Spore Deposition by *Heterobasidion annosum* in Forests of California

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ABSTRACT

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Spore deposition of *Heterobasidion annosum* on fresh pine disks was studied in Jackson State Forest (JSF) in coastal northern California, Stanislaus National Forest (SNF) in the central Sierra Nevada, and San Bernardino National Forest (SBNF) in southern California. Highest spore deposition rates (to 796/m^2/hr) occurred on the SNF; the SBNF had the lowest rates. Spores were deposited throughout the year on the SNF and SBNF. Lowest deposition rates occurred in the summer on the SBNF and in winter on the SNF. Greatest deposition occurred during winter on the SBNF and in autumn on the SNF. Diurnal patterns of spore deposition were studied on the SBNF, where most deposition occurred at night. Spore deposition was not correlated with air-pollution dosage gradients on the SBNF.

Heterobasidion annosum (Fr.) Bref. is a root pathogen that causes extensive losses in mixed-conifer forests throughout California (1). The fungus colonizes freshly wounded xylem, especially stump surfaces, by means of basidiospores (5,11,15,18). Production and deposition of basidiospores vary diurnally (4,10,18), seasonally (2,3,19), and geographically (2,10,13,14,16,18) under the influence of temperature and relative humidity (15,16).

Damage caused by *H. annosum* is of concern, especially within the valuable forests of southern California, where photochemical air pollution stresses conifer ecosystems (12). Previous studies established that photochemical air-pollution damage renders trees more susceptible to stump (8) and subsequent root (6) infection by the pathogen. Ozone, a major component of photochemical air pollution, also restricts growth and conidial production by the fungus (7). Thus, polluted air might influence production, dispersal, and deposition of viable spores of *H. annosum* and might thereby influence disease impact in heavily polluted forest ecosystems. We therefore studied the deposition of germinable spores as one indicator of the infection hazard in three California forests, including one exposed to high levels of photochemical air pollution.

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MATERIALS AND METHODS

Deposition of spores of *H. annosum* was sampled in the Jackson State Forest (JSF) in coastal northern California, the Stanislaus National Forest (SNF) in the central Sierra Nevada, and the San Bernardino Forest (SBNF) in southern California. In the JSF, maritime weather prevails and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and redwood (*Sequoia sempervirens* (D. Don) Endl.) are the predominant conifer species. The SNF is typical of the central Sierra Nevada; the major conifer species at the sample sites were red and white fir (*Abies magnifica* A. Murr., and *A. concolor* (Gord.) Lindl. ex Hildebr.); sugar, ponderosa, and Jeffrey pine (*Pinus lambertiana* Dougl., *P. ponderosa* Dougl. ex P. Laws & C. Laws, and *P. jeffreyi* Grev. & Balf.), and incense cedar (*Calocedrus decurrens* (Torr.) Florin). The SBNF represents the southern Sierra Nevada, where chronic exposures to high levels of photochemical air pollution occur. Except for the absence of red fir, the conifers were the same as on the SNF.

Four sites on the SNF and three on the JSF (Table 1) were sampled at irregular intervals from October 1963 through January 1966 on the SNF and from June 1964 through April 1965 on the JSF. Six sites along two air-pollution dosage gradients on the SBNF (Table 2) were also sampled at approximately monthly intervals for 14 mo beginning in April 1976. Elevations at the sample sites were 100–300 m for the JSF and 1,500–2,250 m for the SNF and SBNF. Root disease caused by *H. annosum* occurred near all sample sites.

Spore deposition was assessed by the wood-disk exposure method (13,14,16, 18,19). Disks of ponderosa pine, about 1 cm thick and 6–8.5 cm in diameter, were cut with a table saw from stem sections that had been swabbed with 95% ethanol after removal of loose bark scales. Disks were placed singly in plastic petri dishes that also contained filter paper and a small piece of absorbent cotton. About 25 ml of sterile distilled water was sprayed on the filter paper and cotton in each dish to prevent drying during exposure. Dishes with wood disks were placed open on the ground or on snow for at least 1 hr. Spore deposition was assessed during the day and early evening on the SNF and JSF. Deposition on the SBNF was sampled sequentially during the day and night of each sample period.

After exposure, petri dish lids were replaced and disks were incubated at about 24 C for 7 days and examined under the dissecting microscope (×20–80) for conidial colonies (*Oedocephalum*) of

Table 1. Deposition of basidiospores of *Heterobasidion annosum* in Stanislaus National Forest and Jackson State Forest in California

Site	No. samples[a]	Average deposition rates (viable spores/m^2/hr)
Stanislaus National Forest		
Gooseberry	17	598
Herring Creek	13	136
Dodge Ridge	16	140
Clarks Fork	2	63
Average	...	298
Jackson State Forest		
Mendocino Road	4	91
Casper Logging	2	20
Willits Road	2	41
Average	...	61

[a] Each sample consisted of 10 or more pine wood disks exposed at a particular site at one time. Deposition rates on disks were averaged.

the fungus. Deposition rates (number of viable spores per square meter per hour) were calculated on the assumption that each colony resulted from deposition of one viable spore (13,14,16,18).

Data for day versus night and for the various locations in the SBNF were subjected to analysis of variance and Tukey's test for block comparisons.

RESULTS AND DISCUSSION

Average spore deposition was greatest in the SNF (mean = 298 spores per square meter per hour), intermediate in the JSF (mean = 61), and least in the SBNF (mean = 37) (Tables 1 and 2). Deposition rates also varied among sites sampled within each forest (Tables 1 and 2). Variation in spore deposition among sample sites within the same geographic area is common in forests because of microclimatic variations, nonuniform basidiocarp distribution, and forest canopy effects on local wind turbulence (4,13).

Relatively few reports have been made of spore deposition of *H. annosum* in western North America. Values in Washington ranged from three to 70 spores per square meter per hour (4). In nearby coastal British Columbia, however, average deposition rates in three mixed conifer stands in one area ranged from 430 to 795 (13). In another area, deposition rates in a stand with basidiocarps of *H. annosum* nearby averaged 1,020, and rates in a stand where basidiocarps were unknown averaged 197 (14). Other average rates reported in North America include 59 in Pennsylvania (19), 218 in Georgia (2), 203–385 in New York (18), and 2 in Ontario (9). Very high values (mean = 16,382) were reported from England (16), and values in Finland ranged from 23 to 88 (10). Thus, spore deposition rates in California varied within the range of those reported in other North Temperate forest ecosystems.

Seasonal trends in spore deposition were apparent (Table 3). In the SBNF, least deposition occurred during late spring and summer, except for one sample taken soon after a light rain shower in July. Highest rates occurred from November through January and apparently were not substantially reduced by snow cover; similar observations have been reported elsewhere (14,19). Deposition rates on the SNF peaked during autumn and lowest colony counts occurred during early spring, when snow depth generally exceeded 1.5 m. Thus, our results generally support those of others, ie, greatest spore deposition usually occurs during the winter in forests of the southern United States (2,3,17), whereas in northern forests, highest rates occur in the spring and autumn (18). Diurnal patterns of spore deposition were evident on the SBNF (Table 2). About five times more spores were deposited during the night than during the day. Previous reports generally affirm greater spore liberation (20) and deposition (4,9,20) at night, but exceptions occur (18).

No relationships between air pollution gradients and spore deposition rates were evident on the SBNF (Table 2), although differences among sample sites were found. Spore deposition by *H. annosum* is apparently not influenced by photochemical air pollution.

Table 2. Deposition of basidiospores of *Heterobasidion annosum* along two gradients of photochemical air pollution in the San Bernardino National Forest in California

	Deposition rates (viable spores/m^2/hr)			
Site	Day	Night	Average deposition[a]	Ozone dose ratio[b]
Gradient I				
Camp Angelus	21	54	38 a	1.20
Barton Flats	3	17	10 b	0.78
Hearts Bar	6	38	22 ab	0.41
Gradient II				
Sky Forest	1	7	4 b	1.00
Camp O-Ongo	1	2	2 b	0.92
Snow Valley	5	41	23 ab	0.66
Averages	7[c]	31[c]	18	...

[a] Means followed by the same letter are not significantly different ($P = 0.05$) using Tukey's test for block comparisons.

[b] Ozone dose ratios are related to a base of 1.00 at Sky Forest. This base indicates an average hourly ozone concentration of 1,650 $\mu g/m^3$. Dosages were computed for May–October 1976–1977 by Miller et al (12).

[c] Day and night average deposition rates are significantly different ($P = 0.05$).

Table 3. Monthly patterns of deposition of basidiospores of *Heterobasidion annosum* in the San Bernardino and Stanislaus national forests and the Jackson State Forest in California[a]

	SBNF		SNF		JSF	
Month	No. samples[b]	Average deposition rate[c]	No. samples[b]	Average deposition rate[c]	No. samples[b]	Average deposition rate[c]
January	12	88	6	47	0	...
February	12	10	0	...	0	...
March	12	10	5	95	0	...
April	24	7	4	90	1	114
May	0	...	6	224	0	...
June	24	8	3	28	3	53
July	12	134	4	405	0	...
August	24	3	3	200	3	5
September	0	...	6	423	0	...
October	24	16	5	662	1	203
November	12	37	3	399	0	...
December	12	40	3	796	0	...

[a] Samples for the San Bernardino National Forest (SBNF) were taken during 1976–1977; those for the Stanislaus National Forest (SNF) and Jackson State Forest (JSF) were taken during 1963–1966 and 1964–1965, respectively.

[b] Each sample consisted of 10 or more pine wood disks exposed at a particular site at one time.

[c] Rate is germinable spores deposited per square meter per hour, assuming one spore per subsequent *Oedocephalum* colony.

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