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Photochemical Oxidant Injury and Bark Beetle (Coleoptera: Scolytidae) Infestation of Ponderosa Pine

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Certain aspects of insect-disease relationships, especially those concerning transmission of pathogens, have been studied extensively and their significance has been well established. However, the role of diseases as factors predisposing coniferous trees to bark beetle infestation has received only minor attention. There has been little effort to determine the extent of the association between disease and bark beetle infestation, the significance of predisposing diseases in the ecology of the beetles, or the effects of disease upon the host that may increase susceptibility to beetle attack.

The series of papers in this issue presents the results of studies to determine (a) the degree of association between photochemical atmospheric pollution injury to ponderosa pine and infestation by bark beetles (paper I), and (b) the changes in the physiology of diseased trees which might influence host susceptibility to bark beetles (papers II and III). The results show that oxidant injury does, in fact, predispose ponderosa pine to beetle infestation, and that the injury leads to physiological changes in the host which may be related to increased bark beetle susceptibility. The significance of these results in relation to the present knowledge on bark beetle ecology and host susceptibility is discussed in paper IV.

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I. Incidence of Bark Beetle Infestation in Injured Trees[1]

INTRODUCTION

MANY WORKERS have observed associations between diseased trees and bark beetle infestation, and speculated that disease is a factor predisposing forest trees to bark beetle attack. Although observations concerning such a relationship between disease and insect have been numerous, few studies have been made to determine the degree of the relationship.

A disease of ponderosa pine, variously called X-disease, chlorotic decline, or ozone needle mottle, has been prevalent in pine stands of the San Bernardino Mountains since the early 1950's. Examination of weather records coupled with observations that affected trees occurred randomly on north or south slopes, valley bottoms or ridge tops, along lake shores or in well watered yards, indicated that drought was not a prominent factor (Parmeter, *et al.,* 1962). Subsequent studies showed that injury was associated with photochemical air pollutants (Miller, *et al.,* 1963; Richards, *et al.,* 1966). A chronic bark beetle problem has existed for several years in the same area. Preliminary observations suggested that beetle attacks might be associated with trees injured by air pollutants, but no investigations were made to determine whether the disease might be predisposing trees to beetle infestation.

This study was undertaken to determine whether those trees showing decline symptoms were attacked in greater numbers by bark beetles than were nonaffected trees. If trees were being predisposed, the second objective was to determine the stage of disease when most beetle attacks occurred.

METHODS

In July 1966, an intensive examination of forest stands in the San Bernardino Mountains was made by three crews, each consisting of an entomologist and a plant pathologist. Each crew searched for ponderosa pines under attack or infested by the previous (spring) generation of the western pine beetle (*Dendroctonus brevicomis* LeConte) or the mountain pine beetle (*D. ponderosae* (Hopkins)). Identity of beetles was determined by removing the bark of the lower boles of standing trees and examining them for brood or characteristic galleries. Each beetle-infested tree and nine uninfested, near-

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est-neighbor trees were carefully examined and the following data recorded:

1. Diameter breast height (dbh) ± 2.5 cm.
2. Crown Class: Suppressed (S), Intermediate (I), Codominant (CD), Dominant (D), and overmature, flat-top dominant (FTD).
3. Total tree height ± 1.5 m.
4. Length of live crown : the length of the living crown from the top of the crown to the lowest living limb ± 1.5 m (before beetles killed the tree).
5. Total crown length : length of the total crown including dead branches ± 1.5 m.

In addition, the following scoring system was applied to five tree characteristics which were considered the most sensitive indicators of damage caused by oxidants (particularly ozone) of photochemical air pollution. Binocular telescopes were used to evaluate needle condition throughout the crown. Many trees under attack at the time of examination had some living foliage, but the foliage of most trees infested by the previous generation of beetles had been killed.

Characteristic	Score Value*
1. Needle (foliage) retention	
Only current year needles	2
Current and preceding year's needles	1
Current and two or more year's needles	0
2. Needle color	
Chlorotic mottle—complete chlorosis	1
Green, no detectable mottle	0
All foliage killed	(dead)
3. Needle length	
Pronounced length reduction	1
Normal length	0
4. Branch mortality	
Pronounced mortality (from bottom up)	1
Normal mortality	0
5. Needle complement (based on entire crown)	
Less than 25 per cent of normal	4
25–50 per cent of normal	2
50–80 per cent of normal	1
80 per cent to normal	0

* The maximum possible score indicating a severely damaged tree was 9; the minimum score of 0 indicated a healthy tree.

Any other abnormality of the tree was recorded, such as dwarf mistletoe infections, root pathogens, or lightning scars. Wherever possible, the tree was carefully examined to determine all insect species present, regardless of whether or not they were instrumental in causing the death of the tree.

In addition to intensive examination of forest stands, a critical evaluation of insect activity in a permanent sample plot was conducted to determine whether insect activity was higher on living trees in various stages of disease. This plot consisted of 150 living trees carefully classified according to the degree of damage caused by air pollution. Fifty trees were considered to be healthy or unaffected, 50 were in an intermediate stage showing some degree of chlorotic decline symptoms, and 50 showed advanced symptoms. Each tree was carefully examined with binocular telescopes for evidence of attempted or successful attack by an identifiable insect. This portion of the study was repeated in February, 1967, on a similar sample of trees in a pine stand near the permanent plot.

TABLE 1
COMPARISON OF THE TOTAL SCORES INDICATING SEVERITY OF CHLOROTIC DECLINE SYMPTOMS OF INSECT-KILLED TREES AND THEIR NINE NEAREST NEIGHBORS

Chlorotic decline symptom score*	Insect-killed		Nearest noninfested neighbors	
	Number of trees	Percentage of total	Number of trees	Percentage of total
0	14	13.1	301	31.3
1	3	2.8	160	16.6
2	8	7.5	137	14.3
3	10	9.3	100	10.4
4	6	5.6	121	12.5
5	12	11 2	67	6.9
6	9	8.4	24	2.5
7 >	45	42.1	53	5 5
	107	100.0	963	100.0

* 0 — healthy tree; highest possible score: 9 — severely damaged tree.

RESULTS AND DISCUSSION

Examination of insect-infested and nearest-neighbor trees

A total of 1,070 trees, 107 infested and 963 noninfested nearest neighbors, were examined. The infested trees were scattered throughout the ponderosa pine type of the San Bernardino Mountains from Cedar Pines Park in the west to the vicinity of Arrowhead Village and Skiforest in the east.

A comparison of the scores of insect-killed trees versus nearest neighbors indicates clearly that trees exhibiting chlorotic decline symptoms are more frequently attacked by bark beetles than those exhibiting less severe or no decline symptoms (table 1). Almost 62 per cent of the insect-killed trees had disease ratings of 5 or greater but less than 15 per cent of the noninfested nearest neighbors were in this category.

Of the insects involved in killing ponderosa pine in westside Sierra Nevada stands, *D. brevicomis* is considered to be the more aggressive, capable of attacking and overcoming more vigorous trees than is *D. ponderosae*. This difference in attack vigor is reflected in the number of trees infested and killed by *D. brevicomis* in the healthy and intermediate classes (table 2). A total of 14 trees had combined attacks, with both *D. brevicomis* and *D. ponderosae* present in the same trees. Both insect species, however, appeared to prefer trees in advanced stages of chlorotic decline.

TABLE 2
PERCENTAGE OF HEALTHY, INTERMEDIATE, AND ADVANCED CHLOROTIC DECLINE TREES ATTACKED BY EACH BARK BEETLE SPECIES SINGLY OR IN COMBINATION

Chlorotic decline symptom score*	Insect species attacking tree		
	D. brevicomis	*D. ponderosae*	Combined attack
	Percentage of total		
Healthy (0-1)	22.2	0	13.5
Intermediate (2-4)	19 1	13.6	30.4
Advanced (5 +)	58.7	86.4	56.1

* 0 — healthy tree; highest possible score: 9 — severely damaged tree.

TABLE 3

PERCENTAGE OF INSECT-KILLED AND NEAREST-NEIGHBOR TREES IN EACH CROWN CLASS AND DECLINE SYMPTOM SCORE

Crown class	Total number of trees	Decline symptom score*			Percentage of total trees	Average decline symptom score*
		Healthy 0–1	Intermediate 2–4	Advanced 5–9		
		Percentage of trees				
Suppressed						
Insect-killed	11	18	27	54	10.3	4.2
Uninfested	97	46	32	21	10.1	2.4
Intermediate						
Insect-killed	23	26	13	62	21.5	4.5
Uninfested	208	42	38	20	21 5	2.4
Codominant						
Insect-killed	23	13	27	62	21.5	5.0
Uninfested	324	52	36	11	33.7	2.0
Dominant						
Insect-killed	50	12	24	64	46.7	4.3
Uninfested	334	50	38	14	34 7	2.3
Total						
Insect-killed	107	16	23	61	100.0	——
Uninfested	963	48	37	16	100.0	——

* 0 — healthy tree; highest possible score: 9 — severely damaged tree.

The proportionate number of trees in each of the four crown classes was approximately the same in the insect-killed and nearest-neighbor groups of trees. Thus, there was no indication that the insects preferred suppressed trees over dominant trees. However, the average disease rating of the insect-killed trees was higher in each crown class (table 3).

Excessive mortality of lower branches which develops acropetally is a symptom of oxidant injury. However, length of live crown did not appear to be correlated with incidence of bark beetle attack. On the other hand, live-crown ratio (length of living crown/total tree height) of dominant and codominant trees was markedly reduced (table 4) and should serve as an indicator of both oxidant injury and host susceptibility to bark beetles. The average live-crown ratio of dominant and codominant, noninfested nearest-neighbor trees was about 58 whereas that of beetle-infested trees in the same crown classes was 48. Through excessive branch mortality, the live-crown ratio of dominant and codominant beetle-infested trees had been reduced to that of suppressed trees.

Disease rating of the insect-killed trees was higher than that of the nearest neighbors regardless of diameter or height class (tables 5 and 6), except possibly for trees taller than 39 meters. No apparent relationship existed between photochemical air pollution injury and either tree diameter or height.

TABLE 4

RELATION OF LIVE-CROWN RATIOS WITHIN CROWN CLASSES TO BEETLE ATTACK

Crown class	Live crown ratio of	
	Beetle-killed trees	Nearest neighbors
	Per cent	
Dominant	47.8	60.1
Codominant	47.5	57.0
Intermediate	54.0	54.0
Suppressed	48.0	49.6

TABLE 5

FREQUENCY OF TREES BY DIAMETER CLASS AND AVERAGE CHLOROTIC DECLINE SYMPTOM SCORE OF INSECT-KILLED AND NEAREST-NEIGHBOR TREES

DBH	Number of trees	Percentage killed by beetles	Average symptom score*	
			Beetle killed trees	Nearest-neighbor trees
cm		*per cent*		
<25	297	6.4	4.6	1.9
25—37	299	11.4	3.8	2.3
38—50	214	13.1	4.5	2.2
51—63	123	5.7	3.8	1.7
64—76	67	9.0	5.2	1.8
77—89	35	6.0	6.0	2.5
>89	36	33.3	3.6	1.9

* 0—healthy tree; highest possible score: 9—severely damaged tree.

TABLE 6

FREQUENCY OF TREES BY HEIGHT CLASS AND AVERAGE CHLOROTIC DECLINE SYMPTOM SCORES OF INSECT-KILLED AND NEAREST-NEIGHBOR TREES

Height class	Number of trees	Percentage killed by beetles	Average symptom score*	
			Beetle killed trees	Nearest-neighbor trees
meters		*per cent*		
3—9	200	7.0	4.8	1.6
10—15	300	6.3	4.8	2.2
16—21	291	11.0	4.8	2.3
22—27	175	16.0	4.0	2.1
28—33	63	14.3	3.5	2.2
34—39	33	15.1	5.0	1.4
>39	9	33.3	4.7	4.3

* 0—healthy tree; highest possible score: 9—severely damaged tree.

Estimates of chlorosis were based on 713 nearest-neighbor trees which were affected to some extent by air pollution. The severity of needle mottle was inversely related to the degree of needle retention (table 7). In all cases, the oldest needles were most affected whether the tree retained two, three, or four years of needles. The reason for this is probably not a greater inherent susceptibility of older needle tissue but the longer period of exposure to photochemical air pollution (Miller and Parmeter, unpublished data).

TABLE 7

FREQUENCY OF CHLOROTIC MOTTLE CAUSED BY CHRONIC EXPOSURE TO PHOTOCHEMICAL AIR POLLUTION BY NEEDLE AGE IN RELATION TO DEGREE OF NEEDLE RETENTION

Length of needle retention	Number of trees*	Percentage of trees with chlorotic mottle of needles			
		Year in which needles were formed			
		1966	1965	1964	1963
Two years.....	500	24.2	100		
Three years...	173	1.7	58.4	100	
Four years....	40	0	10.0	57.5	100

* Based on 713 nearest-neighbor trees which exhibited injury caused by air pollution. Data recorded July 24-30, 1966.

Comparison of bark beetle activity on equal numbers of healthy, intermediate-diseased and advanced-diseased trees

Examination of the 150 trees in the permanent sample plot strongly indicated that trees in an advanced state of chlorotic decline were more frequently selected by bark beetles than either intermediate or healthy trees. A total of 27 trees showed evidence of abortive or current attack by bark beetles. Eighteen were in an advanced state of chlorotic decline, eight were in an intermediate state, and only one was healthy. Of the 18 trees exhibiting advanced chlorotic decline, ten had many pitch tubes while eight had only a few. In the intermediate category, only one of the trees had many attempts, seven had a few. The healthy tree had only a few old, scattered pitch tubes.

An examination of 150 trees in a nearby comparable stand in February, 1967, yielded similar results. Thirty-three trees showed evidence of attempted bark beetle attack. Of these, 18 were in the advanced, 11 in the intermediate, and four in the healthy category.

Only three trees were attacked by *Dendroctonus valens* LeConte, and there was no correlation with chlorotic decline symptoms.

SUMMARY

A total of 107 beetle-killed and 963 nearest-neighbor ponderosa pines were examined to determine the association between severity of atmospheric pollution injury and infestation by bark beetles. Trees exhibiting advanced symptoms of pollution injury were most frequently infested by the western pine beetle, *Dendroctonus brevicomis,* and the mountain pine beetle, *D. ponderosae.* The degree of injury and incidence of bark beetle infestation were not related to total height, diameter, length of live and dead crown or crown class. As severity of oxidant injury increased, live crown ratio decreased and incidence of bark beetle infestation increased.

One hundred noninfested trees in each of three disease categories, advanced, intermediate, and healthy, were examined for evidence of prior beetle attacks. Thirty-six per cent of the advanced-diseased trees versus only five per cent of the healthy trees were attacked. Thus, the beetles may discriminate between healthy and diseased trees at a distance, upon contact with the host, or both.

These studies indicate strongly that atmospheric pollution injury predisposes ponderosa pine to bark beetle infestations.

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