that the most advanced stage found on a particular tree is not necessarily the most common stage found on the tree. Even one needle may contain hysterothecia in different stages of development.

Results

Of the transplanted trees, four on Davis Mountain and five on Pringle Butte succumbed during the summer. Hysterothecial

development of the dead trees never attained ascus formation. For the remaining trees the most advanced stage of development of the hysterothecium on each tree is summarized in Table 1. June data showed that all trees were in the same stage of development. And since the objectives of the experiment were reached with September and October data, the data for July and August was not analyzed.

Comparisons between the treatments are graphically represented in Figures 1 through 4. Figures 1 and 2 compare on a percent basis, the most mature hysterothecial development attained on the trees at Davis Mountain on September 11th and October 14th with that reached by the transplanted trees on Pringle Butte. Figures 3 and 4 exhibit the same relationships between the transplanted trees on Pringle Butte and the trees growing there naturally.

Significance tests for the differences between the treatments were performed using the Wilcoxian two-sample test for the unpaired case (Alder and Roessler, 1964). The results of these tests are tabulated in Table 2.

These results show that transplanting the trees has a profound effect on hysterothecial development. The effect of cooling is much less pronounced, and is significant in October only.

The colder daytime temperatures on Davis Mountain (mean daily high 18 degrees below that on Pringle Butte during the duration of the experiment) correlates with the reduction of the number of

Table 1. Most advanced stage of hysterothecial development attained on September 11th and October 14th by trees equivalent in June. Data for Pringle Butte, 4,500 ft. and Davis Mountain 6,665 ft.

Most advanced stage of fungus per tree		Treatment											
		Pringle Butte transplants				Pringle Butte natural trees				Davis Mt. transplants			
		9/11		10/14		9/4		10/14		9/11		10/14	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
I.	Asci not formed	2	17	1	8	3	13	3	13	4	36	3*	27
II.	Asci formed	6	50	3	25	1	4	1	4	3	27	4	36
III.	Spores evident	1	8	0	0	0	0	0	0	2	18	0	0
IV.	Septa evident	3	25	1	8	2	8	0	0	2	18	0	0
V.	Slit band developed	0	0	7	58	18	75	20	83	0	0	3	27

* One tree died on Davis Mountain between September and October

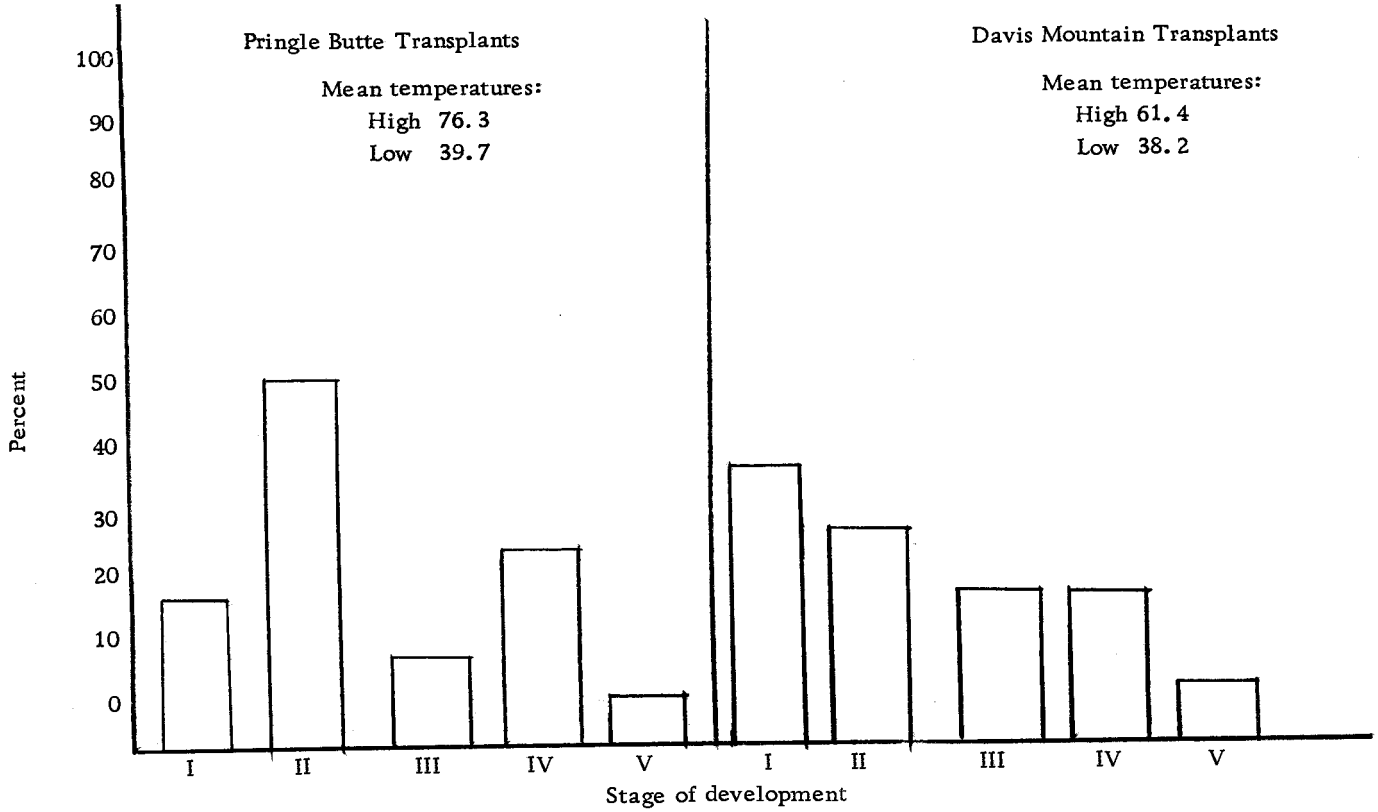

Figure 1. Comparison of the percentage of trees attaining a particular most advanced stage of fungal development at Pringle Butte and Davis Mountain on September 11th. Differences are not significant using Wilcoxian two sample test.

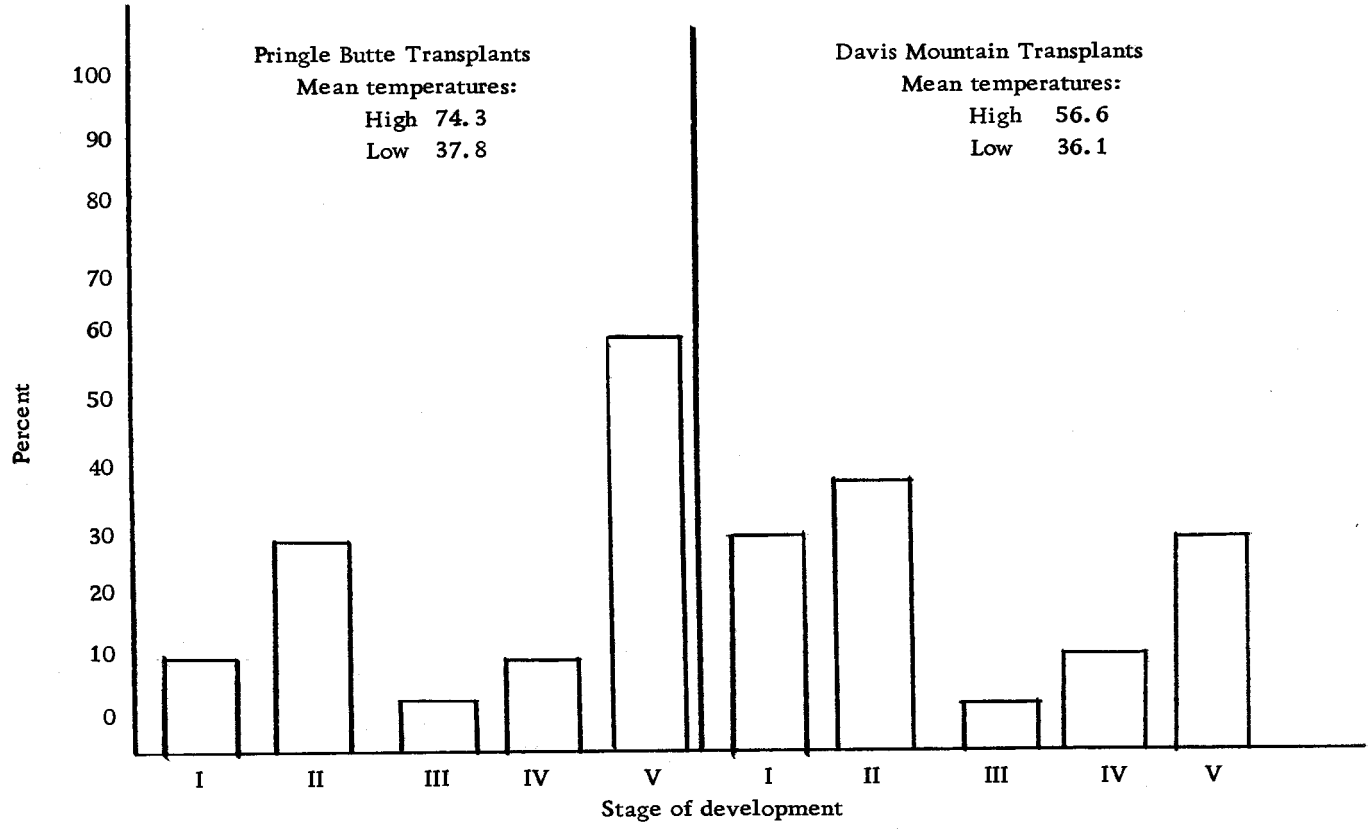

Figure 2. Comparison of the percentage of trees attaining a particular most advanced stage of fungal development at Pringle Butte and Davis Mountain on October 14th. Differences significant at the five percent level.

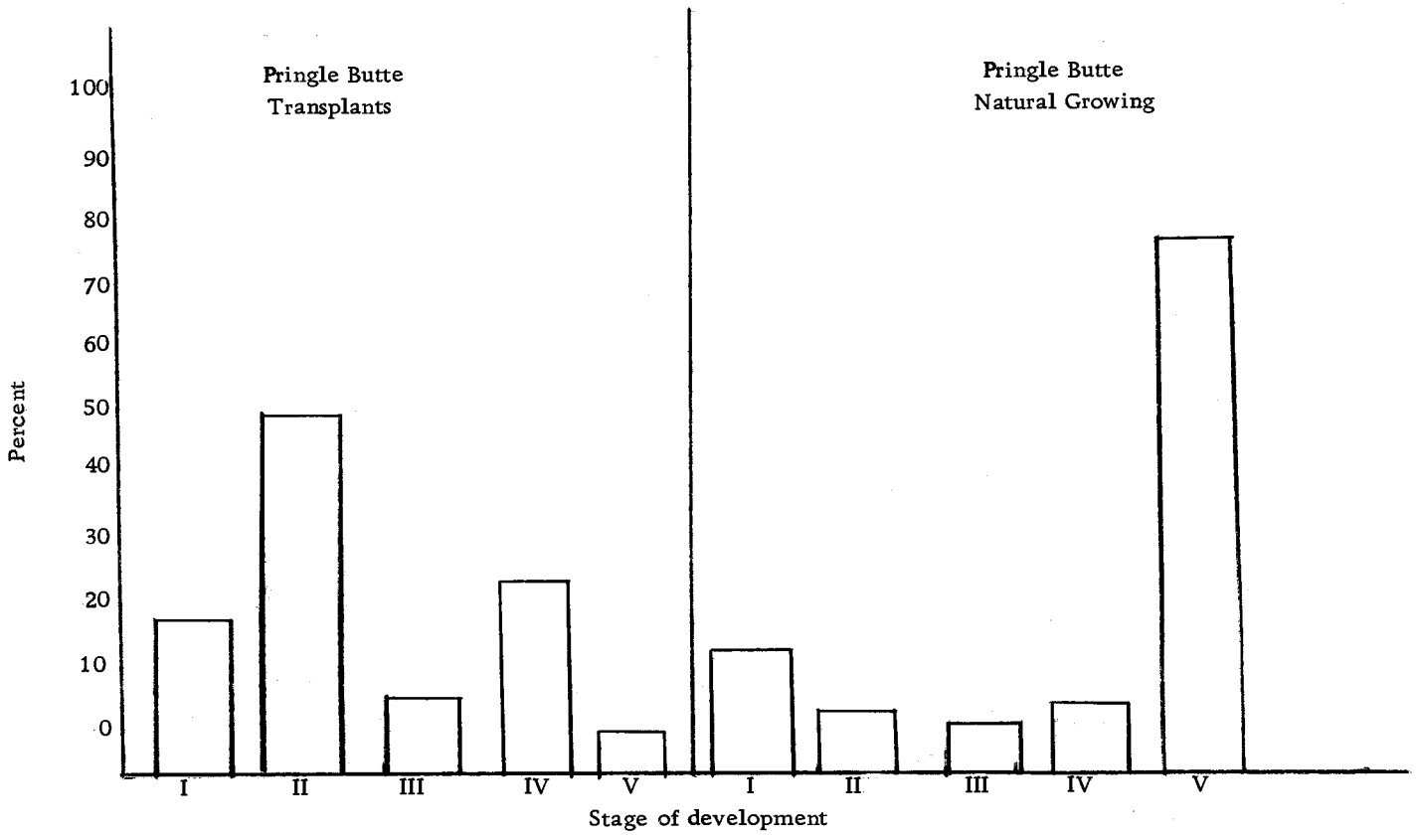

Figure 3. Comparisons of the percentage of trees attaining a particular most advanced stage of fungal development between the transplanted and natural growing trees of Pringle Butte on September 11th. Results significant at the one percent level.

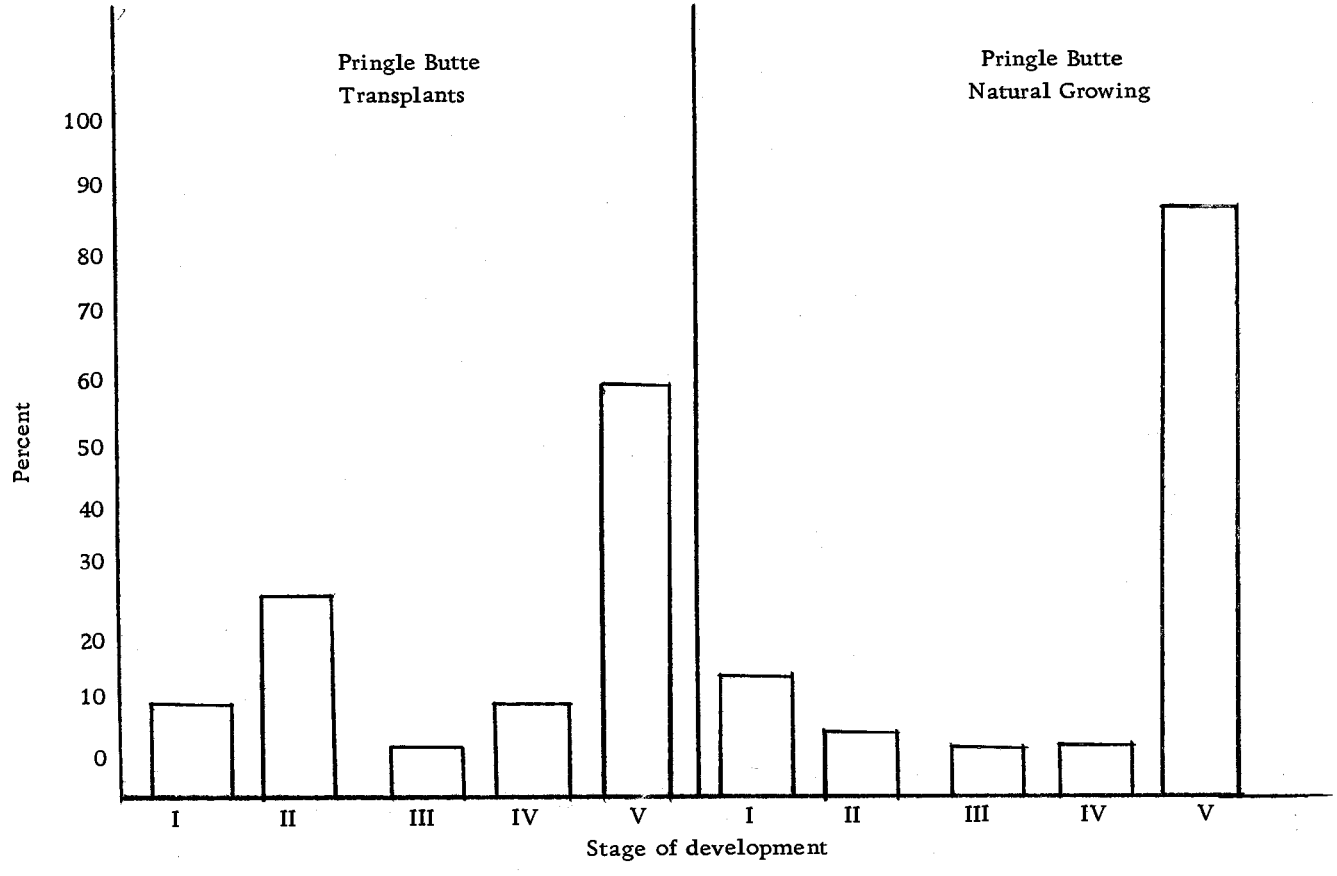

Figure 4. Comparisons of the percentage of trees attaining a particular most advanced stage of fungal development between the transplanted and natural growing trees on Pringle Butte on October 14th. Results significant at the one percent level.

Table 2. Significance tests of differences in hysterothecial development between the treatment of the summer and fall cooling experiments.

Treatments compared	Date	Probability*	Significance
1. Davis transplants Pringle Butte transplants	9/11	28%	none
2. Davis transplants Pringle Butte transplants	10/14	4%	significant
3. Pringle Butte natural Pringle Butte transplants	9/11	.02%	highly significant
4. Pringle Butte natural Pringle Butte transplants	10/14	1%	highly significant

* Probability of the means of the two treatments belonging to the same population.

trees bearing mature hysterothecia from 58 percent on Pringle Butte to 27 percent on Davis Mountain. This reduction is probably due to a combination of indirect and direct factors, the fungus being inhibited indirectly by a reduction of host vigor due to the low temperatures and directly by the effect of the cold temperature on the mycelial growth rate.

An interesting and unexplained result was noted in that in three of the natural growing trees hysterothecial production never progressed beyond the formation of black lines under the epidermis of the needle. This phenomena was also noted on all of the dead trees and some of the transplanted trees. The latter is explainable due to poor vigor or death of the host. Whether this is a host reaction in the natural trees or is due to other causes was not ascertained. Possible other causes might be an effect of saprophytic invasion or the fact that Elytroderma is heterothallic and only one mating strain exists in the trees that the fungus failed to fruit.

The inability of Elytroderma deformans to complete hysterothecial development, even after it had once been initiated, after death of the host and the definite relationship of reduced host vigor (due to transplanting) to delays and diminished hysterothecial production demonstrates the incapability of Elytroderma to act as a saprophyte. These relationships indicate a high degree of parallel evolution between pathogen and host.

THE EFFECT OF HOST VIGOR ON HYSTEROTHECIAL DEVELOPMENT

Data from the preceding experiment indicated that there was a relationship between host vigor and the time and amount of fruiting activity of Elytroderma deformans. However, since the reduction of host vigor in that experiment was artificially induced by transplanting, it was deemed necessary to test the same relationship under natural conditions. The present experiment evaluates the effect of host vigor under natural conditions on fruiting by Elytroderma deformans. It was hoped that the results of the experiment would contribute to a better understanding of the host-parasite relationship between Elytroderma deformans and Pinus ponderosa.

Materials and Methods

Ten trees, each with at least five blighted tips of varying vigor, were selected, marked with surveyor's ribbon and numbered on August 20th. Each individual tip was also marked and labeled. This was done so that comparisons between the tips of varying vigor on one tree could be made as well as comparisons made on all of the tips of varying vigor regardless of which tree they came from. It was thought at the time that if differences in hysterothecial development among the tips of varying vigor of the ten trees could not be

shown, then differences could be shown in hysterothecial development between tips of varying vigor on one particular tree. As it turned out the latter comparison was not required as the relationship of hysterothecial development to host vigor was quite evident using tips of varying vigor regardless of the trees from which they came.

The parameters used to indicate tip vigor were the number and average length of the current year's needles. The average needle length for each tip was determined from measurements on four needles at the base, four at the tip and two from the middle portion of the current year's growth. If the tip had had less than ten needles, then all of the needles were measured and then averaged. The needles were measured while intact with a small ruler split lengthwise to facilitate placement along the needle. The vigor factor for each tip was computed by multiplying the average needle length times the number of needles on the tip.

Hysterothecial development was determined and classified by the methods used in experiment one. The dates of sampling were August 26th and October 14th. In the last sample no effort was made to attain the most advanced stage per tip. Rather all of the blighted needles remaining on the tip were collected. From the last collection the total number of hysterothecia reaching maturity was determined. Maturity in this case was taken as the presence of septate spores.

Results

Of the ten trees selected for the experiment one was omitted because it failed to produce hysterothecia on any of its tips. This phenomena was discussed briefly in experiment one. Results from the other nine trees appear in Table 3. It must be realized the number of mature hysterothecia found on the tree on October 14th is not necessarily the total number produced during the year per tip. This is so because some of the needles bearing mature hysterothecia were undoubtedly cast before October 14th. This assumption is based on the results of an experiment presented later in this thesis.

Of the 50 blighted tips sampled, 24 had vigor factors of less than 100. And it was noted in studying the data that these 24 tips consistently produced fewer mature hysterothecia per tip than did the tips of higher vigor. Consequent to this observation the 50 tips were divided into two groups; one with vigor factors under 100, the other with vigor factors exceeding 100. Comparisons were then made of hysterothecial behavior between the two groups and inferences drawn of the effect of host vigor on hysterothecial development. Table 4 and Figure 5 further show why the tips were divided into two groups at the 100 vigor factor level. Both the table and the graph represent six subgroups of tips based on tip vigor. Group one then consisted of vigor factor subgroups 0-50 and 50-100. Group two was composed

Table 3. The effect of host vigor, as expressed by vigor of branch tips, on production and maturation of hysterothecia.

Tree tip no.	Current year's needles		Vigor factor	Stage of hysterothecial development		No. of mature hyst. 10/14
	no.	Avg. length in cm.		8/26	10/14	
1-1	13	3.0	39.0[1]	1[2]	4[2]	7
1-2	23	1.9	43.7	3	4	2
1-3	1	8.8	8.8	0	4	11
1-4	37	6.6	244.2	3	4	60
1-5	23	4.8	110.4	3	4	43
2-1	20	4.1	82.0	2	4	19
2-2	20	4.1	82.0	1	4	5
2-3	7	4.2	29.4	1	4	1
2-4	40	5.4	216.0	3	4	6
2-5	17	6.0	102.0	3	4	9
3-1	18	2.2	39.6	0	0	0
3-2	59	7.3	430.7	3	4	10
3-3	14	6.4	89.6	1	0	0
3-4	38	6.9	262.2	1	4	2
3-5	17	2.3	39.1	0	0	0
4-1	26	8.1	210.6	0	0	0
4-2	11	6.5	71.5	0	0	0
4-3	10	4.1	41.0	0	0	0
4-4	10	4.6	46.0	0	0	0
4-5	54	6.0	324.0	3	4	19
5-1	43	11.2	481.6	3	4	77
5-2	41	9.6	393.6	3	4	56
5-3	10	4.6	46.0	2	4	6
5-4	38	11.4	433.2	3	4	26
5-5	7	4.0	28.0	1	0	0
5-6	71	11.2	795.2	3	4	9
5-7	26	7.8	202,8	3	0	0
6-1	17	7.0	119.0	0	3	4
6-2	40	7.5	300.0	2	4	2
6-3	25	3.5	87.5	0	3	1
6-4	8	3.0	24.0	0	0	0
6-5	4	2.0	8.0	0	3	1
7-1	29	9.9	287.1	4	4	78
7-2	24	6.8	163.2	4	4	13
7-3	44	8.3	365.2	4	4	11
7-4	6	2.4	14.4	2	3	1
7-5	10	4.2	42.0	2	2	0

Continued on next page

Table 3. Continued.

Tree tip no.	Current year's needles		Vigor factor	Stage of hysterothecial development		No. of mature hyst. 10/14
	no.	Avg. length in cm.		8/26	10/14	
8-1	21	4.4	84.4	3	3	1
8-2	17	3.1	52.7	0	1	0
8-3	41	9.0	369.0	1	1	0
8-4	24	7.2	172.8	3	4	13
8-5	26	8.1	210.6	1	1	0
9-1	17	2.5	42.5	1	1	0
9-2	26	2.9	75.4	0	0	0
9-3	14	1.9	26.6	1	4	2
9-4	57	5.5	313.5	3	4	17
9.5	34	5.1	173.4	4	4	18
9-6	57	7.5	427.5	3	4	22
9-7	10	2.5	25.0	3	4	7

[1] A factor derived by multiplying number of needles times mean needle length.

[2] (0) Hysterothecium formed but hymerium not differentiated, (1) Asci formed but no spores delimited, (2) Aseptate spores only present, (3) Spores septate, (4) Slit band evident.

Table 4. Number of mature hysterothecia per tip on the tips of varying vigor.

Tip vigor subgroups	Number of tips	Number of mature hysterothecia on each tip	Average
I. 0-50	17	7, 2, 11, 1, 0, 0, 0, 0, 6, 0, 0, 1, 0, 1,0, 2, 7	2.2
II. 50-100	7	19, 5, 0, 0, 1, 0, 1	3.7
III. 100-150	3	43, 9, 4	18.7
IV. 150-200	4	6, 13, 13, 18	12.5
V. 200-300	8	60, 3, 2, 0, 0, 2, 48, 0	18.1
VI. 300-800	10	10, 77, 58, 19, 9, 26, 11, 0, 17, 22	24.7

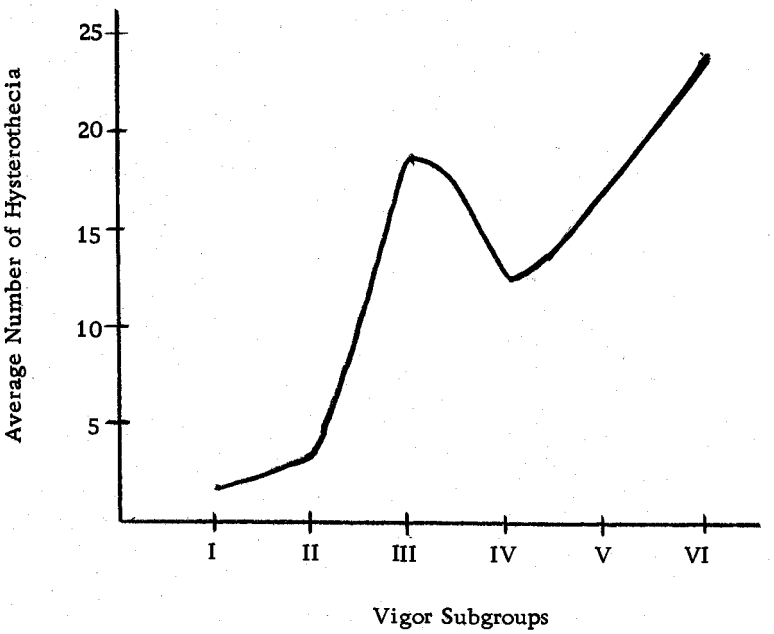

Figure 5. Average number of hysterothecia per tip on tips falling into each of the six vigor subgroups.

of subgroups 100-150, 150-200, 200-300 and 300 and above. The last column of Table 4 lists the average number of mature hysterothecia found per tip on October 14th. From the table it can be noted that the subgroups representing vigor factors of greater than 100 produce conspicuously more mature hysterothecia than the subgroups below 100. Note that great differences exist between the subgroup 50-100 and the subgroup 100-150. With the latter averaging more than four times as many mature hysterothecia per tip as the former. Figure 5 represents these results graphically.

Once the data were divided into two groups the next step was to compare the rates and amounts of hysterothecial development between the groups. Comparisons of the most advanced stage of hysterothecial development reached on August 26th and October 14th were performed and the results tabulated in Table 5. Two columns are listed for each tip vigor factor, hysterothecial development stage and date of sample. The first column represents the number of blighted tips falling into each category of the tip maturity classification, the second column is a percentage expression of the data listed in the first column. These percentages are expressed graphically in Figures 6 and 7. Statistical significance of the differences appear-in Table 5 were tested by the Wilcoxian two sample test (Table 6).

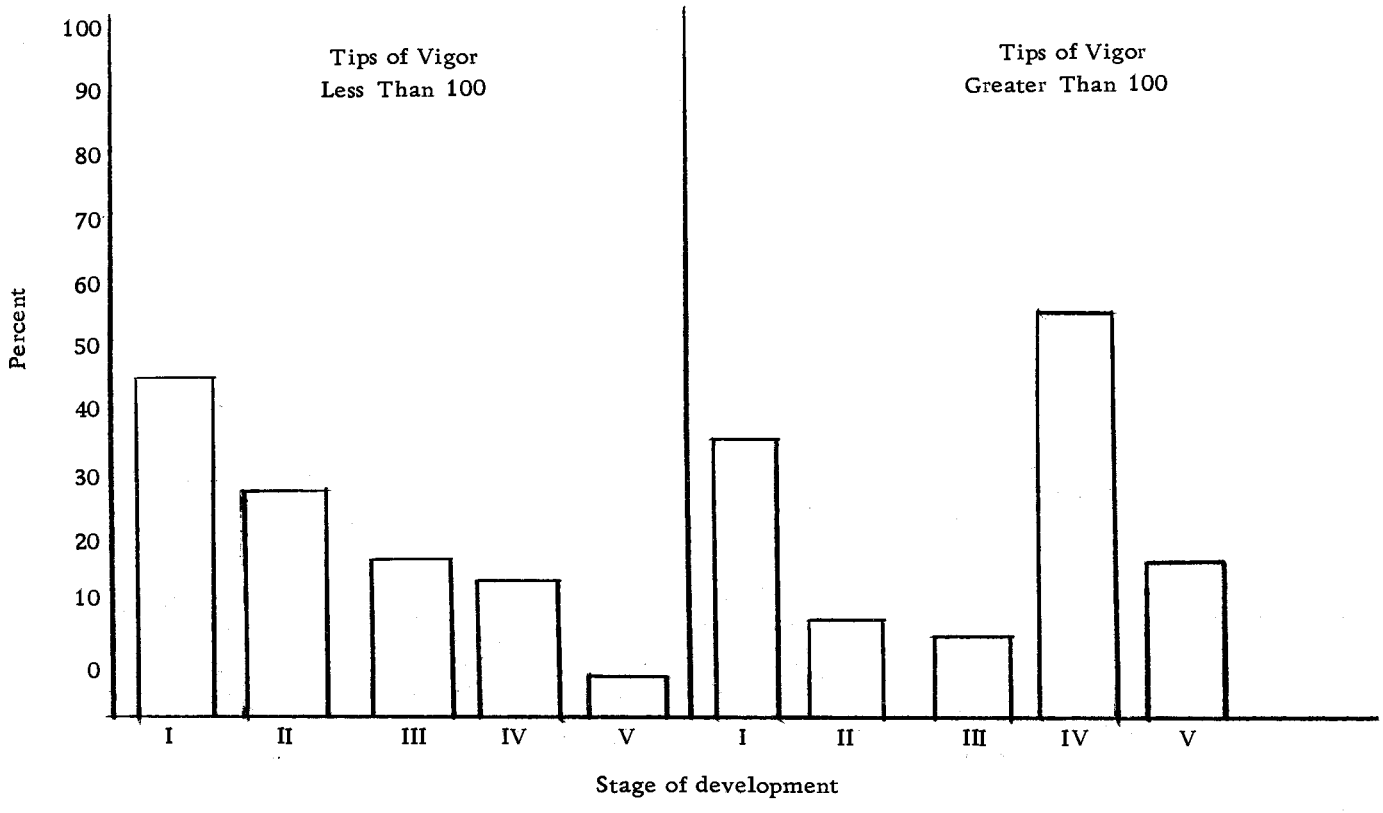

Figure 6. Comparison of the two vigor factor subgroups as to percentage of tips attaining a particular most advanced stage of fungal development on August 26th.

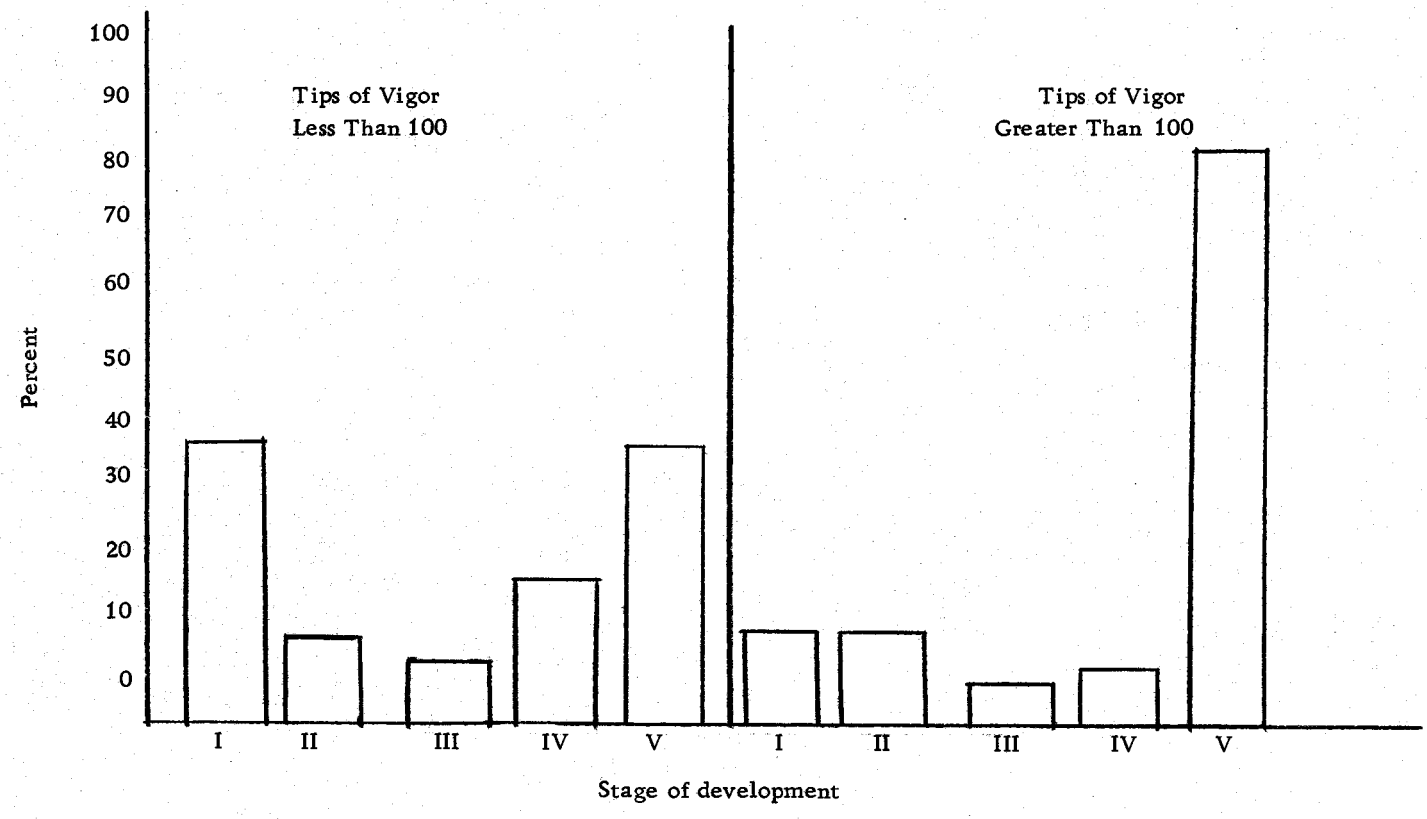

Figure 7. Comparison of the two tip vigor subgroups as to percentage of tips attaining a particular most advanced stage of fungal development on October 14th.

Table 5. Effect of host vigor on the rate of hysterothecial development.

Maturity classification	Group I Tip vigor 0-100				Group II Tip vigor 100-800			
	8/26		10/14		8/26		10/14	
	No.	%	No.	%	No.	%	No.	%
I. Asci not formed	11	44	2	8	9	36	2	8
II. Asci formed no spores	7	28	3	12	2	8	2	8
III. Spores evident	4	16	2	8	1	4	0	0
IV. Spore septa evident	3	12	14	56	4	16	1	4
V. Split band mature	0	0	4	16	9	36	20	80

Table 6. Significance tests of differences between two vigor factor groups with respect to number of hysterothecia and their stage of development.

Comparison between groups	Probability*	Significance
Stage of Development		
8/26	.03%	highly significant
10/14	.08%	highly significant
Number reaching maturity	1.30%	significant

* Probability of the means of the two tip vigor groups belonging to the same population.

The results show that host vigor affects both rate and amount of hysterothecial development by the fungus, tips of low vigor producing fewer hysterothecia at slower rates than tips of high vigor. However other factors also affect the rate and amount of inoculum produced. Note in Table 4 that subgroup VI, the subgroup containing the most vigorous tips shows a range of mature hysterothecia from 0 to 77. Some of the factors which may reduce hysterothecial production are hyper-parasite attack, saprophytic competition, premature casting of the needles due to a host reaction and differences in the strains of Elytroderma among the different tips.

MODIFICATIONS OF HYSTEROTHECIAL DEVELOPMENT BROUGHT ABOUT BY SAPROPHYTES ENTERING THE NEEDLE VIA THE PYCNIDIAL SCAR

It was noted from examination of numerous blighted needles in the spring of 1966 that hysterothecia were initiated only basipetally from the location of the pycnidial scar. Observations during the fall and summer revealed that hysterothecia initiated near the pycnidial scar rarely developed to maturity and that the farther the location of the hysterothecium from the scar the greater the chances of eventual inoculum production. Gordon (1966) reports that the pycnidial scar is a means of rapid entry for saprophytes and hyperparasites into the inner needle tissue. Apparently as these fungi invade the needle tissues Elytroderma is slowly destroyed in a basipetal direction. The purpose of this experiment was to quantitatively determine how much the invading fungi were reducing inoculum production of Elytroderma deformans.

Procedure

Eighty needles collected in the fall of 1966, each containing at least one mature hysterothecium, were used for this experiment. The presence of at least one mature hysterothecium per needle was determined by examination with a dissecting microscope. Mature hysterothecia were easily identified by characteristic swelling

resulting from the presence of the mature spores. The effect of the saprophytes and hyper-parasites was determined by placing groups of ten needles in petri dishes lined with moistened filter paper. The dishes contained just enough free distilled water to cover the surface of the needles. After about 15 minutes the slit bands of mature hysterothecia began to open. The needles were then examined under a dissecting microscope. The distance from the pycnidial scar and the maturity of each ascocarp was then determined. Distances were determined by measuring from the distal end of the hysterotheciium to the basal end of the pycnidial scar. Maturity was determined by the presence or absence of septate spores. Each hysterothecium was then classified according to its distance from the pycnidial scar and its maturity. In a few instances the number of immature hysterothecia under one clypeus was difficult to distinguish. When this situation occurred each centimeter along the clypeus was estimated to be equal to one hysterothecium.

Results

It was hoped that the effect of secondary fungi on hysterothecial development of Elytroderma could be shown by establishing a relationship between the distance from the point of entry (the pycnidial scar) of the invading fungi and the percent of hysterothecia reaching maturity. If the relationship is valid the percent of hysterothecia

reaching maturity should increase as the distance from the hysterothecium to the pycnidial scar increases. The results appear in Table 7 and Figure 8.

Table 7. Hysterothecial maturity relative to distance from pycnidial scar.

Distance from pycnidial scar to hysterothecium	Sterile ascocarps	Fertile ascocarps	
Centimeters	Number	Number	Percent
0-1	85	12	12
1-2	66	40	38
2-3	35	65	65
3-4	18	43	70
4-5	8	34	81
5-6	6	13	69
6-7	2	4	68
7-8	1	2	67
8-9	0	1	100

Data for distances beyond five centimeters probably should be ignored because of their rarity. Data for the first five centimeters are presented in Figure 8.

The results show that the farther the location of hysterothecium from the main point of fungus entry, the pycnidial scar, the better its chance of reaching maturity. Note that the curve represented in Figure 8 is approximately linear. Since fungal growth is known to be linear with time this curve may be postulated to represent the growth

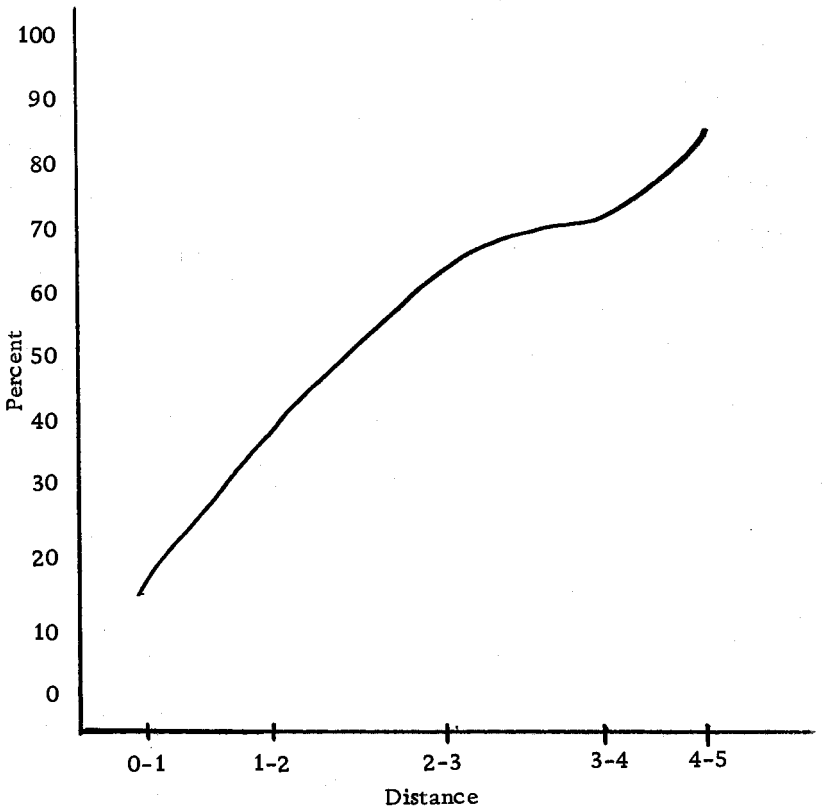

Figure 8. Percent of hysterothecia attaining maturity at distances from one to five centimeters from the pycnidial scar.

of the saprophytes in the dead needle. If this is so Elytoderma apparently offers no resistance to saprophytic fungi.

DETERMINATION OF THE CONDITION OF HYSTEROTHECIA OF CAST NEEDLES

From field observations in Montana Gordon and Laurent (1966) stated that diseased needles are cast only after the hysterothecium has matured and the ascospores have been disseminated. My field observations indicate that this is not the case in Oregon. More needles appear to be cast in the fall no matter what the stage of fungus development.

The objective of the following experiment is to determine whether or not needle casting is dependent on the stage of fungal development. This is an important factor in the disease cycle for if the inoculum is to be delayed until the following spring the needles must remain on the tree through the winter.

Procedure and Results

Ten crenolin bags were tied around blighted tips of ten different trees during the first week of September 1966. On the 14th of October the bags were removed and the fallen needles collected for examination. From 50 needles taken at random, hand sections of each hysterothecium were examined microscopically and the development stage of each hysterothecium was classified, the most advanced stage reached, are as follows: clypeus formation only, acigerous hyphae to

Table 8. Condition of fungus maturity in each of 50 cast needles.

Needle number	Stage of maturity					
	Hystero-thecia	Clypeus	Acigerous-non-septate spores	Asci full	Asci 25-50% empty	Asci 50-100% empty
	number					
1	3	2	0	1	0	0
2	4	3	1	0	0	0
3	4	2	0	1	1	0
4	4	2	0	2	0	0
5	1	0	0	1	0	0
6	1	1	0	0	0	0
7	1	1	0	0	0	0
8	2	2	0	0	0	0
9	1	0	1	0	0	0
12	3	1	2	0	0	0
13	6	0	0	4	2	0
14	3	2	0	1	0	0
16	4	2	1	0	1	0
17	8	0	0	6	2	0
18	2	1	0	0	1	0
21	2	1	0	1	0	0
22	3	2	0	1	0	0
24	3	2	0	1	0	0
25	7	2	0	3	2	0
26	4	1	0	3	0	0
27	5	1	0	3	1	0
28	4	2	0	1	1	0
29	6	0	0	4	2	0
30	4	3	0	0	1	0
31	7	1	0	4	2	0
32	4	3	0	1	0	0
34	3	3	0	0	0	0
35	2	2	0	0	0	0
36	1	0	0	1	0	0
37	2	1	0	1	0	0
38	4	3	1	0	0	0
39	4	2	0	1	1	0
40	8	0	1	5	2	0
41	3	2	0	0	1	0
42	3	3	0	0	0	0
44	3	2	0	1	0	0
46	2	1	0	1	0	0
47	2	2	0	0	0	0
49	5	1	0	3	1	0
50	6	2	0	3	1	0
TOTAL	143	61	7	54	21	0

non-septate spore, asci containing septate spores, 25 to 50 percent of the asci empty, more than 50 percent of the asci empty. Empty asci were taken to indicate that some spore release had taken place. The results appear in Table 8. Needles 10, 11, 15, 19, 20, 23, 33, 43, 45, and 48 showed no hysterothecial development at all and are not included in Table 8.

The results show that needles are cast with the hysterothecia in all stages of development and in no case in this study were the spores more than 50 percent disseminated from hysterothecia of the fallen needles. Thus ascocarp maturation and ascospore release are not a prerequisite for casting of the blighted needles.

THE EFFECT OF TEMPERATURE ON HYSTEROTHECIAL OPENING AND ASCOSPORE GERMINATION

The effect of temperature on hysterothecial opening has not been studied by previous investigators. As noted in the literature review reports on ascospore germination are limited, lacking in agreement and usually not supported by published data.

Since the slit band, when open, is a means of rapid entry into the hysterothecium for secondary fungi, the mechanisms controlling hysterothecial opening are considered important for the survival of overwintering spores. An appreciation of the factors affecting spore germination is mandatory for understanding pathogenesis.

Materials and Methods

All needles used in experiments of this section were collected prior to the fall rains and before the slit band had matured on all but a few of the hysterothecia. Needles collected at later dates were found to be of little value due to the entrance of hyper-parasites into the hysterothecium. The collected needles were kept dry and stored at 34 degrees fahrenheit.

The effect of temperature on the opening of the fruiting bodies was determined in the following manner. Petri plates containing distilled water were placed in temperature chambers set at five

degree intervals from 5 to 40° C. One additional test was made at 90° C. Ten needles bearing at least three mature hysterothecia each were added to the dishes 45 minutes later. This allows time for the water in the dishes to reach the designated temperature prior to the addition of the needles. After a 15 minute exposure to the designated temperature the needles were examined with a dissecting microscope to determine the condition of the slit bands. The effect of temperatures near freezing were tested by placing the needles in petri dishes full of crushed ice. Temperatures were determined using a mercury chemical thermometer. The needles and the thermometer were observed constantly until the slit bands of the hysterothecia opened.

The effect of temperature on ascospore germination was determined as follows. Three petri dishes containing water agar and ten milliliters of distilled water were placed in each of six temperature chambers of a series ranging from 5 to 30 degrees centigrade at five degree intervals. After a period of approximately one hour, ten needles carefully selected on the basis of containing at least three mature hysterothecia per needle, were added to the petri dishes, in the incubators. Shortly after the needles were added to the dishes the slit bands of the hysterothecia opened and the spores were distributed over the surface of the agar medium. The plates were examined for ascospore germination after 12 hours of incubation and at various intervals thereafter. Perhaps it should be emphasized that the

needles were unsterilized. In this way the ascospore germination tests were performed in the presence of many of the organisms that ascospores of Elytroderma encounter in nature.

In order to facilitate counting of germinated ascospores the needles in the petri dishes were arranged to form grids. Each grid was then scanned using the low power objective (100x) of a microscope and the number of germinated and ungerminated spores was tabulated. The first 100 ascospores observed in each petri dish were taken as the sample. Thus the three petri dishes incubated at each temperature yielded a total sample of 300 ascospores. Germinated ascospores where tabulated into one of the following calsses depending on the length of their individual germ tubes.

1. Germ tube twice the length of the ascospore or greater.
2. Germ tube length between one and two times the length of the ascospore.
3. Germ tube length between one-half and one times the ascospore length.
4. Germ tube length between one-fourth and one-half of the ascospore length.
5. Germ tube length less than one-fourth the length of the ascospore.

All of the plates were first read after a 12 hour period in their respective incubation chambers. The plates were read in groups of

three and immediately returned to the chambers from which they were taken, with one exception. Plates incubated at higher temperatures that contained no germinated spores were placed in chambers that had produced good germination for the 12 hour period (in this case the 15 degree chambers). This was done to determine if spores were still capable of germination after the exposure to the higher temperatures. Later readings were taken at 36, 48, 72, and 144 hours.

The effect of subjecting the needles to freezing temperatures prior to the germination tests was determined by placing a petri dish with water agar and distilled water in a freezer at -15 degrees centigrade. After the water was frozen the needles were added.

The petri plates were kept in the freezer for 24 hours then incubated at 15 degrees centigrade.

Results

Hysterothecial opening was found to occur at all temperatures tested in the temperature chambers (0-90°C.). The hysterothecia on the needles covered with crushed ice began opening as soon as the temperature rose above freezing. Thus opening of the slit band is independent of temperature. Apparently free water or conditions of very high humidity will cause the slit bands to open over a wide range of temperatures. The open slit band undoubtedly provides a

means of entry for hyper-parasitic or secondary fungi into the hymenial layer. As previously mentioned hysterothecia collected after mature slit band have opened are of little value in germination tests, since very few contain spores capable of germination. The exact mechanism of how spore viability is reduced or the species of fungi involved was not ascertained.

Ascospore germination results for 12 and 24 hour incubation periods at the various designated temperatures are presented in Table 9. The results show that the optimum temperature range for ascospore germination after 12 hour incubation period on water agar and in the presence of distilled water is near 15 to 20° C. At ten degrees the percentage germination was approximately halved and at 5, 25 and 30° C germination was non-existent. Results after 24 hours of incubation are slightly different. The optimum range for germination approximates 10 to 20° C. However plates incubated at 20 degrees became overrun by contaminating organisms from the needles (mainly bacteria and Actinomycetes) after 24 hours.

After 36 hours all of the plates were overrun by organisms from the needles except for the plates incubated at five degrees. The plates incubated at five degrees were examined every 12 hours up to a maximum of 144 hours (six days). At the end of this time germ tubes were still elongating relatively free from interference from other organisms (Table 10).

Table 9. Ascospore germination after 12 and 24 hours incubation at six temperatures.

Temp.	Germ tube length class			Germination	
	$\frac{1}{2}$-1	$\frac{1}{4}$-$\frac{1}{2}$	0-$\frac{1}{4}$		
degrees C	number			number	percent
	12 hour incubation				
5	0	0	0	0	0
10	4	43	47	94	31
15	107	76	14	197	66
20	104	52	16	172	57
25	0	0	0	0	0
30	0	0	0	0	0
	24 hour incubation				
5	9	41	36	86	29
10	112	69	12	193	65
15	149	61	4	214	72
20	Length not detectable due to presence of competing organisms.			194	85

Table 10. Ascospore germination after 144 hours at 5° C.

Germ tube length class				Germination	
2-∞	1-2	1/2-1	1/4-1/2		
Number				Number	Percent
86	71	31	4	192	65

None of the ascospores initially incubated at 30 degrees and only one percent of those at 25 degrees germinated when placed at the optimum temperature for germination during the last 12 hours of a 24 hour incubation period (Table 11). High temperatures apparently have a lethal effect on Elytroderma ascospores. Prefreezing of the needles had no significant effect on ascospore viability (Table 11).

Table 11. Effect of temperatures above 25 degrees centigrade and below freezing on ascospores.

Temp. and time combinations degrees C and hours	Germ tube length class $\frac{1}{2}$-1	$\frac{1}{4}$-$\frac{1}{2}$	0-$\frac{1}{4}$	Germination	
	number			number	percent
30 @ 12 15 @ 12	0	0	0	0	0
25 @ 12 15 @ 12	0	15	15	30	10
-15 @ 24 15 @ 24	127	46	15	188	63

These results show conclusively that ascospores of Elytroderma germinate best at temperatures below 25° C. Cochrane (Horsfall and Dimond, 1964) states that the average optimum temperature for germination of plant pathogenic fungi is about 25° C. And that the value for saprophytic fungi is a few degrees higher. This with the fact that bacteria are known to be active above 25° C would seem to give Elytroderma a great advantage at lower temperatures. This advantage is evidenced by the fact that Elytroderma germ tubes were still elongating relatively free from competition six days after germination when incubated at 5° C, whereas at higher temperature the plates were completely overrun by competing organisms in 36 hours.

Temperatures above 25° C seemed to have a sterilizing effect on the spores. Whether this deleterious action was due to high temperatures in the presence of water or to rapid action by competing organisms was not ascertained. Contrarily, freezing of the spores had no significant inhibitory effect on the ability of the spores to germinate when later placed under optimum conditions for germination.

THE EFFECT OF TEMPERATURE AND RELATIVE HUMIDITY ON SURVIVAL OF MATURE ASCOSPORES

As mentioned previously, in order for spring infection to occur either an alteration in the cyclic development normally observed for the pathogen or some means of survival of the spores produced in the fall until spring must occur.

The purpose of this experiment is to determine what conditions would be necessary for the mature spores to overwinter in the hysterothecium.

Materials and Methods

Infected needles were collected before the fall rains and prior to their use were kept dry at 34° F. The needles were subjected to controlled temperatures and humidities for a ten week period, after which the condition of hysterothecium and the viability of the spores was determined.

The needles were tested at temperatures from 5° to 30° C at five degree intervals. Temperature was controlled using thermostatically controlled chambers. Five relative humidity ranges were tested at each temperature. Relative humidity was controlled following the method described by Winston and Bates (1960) using saturated solutions of reagent grade salts in closed containers (Table 12).

Table 12. Saturated solutions and their respective relative humidities at temperatures from 5° to 30° C.

Saturated solution	Humidity range at temperatures from 5° to 30° C.
$LiCl \cdot H_2O$	11.0-14.0%
$MgCl \cdot 6H_2O$	32.5-35.0%
$K_2CO_3 \cdot H_2O$	43.5-47.0%
NH_4SO_2	80.0-83.5%
K_2SO_4	96.5-98.5%

According to Winston and Bates, the humidities remain stable in closed containers as long as some solid phase remains beneath the solution. Solutions were made in volumes of 1000 ml. by first dissolving enough solid to saturate at boiling. The solution was then allowed to cool partially and a small amount of chemical was added. Then the solution was allowed to cool further at which time more solid was added until a layer of chemical approximately one eighth of an inch thick covered the bottom of the flask. The solution was then laid aside for one week. At the end of this period the layer at the bottom of each flask was still present and the chemicals were considered ready for use.

Baby food jars served as the humidity chambers. Ten needle sections from one to two centimeters in length, that had been carefully selected for the presence of mature hysterothecia, were wrapped in cheese cloth strips and taped to the underside of the

jar lid. The lid was then tightly screwed on the jar containing the appropriate solution and the whole apparatus was placed in its respective temperature chamber. Three jars of each solution were placed in each of the five temperature chambers.

The ten week test period was initiated on January 10th. Ascospore germination was used as the main criterion of survival. The condition of the hysterothecium was also examined and described as follows. The approximate ratio of alive to dead spores present at the end of the experiment was estimated. The live spores were readily distinguished from the dead ones by their color when observed under low power of the microscope. The live spores were pale olive green and full of protoplasm while the dead spores were void of protoplasm and colorless. Whether or not the hysterothecium contained spores that had germinated within the asci was also noted. The ability of the spores to germinate was tested using the same methods described in the ascospore germination experiment described previously. Needles in this experiment were incubated for 24 hours at 15° C.

The data of the experiment consisted of the following. Spore germination for each treatment was classified as abundant if 50 percent or more of the spores on each plate germinated, as scarce if less than 50 percent germinated and none if all spores failed to germinate. Germination of spores within the asci of the

hysterothecium was simply noted as yes or no. The ratio of alive to dead spores within the hysterothecium was estimated and expressed as percent.

Results

The results presented in Table 13 show that if the ascospores of Elytroderma deformans are to survive for any length of time in the hysterothecium after they have reached maturity dry cool conditions are mandatory. The results in Table 13 represent a summation of the results of all three jars exposed to the temperature and humidity conditions unless specified otherwise.

The total sterilization of the spores by storage at 30° C should be noted. Another interesting result is the fact that in several treatments (11-14% R.H. at 15°, 20° and 25° C and at 32.5-35.0% R.H. at 10 and 20° C) germinated spores were present in the asci within the hysterothecia they were completely absent to scarce in the water over the agar medium, while at optimum conditions (11-14% R.H. at 5-10° C) for survival germinated spores are present both within the asci and on the agar medium.

It is interesting to note that temperatures at 30° C even at the driest humidity is lethal to the ascospores. This fact was previously noted in spore germination tests. However in this case the sterilization was effected in the absence of water. It would be interesting to

Table 13. Effect of temperature and humidity on ascospore survival within the hysterothecium.

Humidity and temperature	Germination on agar	Germination in the ascus	Percent of spores alive*
R. H. 11-14%			
5°C	abundant	yes	95-98%
10°C	abundant	yes	95-98%
15°C	scarce	yes	95-98%
20°C	scarce	yes	95-98%
25°C	scarce	yes	95-98%
30°C	none	no	none
R. H. 32-35%			
5°C	1 abun. 2 scarce	yes	95-98%
10°C	2 scarce 1 none	yes	1@95-98% 2@10%
15°C	none	no	1@10%, 2 at 0%
20°C	none	1 yes, 2 no	1@5%, 2@0%
25°C	none	no	none
30°C	none	no	none
R. H. 43-47%			
5°C	scarce	yes	1@50%, 2@10%
10°C	none	no	none
15°C	none	no	none
20°C	none	no	none
25°C	none	no	none
30°C	none	no	none
R. H. 80-84%			
5°C	none	yes	10%
10°C	none	no	none
15°C	none	no	none
20°C	none	no	none
25°C	none	no	none
30°C	none	no	none
R. H. 96-98%			
5°C	none	no	none
10°C	none	no	none
15°C	none	no	none
20°C	none	no	none
25°C	none	no	none
30°C	none	no	none

*Estimated visually, quantitative values not involved.

determine if the effect is related directly to temperature or if microorganisms are involved.

The fact that the spores, in several treatments, were able to germinate within the asci but were not discharged from the asci onto the medium indicates that mechanism of spore discharge is more easily disrupted by secondary fungi than is the viability of the spores.

DISCUSSION AND CONCLUSIONS

Based on the findings of the experiments presented in this paper the possibility of inoculum initiated during the growing season of one year being delayed or surviving to incite a mass infection and an epiphytotic the following year is highly unlikely if not impossible.

Summer cooling and poor host vigor have been shown to cause delay in hysterothecial maturity, but these same factors also reduce the total amount of inoculum produced. It does not seem probable that a mechanism reducing the amount of inoculum produced could in any way be involved in the creation of epiphytotic conditions. Also since secondary fungi entering through the pycnidial scar have been demonstrated to have a definite relationship with the amount of reduction of Elytroderma inoculum, it seems reasonable to assume that if the inoculum were delayed the probability of it being destroyed by invading fungi or bacteria would be increased. And finally since the needles are cast independently of the condition of the hysterothecium, delayed inoculum would be deposited on the forest floor and subjected to rapid deterioration before it matured.

The possibility of mature inoculum overwintering has also been demonstrated to be rather remote. Dry conditions required for successful survival of the spores could not reasonably be expected to occur in the fall and winter in Central Oregon.

It seems more reasonable to postulate that mass infection would occur under conditions which would speed up fungal development rather than hinder it. Based on the facts that Elytroderma has been demonstrated to be dependent on host vigor and that it is known to reside in the phloem,we can classify the parasitism exhibited by Elytroderma according to the system used by McNew (Horsfall and Dimond, 1960). In this system Elytroderma would be placed in the most advanced class, which includes various rusts, smuts, gall forming parasites and viruses. Diseases of this class according to McNew are not as completely dependent on environmental fluctuations as are diseases of lower classes, for example, storage rots, seedling diseases, root rots and foliage diseases that involve less specialized parasites. The aggressiveness of diseases of this more advanced or specialized class are dependent to a large extent on the genetic makeup and growth of the host. Diseases of this type are especially destructive on rapidly growing tender tissue.

Since the last reported outbreak was preceded by mild, moist weather, which is conducive for rapid and extended growth, and the fact that fungal hysterothecial development has definitely been related to host vigor the hypothesis that epiphytotics occur in the following manner seems reasonable. A mild, moist growing season during the year that the fungus initially infected the needle would promote host vigor and this in turn would speed up fungal

development. So that in the fall of the first year the needles would begin turning brown and hysterothecia would be initiated. A mild, moist spring the second year would facilitate a rapid maturing of the fruiting bodies and extend the length of time that tender young foliage tissue would be susceptible to infection by the hydrophyllic loveing ascospores, which germinate best under cool moist conditions.

Weir (1916) reported disease development that is almost identical to the hypothesis stated above. Trees of his infection studies were inoculated on May 20th. By the following fall the infected needles were turning brown and by the spring of the following year the needles bore mature ascospores. These experiments were conducted in the white pine region of Idaho where conditions are normally milder and more humid than in areas where needle blight is normally found and would be expected to produce conditions favoring vigorous growth of ponderosa pine.

Elytroderma deformans acting on a one year cycle would be very damaging to ponderosa pine. Ascospores produced in the spring or early summer would be relatively unaffected by hyper-parasites and saprophytes since the time between spore maturation and release would be minimal and the competing fungi would be relatively inactive during the cooler spring weather. In addition, infection phenomena would be promoted since the spores have been demonstrated to attain longer germ tube lengths in the absence of competing organisms.

Future experiments should be designed to center around factors that would involve the effect of host vigor on inoculation production. Certainly the effect of cool moist growing seasons should be investigated.

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