

Sulfur Amendment of Soil Improves Establishment and Growth of Firs in a Field Naturally Infested with *Phytophthora*¹

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Abstract

Acidification of soil from pH 6 to 4 by incorporating elemental sulfur reduced mortality and improved color and initial growth of Fraser fir, *Abies fraseri* (Pursh) Poir., and Canaan fir, *Abies balsamea* (L.) Mill. var. *phanerolepis* Fernald, planted into a field that had previously experienced significant losses consistent with phytophthora root rot. Acidifying the soil improved tree color starting the year of planting and persisting through five years. During their second year after planting, extension of terminal growth was 12.5 vs. 5.6 cm (4.9 vs. 2.2 in) for plots with soil pH of 4 and 6, respectively, averaged across tree species. In subsequent years, the growth rate of trees was unaffected by having acidified the soil. Over the course of five years, the average annual mortality rate for the trees was 1.4, 4.0, 9.7, and 12.2% for Canaan fir (pH 4), Canaan fir (pH 6), Fraser fir (pH 4), and Fraser fir (pH 6), respectively. However, all tree mortality for Canaan fir planted into acidified soil occurred during the first two years. A root dip with potassium phosphite at the time of planting only benefitted Fraser fir. Minimizing losses of trees in this field would require planting species less susceptible or resistant to phytophthora root rot infection and soil acidification.

Index words: soil acidification, phytophthora root rot, potassium phosphite, root dip.

Species used in this study: Fraser fir, *Abies fraseri* (Pursh) Poir.; Canaan fir, *Abies balsamea* (L.) Mill. var. *phanerolepis* Fernald.

Chemicals used in this study: acibenzolar-S-methyl (Actigard 50WDG); clothianidin (Arena 50WDG), imidacloprid (Xylect 2F), potassium phosphite (Helena Prophyt), sulfur.

Significance to the Horticulture Industry

Losses due to root rots caused by *Phytophthora* species can be difficult to avoid where the pathogen is present and soils are conducive to disease. For Christmas tree plantations, planting less susceptible Canaan fir in place of the highly susceptible Fraser fir reduced losses by two-thirds. Reducing soil pH from 6 to 4 reduced losses among Canaan fir by an additional two-thirds. The combined actions reduced tree mortality by 89%.

Introduction

True firs (*Abies*: Pinaceae) are especially valued as Christmas trees due to superior needle retention, attractive foliage, and pleasant aroma. However, firs are susceptible to many soil-dwelling pests, including root rot diseases caused by various *Phytophthora* species (Talgø and Chastagner 2012, Li et al. 2019), which are water molds belonging to Oomycota. Under adverse conditions, these organisms form thick-walled oospores (the result of sexual reproduction, usually produced by recombination among differing mating types) and chlamydospores (produced asexually). These spores may remain viable in soil for several years. When conditions are wet, both spore types germinate to develop sporangiophores with sporangia. These, in turn, break open to release zoospores, a free-

living life stage with two flagella that can move within a film of water in soil to roots of potential hosts. Upon contact with the root of a suitable host, the zoospore detaches its flagella and forms a cell wall in a process called encystment, rapidly followed by germination of the cyst, from which threadlike hyphae invade the roots. The life cycle is complete when *Phytophthora* hyphae form either sporangia, oospores, or chlamydospores (Parke and Eberhart 2016). Christmas tree farms in New England are faced with two factors that exacerbate tree losses due to root rot. Soil conditions (soil texture, depth, slope, and drainage) are so variable that even small fields of less than one hectare often contain more than one soil type. This leads to difficulty with losses from root rots when susceptible species are planted in areas (typically, finer textured soils or areas that are poorly drained) more conducive to disease development. Secondly, this region is predicted to receive greater and more variable rainfall resulting from anthropogenic climate change (IPCC 2007), in which precipitation may occur in larger events (e.g., from tropical storms or from persistent low-pressure systems). Conditions leading to more frequent soil saturation events suggests that losses of Christmas trees from *Phytophthora* may increase over time in this region unless we can find effective management options.

Phytophthora root rots of Christmas trees in Connecticut include several species, including *P. abietivora*, *P. cactorum*, *P. kelmaniana*, *P. pini*, and *P. plurivora* (McKeever and Chastagner 2016, Li et al. 2019). World-wide there are many more species of *Phytophthora* found to infect Christmas trees (Talgø et al. 2007, Li et al. 2019). Differences among these species with respect to their ability to infect the roots of various species of fir trees are not known, or of the variations among these species that

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define conditions especially conducive or restrictive for their growth. Current management techniques involve buying healthy plants, using raised beds or installation of drainage tiles, avoiding planting highly susceptible fir species (e.g., Fraser fir) in areas of wet soil or where disease has previously occurred, and either growing resistant species (*A. bornmuelleriana* Mattf. [Turkish fir] or *A. firma* Siebold & Zucc. [Momi fir]), or grafting susceptible trees as scions on these *Phytophthora*-resistant rootstocks (Frampton and Benson, 2012). Use of fungicides has limited practical value under conditions conducive to disease (Benson et al. 2006, Thomas and Pickel 2011).

Methods of growing trees that prevent phytophthora root rots should also enhance the establishment and growth of fir trees, because healthy root systems allow properly functioning plants to reach their full genetic potential. A complete assessment of methods to prevent root rot occurrence should start with the disease triangle: plant disease occurs only when there is co-occurrence of disease inoculum, a susceptible host, and environmental conditions conducive to infection (Francl 2001). Any one of the three sides to the disease triangle could be manipulated to decrease disease.

One method to manipulate the soil environment is to change the soil pH. Previous research has demonstrated that reducing soil pH to about 4 can protect various species from infection by phytophthora root rots, attributed to the negative effects of hydrogen ions on development and germination of sporangia, and survival of oospores and chlamydozoospores (Kong et al. 2009). Fir species native to eastern North America are adapted to highly acid soils (Richter et al. 2011) and so acidification of soil to a pH of 4 can be anticipated to favor growth and survival of *Abies* over *Phytophthora*.

Reducing host susceptibility might be accomplished by growing resistant or less susceptible species or varieties, or by inducing resistance in otherwise susceptible hosts. Induction of the systemic acquired resistance pathway can be accomplished with phosphite-containing products, the insecticides imidacloprid or clothianidin, which are metabolized to form salicylate agonists (Ford et al. 2010), or acibenzolar-S-methyl (Cole 1999). In an earlier study, root dips with products that are known to be able to induce the systemic acquired resistance pathway in plants improved the health of Christmas trees transplanted into a field infested with phytophthora root rot pathogens: Douglas-fir and Fraser fir appeared to benefit from root dips containing potassium phosphite, while Canaan fir and white spruce did not (Cowles et al. 2012).

This work focuses on interactions between host susceptibility, by (1) comparing two species, and (2) using products in a root dip at the time of planting that should activate the systemic acquired resistance pathway, and manipulation of the soil pH. I explored how well we would be able to establish and grow Christmas trees on a site suspected to be unusually uniformly infested with *Phytophthora*.

Materials and Methods

A field trial planted in 2010 investigated the growth performance of exotic firs at a cooperating farm site in

Brooklyn, CT, where the grower had experienced losses consistent with the presence of *Phytophthora* root rot (C. Langevin, personal comm.). By October of 2013, all 60 Fraser firs planted at this site had died, whereas there were few losses among the 660 Turkish, Nordmann, or Trojan firs (*Abies bornmuelleriana*, *A. nordmanniana* (Steven) Spach, and *A. nordmanniana* (Steven) Spach ssp. *equitrojani* Mattf, respectively) (R. Cowles, unpublished data). During May of 2014, the trees from this experiment were removed, including main roots uprooted with the trunks, so that the field could be repurposed for additional experiments. Soils in this field are Paxton and Woodbridge fine sandy loams, averaging 5.5% slope. These are typically well-drained or moderately well-drained soils with a pH of 5.2 to 5.5 within the surface 15 cm (6 in), and are classified as prime farmland (<https://casoilresource.lawr.ucdavis.edu/gmap/>). The short-term history of this field had been Christmas tree production, prior to which it had been used for growing field corn. A history of lime application to grow corn probably explains the soil pH of 6.0 to 6.2 measured in 2014.

To prepare this field for experiments involving soil pH manipulation, pelletized sulfur (Winfield Solutions, St. Paul, MN, containing 90% elemental sulfur) was spread at a rate of 3,370 kg/ha⁻¹ (3,007 lb/A⁻¹) of product on June 18, 2014 into randomized main plots, with each plot sufficiently large (3.4 by 11.7 m) (11.1 by 38.4 ft) to plant 14 trees at a spacing of 1.7 m (5.6 ft) within the row and 1.7 m between rows. There were 23 replicates of paired main plots, either receiving no sulfur or 16.8 kg (37 lb) of sulfur product per plot. Sulfur was manually spread within plots, and then incorporated with a rototiller to a depth of 15 cm (6 in) on June 18, 2014.

The overall experiment was a 2 × 2 × 7 factorial split-split plot randomized complete block design with 23 replicates to investigate the influence of soil pH (consisting of two levels which were main plots of a split-plot design, sulfur or no sulfur), species (two disease susceptibility levels, representing split-split plots), and various root dips (seven levels randomized within subplots) on the initial establishment success and growth of bare-root Christmas trees, for a total of 28 treatment combinations. The seven root dip treatments included a 3 × 2 factorial evaluation of insecticide times potassium phosphite interactions, plus a treatment not balanced with the factorial design to investigate effectiveness of a root dip with acibenzolar-S-methyl (See Table 1). There were 644 trees individually treated at the time of planting: 322 each of Canaan fir (less susceptible to root rot) and Fraser fir (highly susceptible to root rot). Three-year old 30-cm (11.8 in) tall bare root transplants were obtained from Reliable Source Nursery (Star City, WV) and planted April 13 and 14, 2015. Root dips involved submerging the root system into 8 L (2.1 gal) of prepared solutions held in a 20 L (5.3 gal) bucket, and allowing excess liquid to drain back into the bucket immediately prior to planting. Trees were planted into holes, which were backfilled with soil while positioning the root crown just below the soil surface, and then the soil compressed by stepping on the soil to guarantee good soil-to-root contact.

Table 1. Root dip treatments investigating putative SAR-eliciting materials and their interactions

| Treatment | Insecticide ^a | K-Phosphite ^b | Acibenzolar-S-methyl ^c |
|-----------|--------------------------|--------------------------|-----------------------------------|
| 1 | none | none | none |
| 2 | none | yes | none |
| 3 | Imidacloprid | none | none |
| 4 | Imidacloprid | yes | none |
| 5 | Clothianidin | none | none |
| 6 | Clothianidin | yes | none |
| 7 | none | none | yes |

^aImidacloprid, Xyect 2F (Rainbow Treecare, Minnetonka, MN), 33 mL per 8 L; Clothianidin, Arena 50WDG (Valent USA Corp., Walnut Creek, CA), 6.4 g per 8 L

^bPotassium phosphite, Helena Prophyt (Helena Chemical Co., Collierville, TN), 20 mL per 8 L

^cActigard 50WDG (Syngenta Crop Protection, Greensboro, NC), 16 g per 8 L

Composite soil samples were taken to be representative of the rooting zone from each plot on August 31, 2015 and again in September, 2016. Soil pH was measured in the soil testing laboratory at the Valley Laboratory of the Connecticut Agricultural Experiment Station. Deionized water was added to soil to form a slurry, which was allowed to stabilize for about 20 min before taking measurements with a previously calibrated Accumet XL25 pH meter (Fisher Scientific, Hampton, NH). Soil pH measurements from main plots were used to confirm the effectiveness of the sulfur application and the stability of these effects.

Tree condition was evaluated on September 15, 2015, August 17, 2016, September 26, 2017, July 19, 2018, and April 15, 2019. Trees were assigned health ratings according to the following scale: 0, dead; 1, almost dead (yellowed and wilting); 2, very yellow; 3, slight yellowing; 4, fully green. A similar (but mirrored numbering) disease rating system was used in NC to assess Fraser fir root health and underlying phytophthora root rot (Richter et al. 2011). The idea behind the ratings is that they are providing a measure of underlying root health, without taking destructive samples of roots. The length of the current year's growth of the central leader was measured once each year to the nearest cm.

Ten dying Fraser fir trees were sampled in October 10, 2017 to confirm whether the plant losses were due to *Phytophthora* root rot infections. Diseased plants were taken to the laboratory to isolate the causal agent for identification purposes.

Soil pH data were analyzed via t-tests in Excel 2013 (Microsoft, Redmond, WA). Tree health ratings, mortality, and growth were assessed through analysis of variance (ANOVA) with Statistix 9 (Analytical Software, Tallahassee, FL). Analyses of tree health ratings were conducted twice: once with all subplot treatments (including the acibenzolar-S-methyl treatment), and once by excluding the acibenzolar-S-treatment to investigate the remaining factorial design. The general ANOVA feature was used to construct models that followed a split-split plot design, with or without the underlying subplot factorial treatment combinations in subplots.

Results and Discussion

Previous losses in this field were assumed to have been due to phytophthora root rot. Dying trees taken to the laboratory in October, 2017 were used to isolate the disease-causing organism. *Phytophthora* was recovered from stem lesions typical of infection by this genus. The unusually thick oospore walls indicated that it was an undescribed species, and so Koch's postulates were tested to prove its pathogenicity and molecular genetics used to assist in its phylogenetic placement. The full description of the species, *Phytophthora abietivora* D.W. Li, N.P. Schultes, J. A. LaMondia, R. S. Cowles, were then published (Li et al., 2019).

The soil pH measurements taken in 2015 and 2016 demonstrated dramatic acidification within one year following sulfur incorporation. The incorporation of sulfur had the intended effect of reducing pH, as the pH values for the sulfur-incorporated plots vs. no-sulfur plots were 4.06 ± 0.09 (mean \pm se) and 5.95 ± 0.06 , respectively, as measured in August, 2015. Measurements of soil in 2016 were on average 0.4 pH units higher than in 2015, with values of 4.5 ± 0.09 and 6.2 ± 0.09 ; the cause for the shift in pH measurements from the previous year is not known. The pH was not reduced as much in the center of the field where the Paxton soil type occurred (average reduction of 1.6 pH units, $n = 13$), as in the Woodbridge soil type (reduction of 2.0 pH units, $n = 10$; $P < 0.05$, t-test of two populations, averaged over measurements from both years).

In the year of planting (2015), the application of sulfur significantly improved the color of transplants ($F_{(1,22)} = 18.9$; $P < 0.001$). Canaan fir had better color than Fraser fir ($F_{(1,45)} = 9.08$; $P < 0.01$); sulfur incorporation improved the health of both species to a similar degree (sulfur \times species interaction $F_{(1,44)} = 2.61$, $P = 0.11$). The insecticides imidacloprid and clothianidin applied in root dips did not enhance plant health ($F_{(2,447)} = 0.39$, $P = 0.67$). The only root dip factor providing statistically significant benefit was the use of potassium phosphite, which only benefitted the Fraser firs (phosphite main effect, $F_{(1,447)} = 3.51$, $P = 0.061$; species \times phosphite interaction, $F_{(1,447)} = 5.03$, $P < 0.05$) (Fig. 1). This phosphite \times species interaction for Canaan and Fraser firs is consistent with the response reported earlier (Cowles et al. 2012). Potassium phosphite is known to reduce *Phytophthora* infection by activating the systemic acquired resistance (SAR) biochemical pathways in plants (Machinandarena et al. 2012). The different responses of Fraser and Canaan firs to a phosphite root dip could be explained if the SAR pathway is inducible in Fraser fir, but constitutively active in Canaan fir. The influence of soil acidification on the probability of tree death was marginally statistically significant for Canaan fir. Plots with pH 4 vs. 6 soil experienced 3 vs. 11 trees dying out of a starting population of 161 trees per group ($P = 0.052$, Fisher's Exact test). For Fraser firs, this comparison was 21 vs. 27 trees dying ($P = 0.43$).

In the subsequent year (2016), soil acidification resulted in significantly less cumulative mortality in both Canaan fir, with 6.8 vs. 15% in pH 6 soil, and Fraser fir, with 20 vs.

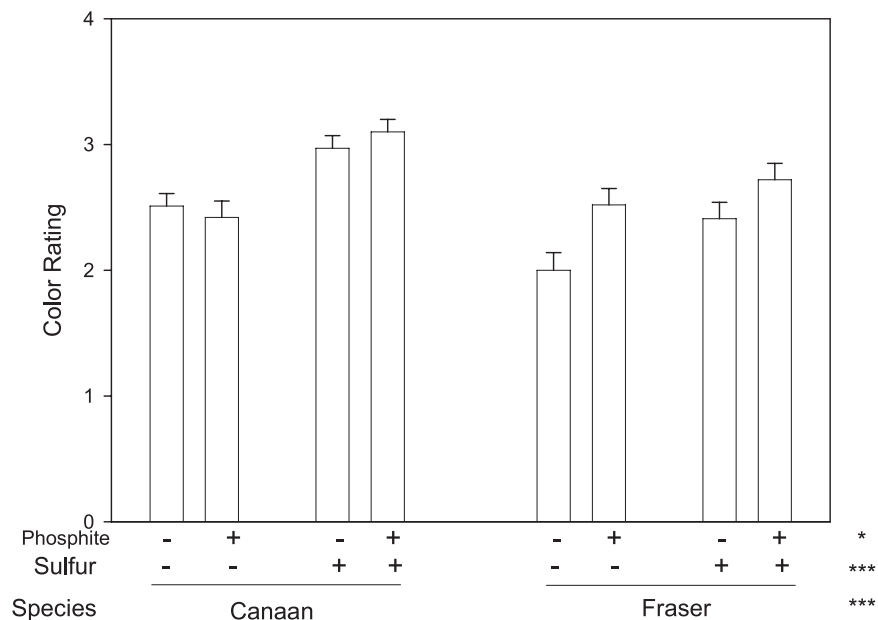


Fig. 1. Root health as measured by tree appearance in the first year of planting (2015). The minus and plus signs signify the absence or presence of a particular factor, respectively. The error bars are the standard error for the treatment combination means. These bars combine various insecticide combinations and represent 69 trees per bar. The statistical significance is given by asterisks: *, $P < 0.05$; ***, $P < 0.001$.

34% in pH 6 soil ($P < 0.05$ for both species, Fisher's Exact test). For mortality in 2016 alone, the sulfur effect was significant for Fraser fir (11 vs. 28 trees dying; $P = 0.003$) but not for Canaan fir (8 vs. 14 trees dying; $P = 0.18$, Fisher's Exact test). Tree color was better in Canaan fir than in Fraser fir ($F_{(1,44)} = 22.6$, $P < 0.001$). For surviving trees, the color of the trees was greatly improved over 2015 (the mean color rating was between 3.5 and 4.0 for all groups in 2016). The growth of leader terminals in the sulfur-amended plots averaged about 12.5 ± 0.5 cm for

both species, and about half that much (5.6 ± 0.3 cm) in no-sulfur plots, which were highly significantly different ($F_{(1,22)} = 37.5$, $P < 0.001$) (Fig. 2). The effects of root dips at the time of planting manifested themselves as contributing to differences in terminal growth in 2016. Of these root dip treatments, only the acibenzolar-S-methyl treatment was significantly different from the water check, and it significantly decreased the terminal growth ($F_{(3,428)} = 5.8$, $P < 0.001$) (Fig. 2). Further experiments would be necessary to determine whether the dose of acibenzolar-S-

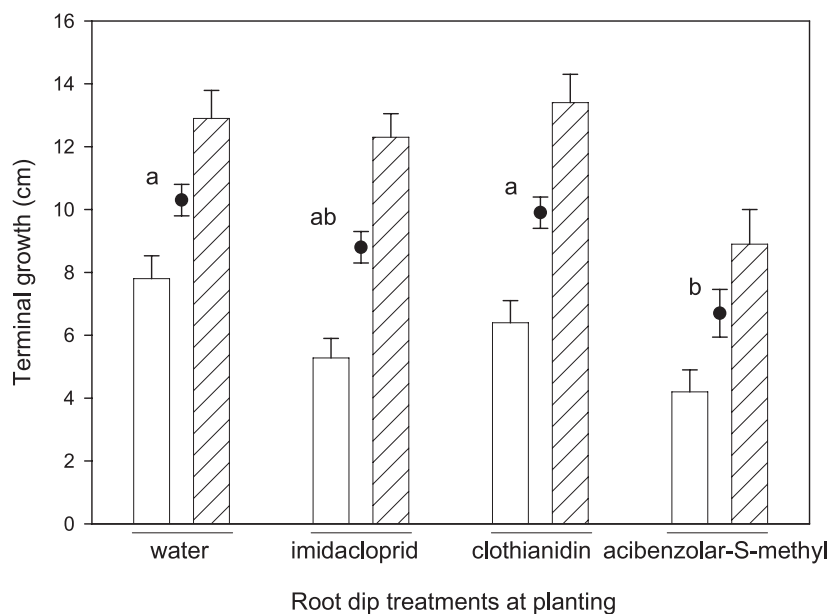


Fig. 2. The effects of root dips at the time of planting (in 2015) on terminal growth (mean \pm se) measured in 2016. There were no effects or interactions from the species or potassium phosphite component of the root dip in 2016, and so data are averaged across these factors. Hatched bars are for trees planted into acidified soil; open bars are data from non-acidified plots. The sulfur incorporation greatly influenced growth, and so hatched bars are significantly different from unhatched bars. The main effects (mean \pm se) of the root dip products are represented by the circles; means given the same letter do not significantly differ (Tukey's HSD test, $P = 0.05$).

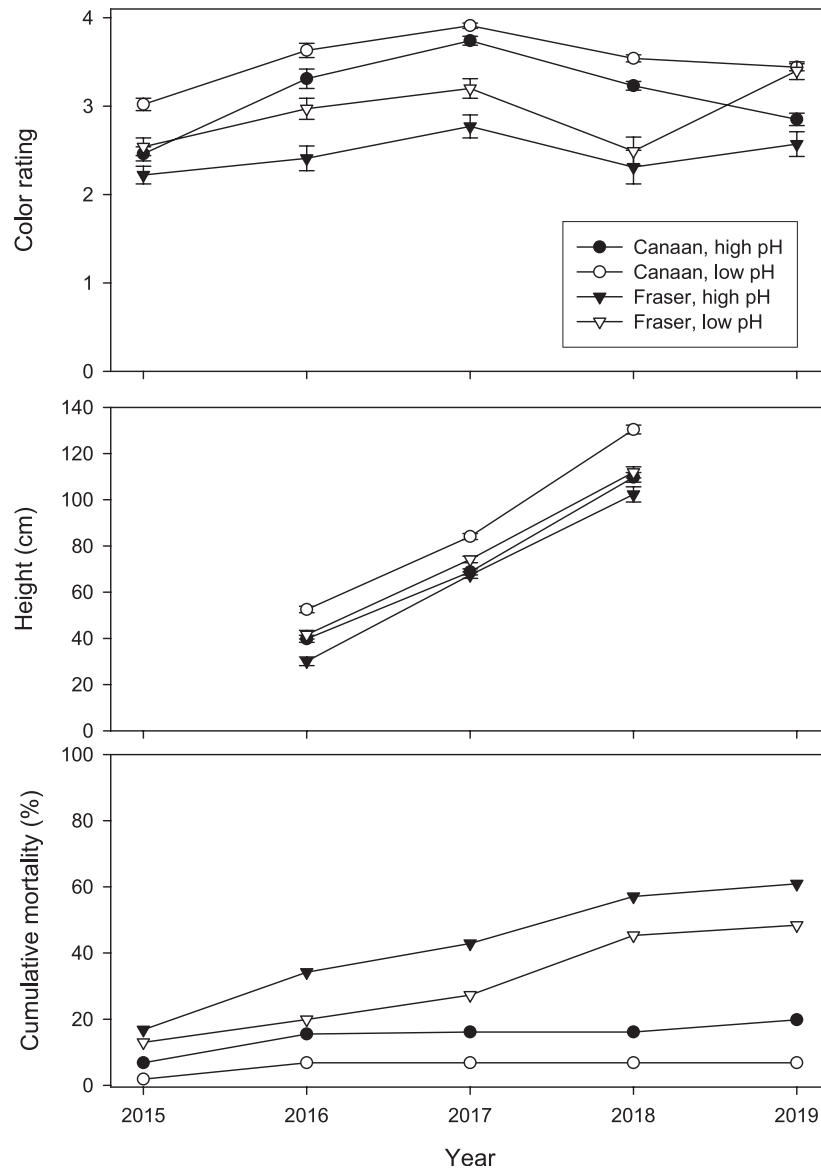


Fig. 3. Comparisons of color ratings, height, and cumulative mortality measured from Canaan and Fraser firs planted in acidified and non-acidified plots. Data have been averaged across root dip treatments conducted at the time of planting. The trees were planted as bare-root nursery stock in April, 2015. Data for color ratings and height are given as mean \pm se. Color ratings: 0, brown and dead; 1, almost dead (yellowed and wilting); 2, very yellow; 3, slight yellowing; 4, fully green.

methyl was phytotoxic, and whether lower doses in a root dip could be beneficial to root health.

The patterns for tree color, growth, and mortality are presented in Fig. 3 for the course of this experiment. For the third through fifth years after planting, the ranking of color qualities for the four treatment combination groups (Canaan vs. Fraser, and acidified vs. non-acidified soils) remained stable, with the exception of the last year of measurements. In 2019, Fraser firs with acidified soil improved in color, whereas color ratings for Canaan fir growing in higher pH soil decreased. This field had not received nitrogen fertilizer, and a decline in the color of the Canaan firs from 2017 to 2019 may reflect nitrogen deficiencies. The improvement in the color of the Fraser firs from 2018 to 2019 may reflect, to some degree, the loss of trees that had previously received poor color ratings, that subsequently died, and were no longer used in calculating

the color rating (a color rating of zero for a dead tree was only used once, and the individual was removed from further ratings). The growth and mortality rates for these four treatment combination groups remained nearly constant from 2016 through 2019, as indicated by the nearly linear results through this period (Fig. 3). The mortality rates from 2016 to 2019 did not significantly differ between acidified and non-acidified soil for Fraser fir ($P = 0.54$, Fisher's Exact test), and so the bulk of the benefit to this species occurred within the first two years of planting, when the mortality probabilities did differ ($P = 0.0056$, Fisher's Exact test). It is notable that there was no additional mortality of Canaan fir following 2016, the second year following planting.

Whereas all 60 Fraser firs in the 2010 previous planting had died within three years, only 64% of Fraser firs in the no-sulfur plots had died at the end of four years in this

experiment. This difference can probably be attributed to a reduction in precipitation. Rainfall through the first two years of the experiment planted in 2015 did not cause frequent, saturated soil conditions conducive to the development of phytophthora root rot to the same extent as in the previous planting in the same field. Rainfall records were assessed from weather stations nearby: T. F. Green Airport, Warwick, RI, 43 km from the field site for May, 2010 to April, 2016, and the East Killingly NEWA (Network for Environmental and Weather Applications, Cornell University) station, 9 km from the field site from May, 2016 to April, 2019. Monthly total precipitation and maximum daily precipitation were compared for the periods from May, 2010 to December 2013 for the earlier experiment, and May 2015 to April 2019 for the present experiment. Trees planted in 2010 experienced 13.9 ± 1.3 cm (mean \pm se) of monthly rainfall, with maximum daily precipitation events per month averaging 6.8 ± 0.7 cm, and the trees planted in 2015 experienced 10.5 ± 0.7 cm (mean \pm se) of monthly rainfall, with maximum daily precipitation events per month averaging 4.1 ± 0.4 cm. Comparison of months with rain events of over 5 cm in daily precipitation are especially striking, with 17 out of 24 months exceeding this rain intensity for the first, versus 3 out of 24 months in the second experiment. There were no precipitation events exceeding 5 cm through all of 2017.

Reduction of soil pH through the incorporation of sulfur clearly improved the health of both a susceptible species (Fraser fir) and a less susceptible species (Canaan fir). Richter et al. (2011) found no benefit to preventing phytophthora root rot in plots amended with sulfur prior to planting. However, in that work, the two field sites had initial pH values of 5.4 and 4.8, and so dropping the soil pH to 4 did not create as great a difference between plots as reported in this study. Furthermore, in the Connecticut trial, only modest protection was observed in Fraser fir (the only species planted in the North Carolina study), whereas a much greater degree of protection was provided to Canaan fir. The North Carolina study found that plant mortality of Fraser fir transplants did not co-vary with soil pH in additional research plots to which sulfur had not been added (Richter et al. 2011): once again, focusing on Fraser firs (for which there may be smaller benefits), the smaller variation in pH, and the smaller sample sizes of trees could obscure the potential for soil pH to influence phytophthora disease.

The effects of sulfur incorporation into soil on protecting the roots from *Phytophthora* infection will require further investigation into the possible mechanisms for the protective effects. Based on a strong inference paradigm, non-mutually exclusive hypotheses that need to be considered are: (1) *Phytophthora* and other root rot pathogens may be intolerant of low pH soils, in which hydrogen ions may be interfering with production of sporangia or causing mortality in zoospores (Kong, et al. 2009). (2) Elemental sulfur could act directly as a biocide, but this effect was not observed by Cooper and Williams (2004). (3) Conversion of elemental sulfur acidifies soil through its microbial oxidation to sulfuric acid. The H^+ produced from this reaction could liberate Ca^{++} into soil

solution from cation exchange sites, which then could interfere with liberation and movement of zoospores (Maloney et al. 2005). (4) A reduction in soil pH changes mineral availability. Richter et al. (2011) especially noted high tissue concentrations of manganese in Fraser firs planted into plots to which sulfur had been incorporated. Elevated levels of several minerals may protect against infection (Duffy 2007, Evans et al. 2007, Thompson and Huber 2007). (5) Lowered pH may favor microbiota antagonistic to *Phytophthora*. Evaluating community structure to identify antagonistic microorganisms and the conditions that specifically encourage them could be made difficult by the extraordinary complexity of soil microbiota and the presence of both generalist and specialist antagonists in the soil (McDonald et al. 2007). (6) Soil at higher pH may favor organisms that exacerbate phytophthora root rot, such as plant pathogenic nematodes that could open infection courts for disease, as is seen in several crops (Chen and Rich 1962, LaMondia 2003, Rowe et al. 1985).

Although the mechanisms for the beneficial effects are unknown, application of elemental sulfur to reduce the pH of soil appears to be a practical approach that, together with planting Canaan fir, a species less susceptible to this disease, can make production of trees economically viable at the studied site. How readily these results may be extended to other field sites with different soil conditions and other *Phytophthora* spp. remains to be seen. As with many pest management challenges, this study has demonstrated that combining multiple tactics provides superior results over planting the less susceptible species or incorporation of sulfur alone. Clearly, other practices already known to limit losses from phytophthora root rot, such as improving drainage, planting into raised beds, and possibly the use of organic mulches (Richter et al. 2011) could be combined with planting less susceptible species and soil acidification to further reduce losses from root rots in Christmas tree plantings.

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