Oak (Quercus spp.) are highly susceptible to the foliar disease powdery mildew (Microsphaera alphitoides Griffon and Maubl.). Conventional control of powdery mildew requires the application of 10 to 22 fungicide applications per season depending on weather conditions (Hibbard et al. 1996; Sabri et al. 1997). The potential for plant pathogens to overcome or to develop insensitivity to conventional fungicides and increased legislative restrictions regarding the use and application of pesticides means new techniques of tree pathogen control are of environmental and economic importance (Agostini et al. 2003).

Plants can defend themselves against pathogen infection through a wide variety of mechanisms that can be local, constitutive, or inducible (Franceschi et al. 2000). Inducible resistance mechanisms such as systemic-induced resistance (SIR) can be acquired by challenging a plant with a weaker strain of a specific pathogen or exposing a plant to natural and/or synthetic compounds (Percival 2001). Formulations of commercial SIR-inducing chemicals such as Messenger (Eden Bioscience Corp., N. Bothell, WA) in the United States, Bion (Syngenta Crop Protection UK Ltd., Whittlesford, Cambridge, U.K.) in Europe, Agri-Fos (Agrichem Ltd., Queensland, Australia) in Australia and the United States, and Oryzemate® (Meiji Seika Kaisha, Ltd., Yokohama, Japan) in Japan now exist. Several studies have found these SIR-inducing compounds to be effective in reducing severity of key tree pathogens such as fireblight (Erwinia carotovora), Phytophthora root rot (P. palmtivora), powdery mildew (Sphaerotheca pannosa var. rosa, Phyllactinia spp. and Uncinula necator), and wilt disease of spruce (Ceratocystis polonica) (Christiansen et al. 1999; Percival 2001). Importantly, the level of disease control achieved was comparable with currently used agrochemicals. Unlike conventional fungicides, a “one-off” SIR application has been shown to provide growing season protection (Kessmann et al. 1994).

RESISTIM is a plant stimulant and fertilizer combined with natural plant betaines (www.mandops.co.uk/resistim.htm). Betaines are naturally occurring amino acid derivatives that function as osmoprotectants within plants (McNeil et al. 1999). Osmoprotectants serve to raise osmotic pressure in the cytoplasm and stabilize proteins and membranes when salt levels or temperatures are unfavorable for plant growth. Osmoprotectants, therefore, play important roles in the adaptation of cells to adverse environmental conditions (Yancey 1994). Manufacturers claim RESISTIM is particularly effective on legumes such as peas and beans, strengthening them against diseases such as mildew (www.mandops.co.uk/resistim.htm). However, a definitive role for betaine as an inducer of plant defense responses has not been clearly shown. More likely, enhanced levels of betaine are as a consequence of pathogen invasion rather than as a cause of resistance (Berglund and Ohlsson 1995).

Phosphites exhibit a complex mode of action, acting both directly on the pathogen and indirectly by stimulating plant host defense responses such as phenolic accumulation that in turn inhibit pathogen growth (Guest and Grant 1991). Likewise, salicylic acid is widely recognized as an inducer of SIR resistance (Enyedi and Raskin 1993) and is shown to be effective in reducing disease incidence against Phytophthora palmivora in cacao, Pseudomonas syringae pv. Maculicola on cucumber and Arabidopsis, and Colletotrichum lagenarium on cucumber and tobacco necrosis virus (Rasmussen et al. 1991; Kessmann et al. 1994; Okey and Sreenivasan 1996).

Harpin protein is a naturally occurring bacterial protein present in several plant pathogenic bacteria to include Erwinia amy-
lovora responsible for fireblight in apples. Manufacturers claim harpin proteins possess wide activity against a broad range of pathogenic viral, bacterial, and fungal diseases and, in addition, enhance resistance to insect attack (www.yardener.com/HarpinProteinProducts.html).

Enhanced leaf peroxidase activity has been associated with SIR against tobacco mosaic virus, alfalfa mosaic virus, and Phytophthora cinnamomi (Van Lelyveld and Brodick 1975; Vegetti et al. 1975; Van Loon 1976). Induced systemic resistance against, for example, the pathogens Colletotrichum lagernarium and Cladosporium cucumerinum is associated with an enhanced ability of the host plant to lignify at points of fungal penetration. Lignification involves the polymerization of hydroxycinnamyl alcohols mediated by peroxidase in the presence of hydrogen peroxide (Gross 1979; Dalisay and Kuc 1995). Likewise, treatment of the lower leaves of potato plants with hyphal wall components of Phytophthora infestans systemically activated enhancement of superoxide dismutase resulting in a significant reduction of hyphal penetration and susceptible lesions (Chai and Doke 1987).

Investigations into SIR-inducing compounds to control oak powdery mildew have received limited study. In addition, the majority of studies regarding the efficacy of SIR-inducing chemicals have been conducted primarily under laboratory and glasshouse conditions that do not reflect field or landscape environments. Finally, assessments of SIR efficacy in the majority of cases reflect applications applied as preventive (before visible symptoms of diseases expression) rather than therapeutic (when disease expression is visible). The objectives of this project were to investigate 1) the efficacy of commercially available SIR compounds on powdery mildew infection of English oak under field conditions as therapeutic rather than preventive treatments; and 2) the role of leaf peroxidase and superoxide dismutase activity on powdery mildew infection.

MATERIALS AND METHODS

Plant Material and Experimental Design

The trial site consisted of a 2.0 ha block of English oak (Quercus robur L.) at the University of Reading Shinfield Experimental Site, Berkshire, U.K. Planting distances were based on a 2 x 1 m (6.6 x 3.3 ft) spacing. Trees were planted in early November 2001 and trained to produce a central-leader system to an average height of 1.5 ± 0.15 m (4.95 ± 0.5 ft) with mean trunk diameters of 10 ± 2 cm (4 ± 0.8 in). Weeds were controlled with glyphosate (Roundup; Green-Tech, Sweethills Park, Nun Monkton, York, U.K.) at applied at 15 mL (0.45 fl oz) per liter (0.26 gal) of water four times during the growing season. Supplementary irrigation was applied during the 2005 and 2006 growing seasons as required. Trees were fertilized annually through a broadcast application of granular 29N–7P–9K fertilizer (Bartlett BOOST; The Doggett Corporation, Lebanon, NJ, U.S.) applied at 40 g (1.4 oz) m⁻² (11 ft²) in early May. The soil was a sandy loam containing 4% to 6% organic matter, pH of 6.2; available phosphorus, potassium, magnesium, sodium, and calcium were 52.0, 659.1, 175.2, 49.4, and 2188 mg/L (0.0001, 0.005, 0.002, 0.001, and 0.02 oz/gal), respectively, at the time treatments began.

Historically, the oaks suffered annually from powdery mildew infections. Consequently, before the trial began in 2005 and 2006, trees were inspected in September 2004 and 2005 and only those trees visually rated with 50% to 80% of leaves affected, representing severe foliar discoloration and powdery mildew infection, were used in the 2005 and 2006 trial. The insecticide deltamethrin (Bandu; Headland Agrochemicals Ltd., Saffron Walden, Essex, U.K.) was applied in July and August every other month through a broadcast application with a Rig sprayer at 40 mL (1.2 fl oz) deltamethrin per 100 L (26 gal) of water. Trees were sprayed until runoff, generally 0.25 L (0.07 gal) deltamethrin per tree.

Systemic-Inducing Resistance Treatments

Seven trees with 5% to 20% of leaves affected with powdery mildew, i.e., some yellowing but little or no defoliation, were treated per SIR product. These occurred on 23 July 2005 and 31 July 2006. During SIR spray treatments, polythene screens 1 m (3.3 ft) high were erected around each tree to prevent dispersal of sprays and possible cross-contact with other trees. The base of the tree was covered with a 0.5 m x 0.5 m (1.65 x 1.65 ft) polythene mulch to prevent potential soil percolation. The treatments (Messenger [harpin protein], Agri-Fos [potassium phosphate], Aspin [salicylic acid], RESISTIM [Betaine, amino acid derivatives], two fungicide [penconazole] regimes, and a water control) were applied in seven randomized complete blocks with a single tree as the experimental unit, giving a total of 49 observations per response variable. Foliar sprays of each chemical were applied until runoff using a 10 L (2.6 gal) backpack sprayer at the manufacturer’s recommended rate:

RESISTIM (a.i. betaine): 10 mL (0.3 fl oz) per liter (0.26 gal) of water (Mandops UK Ltd., Eastleigh, Hampshire, U.K.);
Topas (a.i. penconazole): 1.5 mL (0.045 fl oz) per liter (0.26 gal) of water (Syngenta Crop Protection UK Ltd., Whittlesford, Cambridge, U.K.);
Messanger (a.i. harpin protein): 4 g (0.14 oz) per 100 m² (1,111 sq ft) (EDEN Bioscience Corporation, N. Bothell, WA);
Agri-Fos (a.i. potassium phosphate): 3 mL (0.09 fl oz) per liter (0.26 gal) of water (Shelton Technology Ltd., Boundary House, Charwelton, Northamptonshire, U.K.); and
Salicylic acid: 3 mL (0.09 fl oz) per liter (0.26 gal) of water (Shelton Technology Ltd.).

In addition, a comparative evaluation of a conventional spray program used within the United Kingdom for powdery mildew control was conducted. Trees were sprayed with the fungicide Topas (a.i. penconazole), a protectant conazole fungicide with antisporulant activity, at the recommended rate of 1.5 mL (0.045 fl oz) per liter (0.26 gal) of water. Penconazole treatments began at the same time as application of SIR products and every 3 weeks thereafter until the cessation of the experiment (27 September 2005 and 2006).

Disease Severity

Disease severity of whole trees was assessed visually on 27 September 2005 and 2006. Each tree was rated on a 0 to 5 rating scale using a visual indexing technique and ratings on the scale: 0 = no powdery mildew observed; 1 = less than 5% of leaves affected and no aesthetic impact; 2 = 5% to 20% of leaves affected with some yellowing but little or no defoliation; 3 = 21% to 50% of leaves affected, significant defoliation, and/or leaf yellowing; 4 = 51% to 80% of leaves affected, severe foliar discoloration; and 5 = 81% to 100% of foliage affected with 90% to 100% defoliation.

Leaf disease severity was assessed at days 10, 20, and 60 after application of the SIR-inducing chemical to determine the short- and long-term effects of each product using a similar indexing
technique as follows: \(0 = \text{no powdery mildew observed; } 1 = \text{less}
\frac{5}{\text{than 5\% of leaf surface covered with hyphal growth; } 2 = 5\%}
\text{to 20\% of leaf surface covered; } 3 = 21\% \text{ to 50\% of leaf surface}
\text{covered; } 4 = 51\% \text{ to 80\% of leaf surface covered; and } 5 = 81\%
\text{to 100\% of leaf surface covered.}

**Superoxide Dismutase Activity**

Superoxide dismutase activity (SOD) was based on the method described by
Kraus and Fletcher (1994). In summary, extracts were prepared at 4°C (39.2°F)
by homogenizing 0.2 g (0.07 oz) of leaf tissue (generally six leaves per tree
in 4 mL [0.12 fl oz] of 0.1 M Na2HPO4/NaH2PO4 buffer [pH 7] with
a mortar and pestle and centrifuged at 16,000 × g for 10 min). The
supernatant was filtered through Whatman paper (No. 1) and 1 mL
(0.03 fl oz) was applied to a Pharmacia PD-10 chromatography
column containing Sephadex G-250 equilibrated with 50 mM Na2CO3 buffer
(pH 10.2) to remove low-molecular-weight components and exchange the buffer. The assay was performed
using 0.1 mM diethylenetriaminepentaacetic acid in the reaction
mixture and the subsequent increase in absorbance at 550 nm
followed on a spectrophotometer (PU8800 Pye Unicam, Ports-
mouth, U.K.) equipped with a kinetics module for 6 min at 24°C
(75.2°F). SOD activity was assessed at days 10, 20, and 60 after
application of the SIR-inducing chemical to determine the short-
and long-term effects of each product on enzymatic activity.

**Peroxidase Activity**

A total of 0.3 g (0.01 oz) of foliar tissue (generally six leaves per
tree) were homogenized in 5 mL (0.15 fl oz) of 0.2 M Tris-Cl−
(buffer pH 7.8) containing 0.13 mM EDTA and 80 µM soluble
polyvinylpyrrolidone with a Polytron homogenizer (Glen Mills
Inc., Clinton, NJ) for 30 sec on ice and centrifuged at 3,000 × g
for 10 min. Catalase activity was determined by following the
consumption of hydrogen peroxide (extinction coefficient 39.4
mmol I/cm²) at 240 nm for 2 min. The reaction mixture
contained 2 mL (0.06 fl oz) of 100 mM Na2HPO4/NaH2PO4 buffer
(pH 6.5) and 50 µL of plant extract, and the reaction was initi-
ated by adding 10 µM of 30% (w/v) hydrogen peroxide. Leaf
peroxidase activity was assessed at days 10, 20, and 60 after
application of the SIR-inducing chemical to determine the short-
and long-term effects of each product on enzymatic activity.

**Statistical Methods**

Before the analysis, data were examined to ensure normality and
genomegity of variance (Anderson-Darling test) were met to
meet the assumptions for the analysis of variance. Data were then
analyzed as a randomized complete block using an analysis of
variance (ANOVA). If trial data violated the basic assumptions
required by ANOVA, data were log-transformed and then back-
transformed for presentation in tables. Differences in levels of
disease severity, leaf superoxidase dismutase, and peroxidase-
specific activity from control values were determined and means
were separated at the \(P < 0.05\) level of significance using the
Genstat for Windows program (VSN International Ltd., Hemel
Hempstead, U.K.). A simple linear mathematical model was
used to record relationships between leaf superoxidase dismutase
and peroxidase-specific activity versus leaf disease severity us-
ing goodness-of-fit R² values.

**RESULTS**

In both the 2005 and 2006 trials, damaging outbreaks of powdery
mildew were recorded on control trees as indicated by disease
severity ratings of 5.0 to 5.5, respectively, on leaves of English
oak (Figure 1). During the study, none of the treated or control
trees died as a result of pathogen attack. None of the SIR agents
or fungicide evaluated was phytotoxic to the test trees. The SIR-
inducing compound RESISTIM (a.i. betaine) and a single spray
treatment of penconazole had no significant influence on disease
severity and specific activity of peroxidase and superoxide dis-
mutase in both the 2005 and 2006 trials (Figures 1 to 4). Con-
sequently, results for RESISTIM are shown that reflect those of
a single penconazole spray treatment. Results of this study indi-
cate that the commercially available compound RESISTIM
and a single spray of penconazole have no significant role in the
control of powdery mildew when applied as a therapeutic treat-
ment (Figure 1).

**Disease Severity**

In both the 2005 and 2006 trials, salicylic acid and potassium
phosphite had no significant effect on disease severity at the
cessation of the growing season (Figure 1). Consequently, results of
this study indicate no beneficial long-term effects of salicylic
acid and potassium phosphite on reducing powdery mildew se-
verity when used as a single therapeutic spray treatment. Appli-
cation of the SIR-inducing agent harpin protein significantly
\((P < 0.05)\) reduced disease severity of powdery mildew from 5.5 to 2.1
in the 2005 trial. No significant effects, however, on disease
severity were recorded in the 2006 trial. The fungicide Topas
(penconazole) applied at three weekly intervals after the visible
observation of powdery mildew resulted in a significant
\((P < 0.05)\) reduction in disease severity (Figure 1). Disease severity rates in
this instance were reduced from 5.5 to 1.9 (2005 trial) and 5.0 to
1.8 (2006 trial).

**Leaf Superoxidase Dismutase,**
**Peroxidase-Specific Activity, and Disease Severity**

The SIR-inducing agents harpin protein, salicylic acid, and
potassium phosphite increased leaf-specific activity of superoxidase
dismutase and peroxidase by 16% to 28% at days 10 and 20 post-
application compared and nontreated controls (Figures 2 and 3). In
all cases, such an increase in activity was significant at \(P < 0.05\). By
day 60, however, specific activity of both enzymes in leaves was
nonsignificant when compared with controls (Figures 2 and 3).
Such a result indicates a single spray of harpin protein, salicylic
acid, and potassium phosphite induces superoxidase dismutase
and peroxidase activity 20 days or more but less than 60 days.
Concomitant with an increase in superoxidase dismutase and
peroxidase activity at days 10 and 20, a significant \((P < 0.05)\)
reduction in disease severity was recorded at these time intervals.
Such a result indicates an association between enhanced super-
oxidase dismutase and peroxidase activity and resistance against
oak powdery mildew. Applications of penconazole had no sig-
nificant effect on specific leaf activity of superoxidase dismutase
at days 10, 20, and 60, although the level of activity was always
higher than controls (Figure 3). However, a significant increase
\((P < 0.05)\) in leaf peroxidase activity was recorded at days 10 and
20 (Figure 3). At day 60, levels were higher than controls, only
not significantly so. At days 10, 20, and 60, penconazole applica-
tion significantly \((P < 0.05)\) reduced disease severity com-
pared with nontreated controls (Figure 4).
Figure 1. The influence of systemic-inducing resistance (SIR) and a fungicide treatment on disease severity of powdery mildew on English oak growing under field conditions. Trials were conducted in 2005 and 2006. All values mean of seven trees. *Significantly different from controls according to least significant difference at $P < 0.05$; no annotations = not significant different from control value. Significance of SIR-inducing agents in 2005 = $P < 0.05$, nonsignificant; significance of SIR-inducing agents in 2006 = nonsignificant (analysis of variance effect).

Figure 2. The influence of systemic-inducing resistance (SIR) and a fungicide treatment on leaf superoxidase dismutase activity in English oak at days 10, 20, and 60 after application. Trees were growing under field conditions. Powdery mildew infection was visibly present on the leaf at the time of SIR application (disease severity = 2). Measurements were taken only in the 2006 trial. All values mean of seven trees, two superoxidase dismutase measurements per tree with each superoxide dismutase activity measurement comprised of six leaves. *Significantly different from controls according to least significant difference at $P < 0.05$; no annotations = not significant different from control value. Significance of SIR-inducing agents at days 10 and 20 = $P < 0.001$ (analysis of variance effect). Significance of SIR-inducing agents at day 60 = nonsignificant (analysis of variance effect).
Figure 3. The influence of systemic-inducing resistance (SIR) and a fungicide treatment on leaf peroxidase activity in English oak at days 10, 20, and 60 after application. Trees were growing under field conditions. Powdery mildew infection was visibly present on the leaf at the time of SIR application (disease severity = 2). Measurements were taken only in the 2006 trial. All values mean of seven trees, two peroxidase measurements per tree with each peroxidase measurement comprised of six leaves. *Significantly different from controls according to least significant difference at $P < 0.05$; no annotations = not significant different from control value. Significance of SIR-inducing agents at days 10 and 20 = $P < 0.001$ (analysis of variance effect). Significance of SIR-inducing agents at day 60 = nonsignificant (analysis of variance effect).

Figure 4. The influence of systemic-inducing resistance (SIR) and a fungicide treatment on leaf disease severity in English oak at days 10, 20, and 60 after application. Trees were growing under field conditions. Powdery mildew infection was visibly present on the leaf at the time of SIR application (disease severity = 2). Measurements were taken only in the 2006 trial. All values mean of seven trees, 12 leaves per tree. *Significantly different from controls according to least significant difference at $P < 0.05$; no annotations = not significant different from control value. Significance of SIR-inducing agents at days 10 and 20 = $P < 0.001$ (analysis of variance effect). Significance of SIR-inducing agents at day 60 = nonsignificant (analysis of variance effect).
Relationship of Leaf Superoxidase Dismutase and Peroxidase-Specific Activity versus Leaf Disease Severity

Figure 5 shows the relationships between leaf superoxidase dismutase and peroxidase-specific activity versus leaf disease severity. A simple linear mathematical model best fit the relationship between these parameters. Goodness-of-fit $R^2$ values of 0.56 (day 10) and 0.43 (day 20) and 0.59 (day 10) and 0.65 (day 20) were recorded between the specific leaf activity of peroxidase and SOD, respectively, and leaf disease severity (Figure 5). These relationships were highly significant at $P < 0.001$. Such a result indicates enhanced levels of peroxidase and SOD activity may contribute to reduced leaf disease severity caused by oak powdery mildew. At day 60 post-SIR application, no relationship was found between peroxidase and SOD activity and leaf disease severity with $R^2$ values of 0.06 and 0.04 recorded coupled with a lower and a nonsignificant $P$ value (Figure 5).

DISCUSSION

The phenomenon of inducing resistance in plants by biologic and/or natural compounds such as jasmonic acid, salicylic acid (aspirin), phosphates, fatty acids, and so on, potentially offers an alternate, more environmentally benign approach to tree protection (Friedrich et al. 1996; Sticher et al. 1997). Several studies have found SIR-inducing compounds to be effective in controlling fireblight (*Erwinia carotovora*), *Phytophthora* root rot (*P. palmivora*), powdery mildew (*Sphaerotheca pannosa* var. *rosa*, *Phyllactinia* spp., and *Uncinula necator*), and wilt disease of spruce (*Ceratocystis polonica*) with the level of disease control achieved comparable with currently used agrochemicals (Sparla et al. 2004). Few reports exist evaluating the effects of salicylic acid, potassium phosphite, betaines, and harpin protein on reducing disease severity of oak powdery mildew (*Microsphaera alphitoides*) under field conditions. Results of this study indicate that salicylic acid, potassium phosphite, and betaine do not provide long-term protection against oak powdery mildew (*Microsphaera alphitoides*).
alphitoides) when applied as a single therapeutic spray treatment. A short-term (20 day) reduction in leaf disease severity was, however, recorded with salicylic acid and potassium phosphate. Research by the author also indicated a single therapeutic spray treatment of the four SIR agents used in this investigation have no long-term effects on disease severity of other foliar pathogens such as apple scab (Venturia inaequalis) and Guignardia leaf blotch (Guignardia aesculi) (Percival, unpublished data).

Induction of antioxidant and defensive enzymes such as superoxide dismutase and peroxidase are recognized as initial SIR responses in plants (Kessmann et al. 1994). No such response was recorded in this investigation after RESISTIM application indicating no SIR-inducing properties. In addition, no significant role of betaine in the form of RESISTIM in enhancing tree resistance against oak powdery mildew was recorded when applied as a single therapeutic treatment.

Research in Australia and the United States have found phosphites to be effective in the control of diseases, particularly those that belong to the oomycetes group such as Phytophthora spp., Pythium spp., and the Downy Mildew diseases (Jackson et al. 2000; Wilkinson et al. 2001; Miller et al. 2006). In addition, phosphites control other diseases that fall outside this group such as the bacterial disease Erwinia amylovora (apple fireblight). Potassium phosphate has been shown to provide a significant degree of control against Venturia inaequalis when applied as foliar sprays at 10 to 12 day intervals (MacHardy and Jeger 1983). Application of phosphites and salicylic acid as a single therapeutic spray treatment, however, appeared to offer a short-term reduction in disease severity up until day 20 after application, but by the cessation of the growing season, no long-term control of oak powdery mildew under field conditions was recorded.

The use of the harpin protein (trade name Messanger) has been shown to reduce disease severity of Botrytis cinerea on leaves and fruit of pepper (Capsicum annum L. var. cvs. ‘Demere’, ‘Yalova Charleston’, and ‘Sari Sivi’) as measured by leaf chlorophyll content (Abudak et al. 2006). In this study, application of harpin protein provided a significant degree of protection against oak powdery mildew in the 2005 trial. No significant long-term effects, however, were recorded in the 2006 trial. Such a response reflects those recorded by Agostini et al. (2003) who evaluated the influence of harpin protein (Messenger) on enhanced resistance of potted lemon seedlings against citrus scab (Elsinoe fawcettii), grapefruit against melanine (Diaporthe citri), and Dancy tangerine against Alternaria brown spot (Alternaria alternata pv. citri). In the case of Diaporthe citri and (Alternaria alternata pv. citri), no enhanced resistance effects were recorded after application of harpin protein. In the case of citrus scab, Messenger provided a significant degree of control in some studies but not others. A number of reasons were postulated for this lack of consistency. Plant phenology has been shown to be important, with harpin protein showing greater effectiveness when applied at budbreak before inoculum buildup. Efficacy was also influenced by the weather conditions that prevailed at the time of application with cool wet weather not conducive for efficacy (Agostini et al. 2003). The potential shelf life and batch-to-batch variation of biologic propagules in terms of reduced viability has been highlighted by Downer (2007) that may also partially explain the lack of consistency shown by the harpin protein. These problems should not distract from the fact that a single spray treatment of harpin protein during the 2005 growing season provided season-long control of oak powdery mildew comparable with repeat three-weekly applications of a commercially available triazole fungicide. Such a response indicates that further research to clarify phologenic and climatic influences on the efficacy of SIR-inducing chemicals may help develop important tree protectant compounds. In addition, results of this study indicate a short-term (20 day) reduction in leaf disease severity after spray application of harpin protein.

A positive relationship between enhanced leaf peroxidase and superoxide dismutase activities and reduced oak powdery mildew were observed up to 20 days after systemic induction. By day 60 after SIR treatment, however, any induced protection was no longer manifest with disease severity reflecting those of controls. Such a result indicates repeat application of systemic induction at 20 day intervals may be warranted to enhance resistance against oak powdery mildew over time.

Repeat spray applications of penconazole resulted in a significant increase in peroxidase activity in English oak. Likewise, repeat spray applications of penconazole resulted in higher leaf activities of superoxide dismutase compared with controls, if not significantly so, in all cases. Reductions in disease severity as a result of direct fungicidal properties of penconazole is through inhibition of the C4-demethylase reactions in sterol biosynthesis of fungi (Allingham 2005). However, all triazole-based fungicides have been shown to induce a suite of morphologic adaptations to include promotion of leaf catalase and superoxide dismutase activity that allow plants to tolerate a range of environmental stresses (Kraus and Fletcher 1994). These antioxidant enzymes and pigments are vital in quenching high-energy reactive oxygen species (ROS) such as superoxide and singlet oxygen produced in response to abiotic stresses such as salinity, drought, and atmospheric pollutants (Apel and Hirt 2004). Consequently, a number of authors suggest that triazole-induced protection from abiotic stress is an important factor in improving tree vitality that in turn allows the tree’s own natural defense mechanisms to reduce subsequent pathogen attack (Zhang et al. 1994; Fletcher et al. 2000).

In conclusion, results of this investigation indicate that in the case of oak powdery mildew, a positive association was noted between increased activities of peroxidase and superoxide dismutase and reduced disease severity in the short term. Such benefits were, however, not manifest over a longer time period indicating repeat 20 day interval sprays are required. Further research evaluating the influence of repeat SIR treatments are ongoing against a range of foliar and root pathogens.

**LITERATURE CITED**


Berglund, T., and R. Ohlsson. 1995. Defensive and secondary metabolism in plant tissue cultures, with special reference to nicotinamide,
foliaire tandis qu’une faible diminution de la sévérité de la maladie qui a été enregistrée fut associée avec une amélioration de l’activité en peroxydase et en superoxide dismutase foliaire. Une application thérapeutique unique de l’agent protéine harpine qui induit une résistance systématique a permis de réduire significativement la sévérité du blanc des feuilles au cours de l’essai de 2005 uniquement. Seuls des vaporisations répétitives de penconazole ont permis de diminuer significativement la sévérité du blanc des feuilles chez le chêne au cours des essais de 2005 et de 2006. Une activité foliaire accrue de superoxide dismutase et de peroxydase a été enregistrée suivant les traitements répétitifs avec le penconazole.


Resumen. Se condujo un ensayo de dos años, usando encinos establecidos (Quercus robur L.), para evaluar la eficacia de sistemas comercialmente disponibles que inducen los compuestos de resistencia (SIR, por sus siglas en inglés) (ácido salicílico, fosfato de potasio, proteína harpin, betaína); aplicados como un solo tratamiento de aerosol terapéutico contra el patógeno foliar del encino (Microsphaera alphitoides). Los compuestos del SIR que incluyeron betaína y un tratamiento con aerosol de penconazol no tuvieron influencia significativa en la severidad de la enfermedad, emisiones de fluorescencia de clorofila, contenido de clorofila en la hoja y actividad específica de peroxidase y superóxido dismutase, en ambos ensayos de 2005 y 2006. El ácido salicílico y el fosfato de potasio no tuvieron efecto significativo a largo plazo en la severidad de la enfermedad, clorofila foliar, emisiones Fv/Fm y contenido de clorofila en la hoja, a pesar de que fue registrada reducción a corto plazo en la severidad de la enfermedad, que estuvo asociada con la actividad del peroxyd y superoxido dismutate. Una sola aplicación de SIR, induciendo el agente proteínico harpin, redujo significativamente la severidad de la enfermedad, en el ensayo de 2005, únicamente. Aplicaciones repetidas de penconazol, solamente, redujeron significativamente la enfermedad del encino en los ensayos de 2005 y 2006. Se registró una mayor actividad del superoxidi dismutase y peroxidase después de las aplicaciones repetidas de penconazol.