Sphaeropsis sapinea and Water Stress in a Red Pine Plantation in Central Wisconsin

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ABSTRACT

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A study was conducted to determine the effects of water stress resulting from competing vegetation on disease development of *Sphaeropsis sapinea* in red pine plantations. A 9-year-old plantation was selected in 1992 and experiments were conducted for three consecutive years. Four treatments were assigned at random to individual trees: no treatment, herbicide to kill surrounding weeds, supplemental water, and both herbicide and supplemental water. Two isolates of each *S. sapinea* morphotype (A and B) were used to inoculate wounded lateral shoots. Disease development was measured as the maximum distance below the inoculation site at which necrotic needles were observed. Nonwatered trees with competing vegetation (nontreated condition) had significantly lower predawn needle water potentials (more water stress) and more severe disease development than trees that received the herbicide, water, or combined herbicide and water treatments. The most severe disease occurred in the driest year and the least in the wettest year. Competing vegetation indirectly affected disease development by inducing water stress, even in relatively moist years, on trees previously considered well established. Isolates of morphotype A were more aggressive than isolates of morphotype B. Conclusions from this research have implications for sustainable management of the region's conifer forests.

Additional keywords: *Diplodia pinea*, drought, predisposition.

Sphaeropsis shoot blight and canker, caused by *Sphaeropsis sapinea* (Fr.:Fr.) Dyko & Sutton in Sutton (syn. *Diplodia pinea* (Desmaz.) J. Kickx fil.), has caused extensive damage to conifers throughout the world. Pines are affected from the seedling stage to mature size and damage occurs in nurseries, plantations, Christmas tree and ornamental plantings, and natural stands (7,14,22). In the United States, some of the greatest damage caused by *S. sapinea* has occurred on red pine in the Great Lakes region (21,22,24).

Field studies have associated losses caused by *S. sapinea* with predisposing stresses, including drought (21,23,30). In a survey by Nicholls and Ostry (21) of stressed red and jack pine trees in Minnesota and Wisconsin, tree mortality within plots was as high as 30% for red pine and 51% for jack pine. In a survey of red pine seedling and sapling plantations in Wisconsin, mortality was as high as 95% for seedlings and 30% for saplings (30). In these surveys, reported reasons for the stresses included drought, poor site, hail, snow, and insects. Such field surveys, however, do not provide information on the quantitative effects of water stress in disease development.

Some controlled studies examining the effects of host water stress on disease development have been conducted in greenhouse and growth chambers using hosts other than red pine (1,9,18,35). In these studies, either extremely low host water potentials (–3.0 MPa or lower) were used, or results were not analyzed statistically. Shoot colonization was greater on red pine seedlings that experienced only moderate water stress (above –1.9 MPa) in a greenhouse and growth chamber study that examined the aggressiveness of *S. sapinea* isolates (4). Colhoun (10), however, has suggested that studies of environmental stress under controlled conditions may not reflect trends that occur in the field.

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Two *S. sapinea* morphotypes (A and B) are recognized in the north central United States (25). Morphotype is defined as "a group of morphologically differentiated individuals of a species of unknown or of no taxonomic significance" (15). The two *S. sapinea* morphotypes differ in colony morphology and growth rates on potato dextrose agar (25), and aggressiveness on red pine in a greenhouse study (3).

The objectives of this study were to determine whether competing vegetation affects disease development by *S. sapinea*, and if the morphotypes differ in aggressiveness on red pine under field conditions. Host water potential was manipulated by herbicide applications to control competing vegetation and by supplemental water. The null hypotheses were (i) competing vegetation does not affect red pine growth or colonization by *S. sapinea*, (ii) the effect of competing vegetation on disease development is not associated with water stress, and (iii) the two morphotypes of *S. sapinea* produce similar disease severity on red pine under field conditions.

MATERIALS AND METHODS

Plots were established in a 9-year-old red pine plantation in northern Adams County, central Wisconsin, in early July and maintained for three consecutive years (1992 to 1994) in the same stand. A total of 40 trees were selected in 1992 and the same trees were used in 1993. To avoid any effect of repeated branch removal, a new set of 40 trees was selected in 1994. Trees were selected for uniform height (1.93 m ± 0.03 [standard error] in 1992; 2.43 m ± 0.03 in 1994), competing vegetation (ground cover of 88% ± 2 in 1992; 96% ± 1 in 1994), and tree health. A minimal spacing of 4.9 m occurred between selected trees and trees were located at least 12.2 m from the plantation edge. The soil type in the area is Plainfield sand (well-drained to excessively well-drained; containing 89% ± 0.4 sand and 7% ± 0.4 silt).

Four treatments were assigned at random to individual trees: no treatment, herbicide only, water only, and herbicide and water. In early July of each year, the herbicide glyphosate (Monsanto Enviro-Chem Systems, Inc., St. Louis) was applied in accordance with label directions within a 1.8 m radius around the experimental trees 3.5 weeks before branches were inoculated. Water (67 liters per tree) was applied within a 0.9 m radius around sample trees, twice per week. Watering started in mid July, 2 weeks before branches were inoculated.

Total ground cover (percentage of ground area covered by living vegetation) was visually estimated within a 1.8 m radius around sample trees before and 2 weeks after the herbicide treatment in all 3 years. Species composition (ground cover of each species as a percentage of total ground cover) was visually estimated within a 1.8 m radius around sample trees. Species composition was recorded in late August of 1993 only.

Predawn needle water potentials (ψ_{PD}) were measured two to four times per week with a pressure bomb (29). On each day of measurement, one needle fascicle from a noninoculated lower branch on each of several randomly selected trees was used for determination of ψ_{PD}. Four trees per treatment were used in 1992, six in 1993, and seven in 1994.

Two A and two B morphotype isolates of *S. sapinea* (Table 1), as well as a wounded and a nonwounded control, were evaluated in this study. Each of the six treatments were assigned randomly to a branch on each tree in late July of each year. Monoconidial isolates of *S. sapinea* used in this study were the same as used in a previous study (3). A wound, 3 × 1.5 mm, was made by removal of a needle fascicle with a scalpel cut flush to the stem base, approximately 3 cm below the shoot apex. A plug of colonized 1.5% water agar (WA) (Difco Laboratories, Detroit) 4 mm in diameter was placed fungus-side-down on wounds. A noncolonized WA plug was applied to wounded controls. Parafilm (American National Can Co., Chicago) was wrapped around shoots for 7 days.

Symptom severity was measured in late August and was evaluated as the maximum distance below the inoculation site at which necrotic needles were observed 4 weeks after inoculation. After needles were removed, 25-cm-long shoots were surface disinfected for 10 s in 95% ethanol followed by 4 min in 1.05% NaOCl solution with two drops of Tween 80 (Fisher Scientific Co., Toronto, Ontario, Canada) per liter. A small piece of each shoot segment, centered at the site of inoculation, was cut aseptically to determine recovery success of *S. sapinea*. These pieces were placed in individual slants containing 2% WA and incubated for 3 months at ambient laboratory temperature (approximately 23°C) and light. The presence of *S. sapinea* in incubated pieces was determined by examining the resulting mycelia, pycnidia, and conidia.

Stem diameters at 0.3 m and tree heights were measured in mid-July of 1992 to 1995. Percentage growth was calculated as follows: percentage of growth = [(final size – initial size) / initial size] × 100. Final stem diameters and tree heights were determined after 1 year. Percentage of growth was used to standardize growth among trees that had different initial sizes. Precipitation was not recorded at the study site in 1992, but was recorded at the study site for July and August in 1993 and 1994. Soil temperatures of the top 20 cm were recorded from the south side of trees used for ψ_{PD}. Temperatures were recorded from 11:30 a.m. to 12:00 p.m. for 3 days in 1992 and 1994, and 5 days in 1993. Climate data were obtained for Hancock, 23 km east of the study site, from the National Weather Service and the University of Wisconsin Agricultural Weather Station.

Statistical analyses. Symptom severity was analyzed by two-factor analysis of variance with interactions. Factors used as main effects were tree treatment and branch treatment. A split plot model was used with the tree as the whole plot and branches as subplots. The symptom severity data were analyzed both untransformed and after $\ln(x+1)$ transformation was applied. The *P* values and resulting conclusions were similar for both forms of analysis, therefore, results are reported here only for the untransformed data. Quantitative data for trees (daily ψ_{PD} and height and diameter growth) were analyzed by one-way analyses of variance with tree treatment as the factor. If significant differences were found ($P \leq 0.05$), means were separated using Fisher's least significant differences (LSD) at $P = 0.05$. Two different LSD values were determined for symptom severity because of the split plot nature of the experimental design (20). Simple linear regression analyses were used to examine relationships between symptom severity and mean ψPD and between precipitation recorded at the study site in 1993 and 1994 and precipitation at Hancock. Analyses of variance (using general linear model procedure) and linear regression analyses were performed with the Minitab for Windows program (release 10.2; Minitab Inc., State College, PA).

RESULTS

Competing vegetation at the study site consisted mainly of grasses or grass-like species. The vegetation was dominated by Pennsylvania sedge (*Carex pensylvanica* Lam.), which made up 83% ± 3 (standard error) of the ground cover. Horseweed (*Conyza canadensis* (L.) Cronq.) was the next most common single species making up 4% ± 1 of the ground cover. A combination of grass species and other sedges made up 6% ± 3 of the ground cover. The most common grasses were little bluestem (*Andropogon scoparius* Michx.), big bluestem (*A. gerardii* Vitman.), and other prairie grass species typically found in pine barrens and early successional northern dry forests. The remaining 7% consisted of various woody species and forbs consisting primarily of composites. Indicator species typically found in pine barrens such as American hazelnut (*Corylus americana* Marsh.), flowering spurge (*Euphorbia corollata* L.), and wild rose (*Rosa* sp.) also were present. Unplanted areas surrounding the study site were dominated by jack pine and include other tree and ground cover species (2) typical of northern dry forests (such as *Quercus* sp., *C. americana*,

TABLE 1. Origin of *Sphaeropsis sapinea* isolates used in a field study in central Wisconsin during 1992 to 1994

Isolate[a]	Isolate no.[b]	Host	Geographic origin
A1	411	*Pinus resinosa*	Clearwater Co., MN
A2	128	*P. resinosa*	Grant Co., WI
B1	124	*P. banksiana*	Jackson Co., WI
B2	215	*P. resinosa*	Douglas Co., WI

[a] Morphotype and isolate number.
[b] Culture collection numbers of M. A. Palmer.

TABLE 2. Total monthly precipitation at Hancock, WI

Year/month	Precipitation (cm)[a]	Surplus or deficiency (cm)[b]
1992		
June	4.40	–4.85
July	10.57	+1.43
August	8.23	–1.73
1993		
June	17.42	+8.17
July	21.59	+12.45
August	13.54	+3.58
1994		
June	9.42	+0.17
July	17.37	+8.23
August	9.58	–0.38

[a] Precipitation as reported by the National Weather Service.
[b] The difference between total monthly precipitation and 30-year monthly average (1961 to 1990) at Hancock.

Prunus sp., *Rubus* sp., *Rosa* sp., and *C. pensylvanica*) that often replace pine barrens.

The herbicide treatment was effective at reducing overall ground vegetation. Initial percentage of cover was 88% ± 2 in 1992 and 96% ± 1 in 1994. Since the same trees were used in 1992 and 1993, initial ground covers were 87% ± 4 for nonherbicide and 7% ± 1 for the herbicide treatment in 1993. The herbicide treatment reduced ground cover to 3% ± 0.4 in 1992; 1% ± 0.4 in 1993; and 0.2% ± 0.2 in 1994.

Precipitation recorded at the study site in 1993 and 1994 was highly correlated with the precipitation data obtained from the National Weather Service for Hancock (r = 0.87 in 1993 and 0.91 in 1994; $P \leq 0.001$ for both years). Precipitation at Hancock was lowest in 1992 and highest in 1993 (Table 2). Among the 3 years,

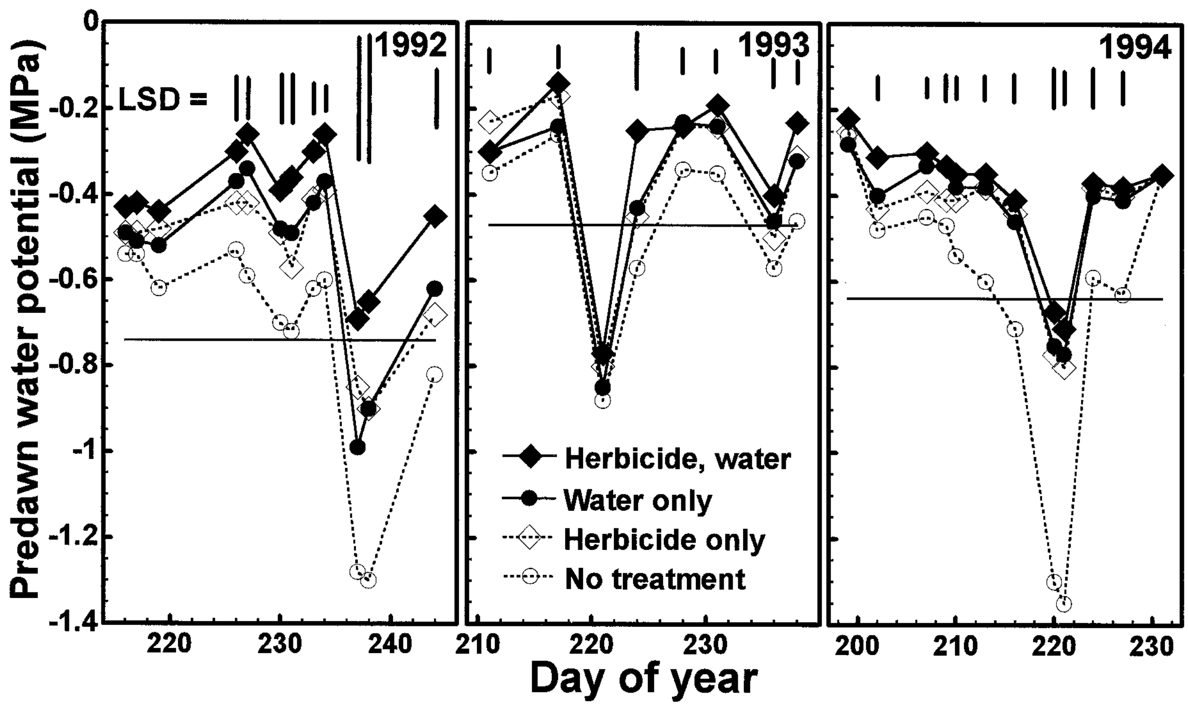

Fig. 1. Mean predawn needle water potentials for red pine (*Pinus resinosa*) trees by tree treatment. Four trees per treatment were used in 1992, six in 1993, and seven in 1994. Vertical lines show Fisher's least significant differences for separating the means for a given day at P = 0.05. The horizontal line in each panel is the average predawn needle water potential of all nontreated trees (no treatment) in a given year.

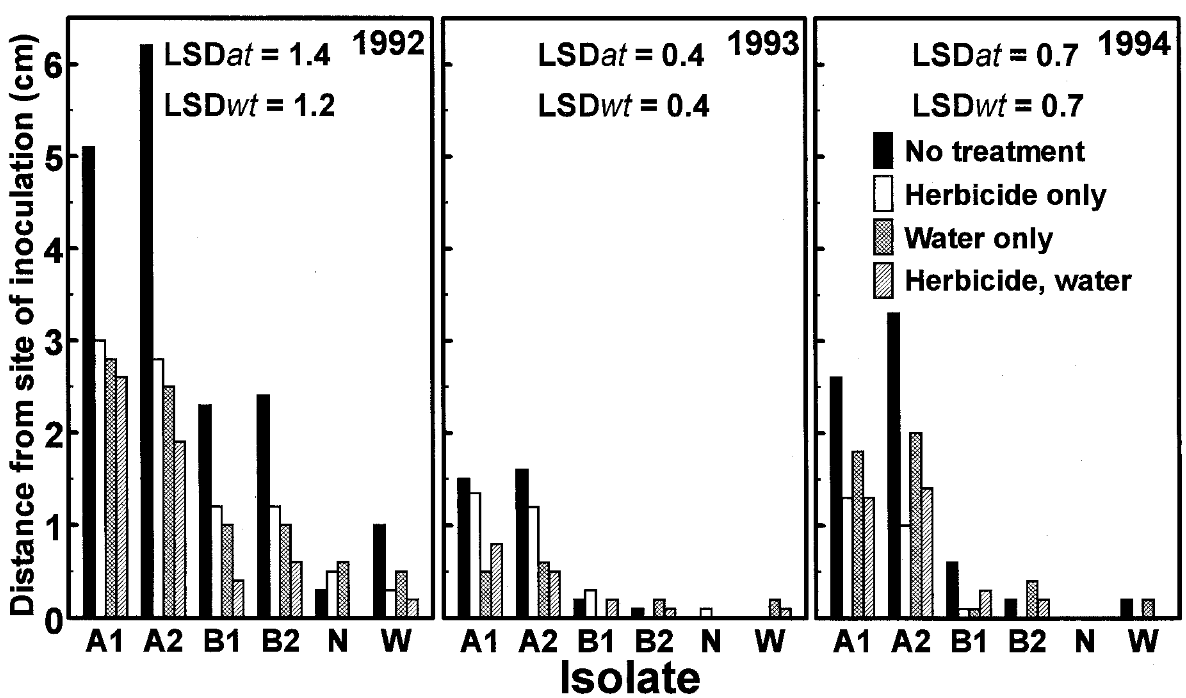

Fig. 2. The average maximum distance below the inoculation site at which necrotic needles were observed on wounded red pine (*Pinus resinosa*) trees inoculated with agar plugs colonized by *Sphaeropsis sapinea* isolates of morphotype A and B. Forty trees were used each year, 10 per treatment. Branch treatments include two A (A1 and A2) and two B (B1 and B2) isolates and both nonwounded (N) and wounded (W) controls for each tree. The LSD values are Fisher's least significant differences for separating the means at P = 0.05. The LSD*at* is for separating the means of branch treatments across (for different) tree treatments. The LSD*wt* is for separating the means for branch treatments within the same tree treatment.

relationships were not apparent between symptom severity and climatic variables measured at Hancock (air temperatures, relative humidity, vapor pressure deficit, wind speed, and total solar radiation) other than precipitation (2).

The mean soil temperature of the top 20 cm differed among tree treatments ($P < 0.001$ in 1993 and 1994; $P = 0.050$ in 1992). Higher soil temperatures were measured in herbicide treated plots compared with those not treated with herbicide. However, in none of the 3 years was symptom severity related to soil temperature measured under experimental trees.

There were distinct differences in ψ_{PD} among years (Fig. 1). Mean ψ_{PD} of nontreated trees, for all days, were lowest in 1992 (–0.74 MPa ± 0.04), followed by 1994 (–0.64 MPa ± 0.01), and highest in 1993 (–0.46 MPa ± 0.01). There also were significant differences in the mean ψ_{PD} among tree treatments during all 3 years (Fig. 1; $P < 0.001$ for all 3 years). Nontreated trees had consistently lower mean ψ_{PD} compared with all other tree treatments. The lowest mean ψ_{PD} of nontreated trees, for a single day, was –1.30 MPa ± 0.10 in 1992, –0.88 MPa ± 0.02 in 1993, and –1.35 MPa ± 0.02 in 1994.

Distinct differences in symptom severity occurred among years (Fig. 2). The average maximum distance below the inoculation site at which necrotic needles were observed on nontreated trees inoculated with isolates of morphotype A was greatest in 1992 (5.7 cm ± 0.5), followed by 1994 (3.0 cm ± 0.4), and lowest in 1993 (1.6 cm ± 0.2). Symptom severity among years was consistent with ψ_{PD} among years (Figs. 1 and 2).

Distinct differences in symptom severity also occurred among tree treatments and branch treatments (Fig. 2). Trees that received herbicide and water treatments had less severe symptoms than nontreated trees in all 3 years ($P < 0.001$ for tree treatments in 1992 and 1994 and $P = 0.004$ in 1993). Branches inoculated with isolates of morphotype A had more severe symptoms than branches inoculated with isolates of morphotype B of the same tree treatments ($P < 0.001$ for isolates in all 3 years). The interaction between tree treatment and branch treatment was significant ($P = 0.012$ in 1992, $P < 0.001$ in 1993 and 1994), indicating that different isolates responded differently depending on the tree treatment. Differences in symptom severity among tree treatments were only significant for isolates of morphotype A, based on LSD.

Symptom severity and mean ψ_{PD} (averaged over all days) were negatively correlated for branches inoculated with isolates of morphotype A. For A1: $r = –0.58$, $P = 0.019$ in 1992; $r = –0.23$, $P = 0.289$ in 1993; and $r = –0.62$, $P < 0.001$ in 1994. For A2: $r = –0.77$, $P < 0.001$ in 1992; $r = –0.47$, $P = 0.022$ in 1993; and $r = –0.59$, $P = 0.002$ in 1994. Correlations were not significant for branches inoculated with isolates of morphotype B.

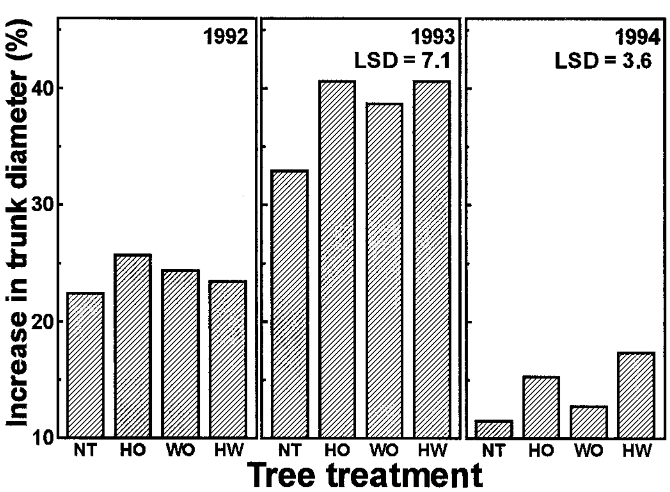

Fig. 3. Percentage of increase in trunk diameter of red pine (*Pinus resinosa*) trees by tree treatment for the period from 1992 to 1995. Four treatments were assigned at random to individual trees: no treatment (NT), herbicide only (HO), water only (WO), and herbicide and water (HW). Values are means of 10 trees per treatment. The LSD values are Fisher's least significant differences for separating the means at $P = 0.05$.

S. sapinea was recovered from branches inoculated with either morphotype. For all tree treatments, isolates of morphotype A were successfully recovered at the inoculation point 68% ± 7 of the time in 1992, 89% ± 5 in 1993, and 90% ± 2 in 1994. For isolates of morphotype B, *S. sapinea* was successfully recovered at the inoculation point 48% ± 8 of the time in 1992, 69% ± 7 in 1993, and 71% ± 7 in 1994. For all controls it was recovered 7% ± 4 of the time in 1992, 4% ± 2 in 1993, and 1% ± 1 in 1994.

Differences in trunk diameters among treatments were not significant when trees were selected ($P = 0.911$ in 1992; $P = 0.977$ in 1994). Differences in percentage of growth of trunk diameters among tree treatments were measured for 2 of the 3 years ($P = 0.102$ in 1993; $P = 0.011$ in 1994) (Fig. 3). The diameter growth was consistently less for nontreated trees compared with trees that received the herbicide or water treatments. When the same trees were compared, greater diameter growth occurred in the wettest year (1993) than in the driest year (1992). Differences in height growth among tree treatments were not significant in any year.

DISCUSSION

This study demonstrates the importance of considering both environmental factors and variation within the pathogen population when examining host susceptibility to *S. sapinea*. Environmental predispositions from a variety of sources have been shown to affect woody plant disease severity. These include water and temperature extremes, and defoliation, transplant, soil nutrient, and light stresses (26,28). Increased disease development by *S. sapinea* has been associated with water stress (1,4,9,18,35), high soil nutrition (34), and hail damage (33,37). Temperature and humidity are important factors in infection (5,8). Seasonal variations (32) and climate differences (17) also have been related to differences in the amount of disease caused by *S. sapinea*. The current study shows that competing vegetation and *S. sapinea* morphotype also are important factors to consider when managing pine plantations.

Water stress caused by the competing vegetation appeared to be the dominant factor involved in the increased disease severity observed. Previous field studies that associate losses caused by *S. sapinea* to drought did not demonstrate a clear, quantitative relationship between host water stress and colonization by the pathogen (21,23,30). In the current study, the yearly differences in symptom severity were consistent with differences in precipitation, ψ_{PD} data, and reductions in symptom severity due to watering. However, severity of water stress due to competition is also an important factor as indicated by reduction in symptom severity on trees treated with herbicide in the two driest years. Although higher soil temperatures were measured under the herbicide trees compared with nonherbicide trees, soil temperatures did not explain differences in symptom severity on trees that received water only and not the herbicide treatment. Therefore, water availability is likely involved in the differences in aggressiveness of *S. sapinea* both among years and among treatments.

The observed effects of competition on tree water relations and growth are consistent with previous reports. Thinned red pine stands have more water in the upper soil during the growing season than do unthinned stands (12,31). Sucoff and Hong (31) also found ψ_{PD} to be higher in thinned stands. In the southern United States, competing vegetation can affect the water status of southern pines in plantations (13,19). Miller et al. (19) found that competition of both herbaceous and woody vegetation resulted in a significant reduction in height and diameter growth, with herbaceous competition having the greatest effect. Caldwell et al. (6)

found that grass competition limited resource availability (water, soil nutrients, and light) and resulted in reduced growth of red pine seedlings in Minnesota. In the current study, competing vegetation significantly lowered ψ_{PD} and resulted in reduced diameter growth and increased disease severity by *S. sapinea*. The observed effect on tree growth is evidence of the reduction of many physiological processes in trees (16,27) that may affect the ability of a host to defend itself (27).

Previous results from greenhouse and growth chamber experiments demonstrating differences in aggressiveness between isolates of morphotype A and B (3,4) and in their response to host stress (4) were confirmed in this field study. Using potted seedlings, Blodgett et al. (4) found significant increases in aggressiveness for morphotype A isolates, but not for isolates of morphotype B when hosts were moderately water stressed (ψ_{PD} at or above –1.9 MPa) in a greenhouse and growth chamber study. In that study, neither a discrete threshold level of water potential nor a prolonged water stress were necessary to enhance colonization by *S. sapinea*. The similarity of results from our greenhouse studies adds additional support to our conclusions on the relative aggressiveness of *S. sapinea* morphotypes on red pine and their responses to host water stress.

The red pine plantation used in this study, although representative of many in the region, may not be within an ideal area for sustainable production of red pine. Fire-suppression practices, fragmentation of land by constructing roads and farming, and the sandy-dry-infertile soil at this site tends to favor jack pine over red pine (11). Studies of the early vegetation of Wisconsin classified this area as a pine barren composed of jack pine and prairie grasses (11). Vegetation in the plantation and surrounding vegetation would categorize the study site as a jack pine forest or jack pine barren (11,36). Establishment of red pine on a site for which it was not well adapted may have contributed to the water stress observed in this study.

Because isolates of morphotype A are more aggressive than isolates of morphotype B, identification of the morphotype(s) in a plantation may provide some indication of risk of damage from this disease and may help to determine if management is required to control the disease in an area. Water stress at levels observed for short periods in wet years and at levels typically observed during any year (above –1.7 MPa), can result in greater disease development by *S. sapinea* morphotype A on red pine. Competing vegetation has substantial effects on water status, even in relatively wet years, on trees previously considered well established. Therefore, planting on drought-prone sites should be avoided. If planting on drought-prone sites, reducing water stress is an important factor in controlling Sphaeropsis shoot blight. Management of competing vegetation, stand thinning, planting techniques that reduce drought, and selection of a tree species compatible with a site should reduce losses due to Sphaeropsis shoot blight and foster sustainable use of forest resources.

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