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Harringtonia lauricola Spread in Sassafras Root Systems in the Absence of Its Vector, the Redbay Ambrosia Beetle (*Xyleborus glabratus*)

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ABSTRACT

Laurel wilt is a vascular disease caused by a non-native pathogen (*Harringtonia lauricola*) and an associated beetle vector (redbay ambrosia beetle; RAB; *Xyleborus glabratus*) affecting several members of the Lauraceae family in North America, including the ecologically and culturally important sassafras (*Sassafras albidum*). Since discovery of the vector in 2002 and the disease in 2004 near Savannah, GA, laurel wilt has spread widely throughout the eastern United States, causing widespread mortality to redbay, sassafras, and other lauraceous species. The objective of this study was to assess the spread of *H. lauricola* through sassafras roots in the absence of the beetle vector. Four spatially independent forest plots containing sassafras were identified in the Clemson Experimental Forest, and 1–2 mature trees in each stand were inoculated with *H. lauricola* in May of 2020. All sassafras in each plot were counted and categorized by size class and crown damage over a 4-year period. *Harringtonia lauricola* was confirmed in sassafras roots up to 3.6 m from inoculated trees 1-year post-inoculation in the absence of RAB. Sassafras stems closer to the inoculated tree experienced greater wilt symptoms and mortality. Despite significant mortality and wilt, nearly 50% of the sassafras stems across all sites were still living 4 years post-inoculation. These results demonstrate that laurel wilt can spread from one sassafras stem to others via underground movement of the pathogen through root suckers in natural stands, but that many trees can survive years after inoculation. Development of management strategies for laurel wilt in sassafras will need to account for this mechanism of disease spread.

1 | Introduction

Laurel wilt is a vascular wilt disease caused by a complex that includes a beetle vector (redbay ambrosia beetle, RAB; *Xyleborus glabratus* Eichhoff) and its symbiotic fungus (*Harringtonia lauricola*) (T.C. Harr., Fraedrich & Aghayeva) Z.W. de Beer & M. Procter (formerly *Raffaelea lauricola*) in the Ophiostomatales, both of which are not native to North America. The fungus acts as an aggressive pathogen in North American Lauraceae, a plant family which includes several economically and ecologically important species, some of which are hosts for a variety of specialist insects (Riggins et al. 2019). Laurel wilt was first discovered outside the Port of Savannah, GA, USA in 2004, when extensive mortality began occurring in redbay trees (*Tamala borbonia* L.), followed soon after by mortality in other lauraceous species such as the native and culturally important sassafras (*Sassafras albidum* (Nutt.) Nees), and the economically important avocado (*Persea americana* Mill.) (Fraedrich et al. 2008; Evans et al. 2010; Gramling 2010; Kendra et al. 2013). Species in Lauraceae

also serve as important food sources for wildlife species including deer, rabbits, birds and insects (Sullivan 1993; Van Deelen 1991), and laurel wilt has been implicated in the decline of these trees and their specialist herbivores, such as the Palamedes swallowtail [*Papilio palamedes* Drury (1773)], which feeds exclusively on Lauraceae (Lederhouse et al. 1992; Gezon et al. 2019; Riggins et al. 2019). Since its discovery, laurel wilt has spread north to Tennessee, Kentucky, and New York, west to Texas and Arkansas, and south through Florida (Olatinwo et al. 2021; New York Department of Environmental Conservation 2025). Depending on host species, symptoms of laurel wilt include discoloured or wilted leaves, stunted growth, and discoloured xylem (Fraedrich et al. 2008), with time to mortality ranging from a few months to multiple years.

The term 'vascular wilt' describes a damage caused by any microorganism, including *H. lauricola*, in which the vascular system of the plant (i.e., xylem) is disrupted through one or more mechanisms, and this group of diseases is considered one of the most destructive worldwide (Yadeta and Thomma 2013). The Ophiostomatales contains the causal agent of laurel wilt as well as several other well-known, and highly destructive, tree pathogens such as the causal agents of Dutch elm disease (*Ophiostoma* (= *Ceratocystis*) *ulmi*) (Strobel and Lanier 1981; Juzwik et al. 2011). Diseases like Dutch elm disease are spread aboveground by beetle vectors carrying spores to new stems, and belowground via pathogen movement through root suckers and grafts. Due to the potential for underground spread, severing root connections with a vibratory plough or trenching machine is part of the sanitation strategy for Dutch elm disease in high value stands of elms (Rebek and Olson 2017).

The widespread, patchy distribution of sassafras across the eastern half of North America, as well as its ecological importance as an early successional species, makes it of particular concern to ecologists (Randolph 2017). Sassafras holds significant cultural importance in many Indigenous tribes who use it in medicines, teas, and tinctures (Cummings 2012; Perlmutter et al. 2022). Sassafras also has the ability to reproduce vegetatively by root sprouts from stumps as well as from severed roots which remain shallow in the soil (Griggs et al. 1990; Sullivan 1993), potentially aiding in the spread of the laurel wilt pathogen by allowing infected roots to be easily picked up and transported to new areas by animals, people, and equipment.

Previously reported field observations strongly suggest that the laurel wilt pathogen can travel from one infected stem to another through interconnected roots (Mayfield et al. 2022). This has been evidenced by the recovery of the laurel wilt pathogen from small, wilted sassafras ramets that displayed no evidence of ambrosia beetle attack, located within several feet of larger sassafras trees with laurel wilt (Mayfield et al. 2022). Because the RAB was present in the area; however, transmission by beetles could not be conclusively ruled out. To address this knowledge gap regarding root transmission of laurel wilt, we conducted a field experiment to confirm the spread of *H. lauricola* from stem to stem through sassafras roots in stands where no RAB were present, and to quantify underground movement of the pathogen in the absence of RAB.

2 | Methods

2.1 | Site Selection

We identified four study plots within the Clemson Experimental Forest (CEF): a 7081-ha (17,498 acres) forest managed by Clemson University, which includes a variety of habitats across multiple counties in South Carolina including Oconee, Pickens, and Anderson Counties. Elevations in the CEF range between 198 and 304 m above sea level and the predominant soil type is Pacolet (fine, kaolinitic, thermic Typic Kanhapludults) (USDA Web Soil Survey 2022). The climate of the CEF is humid subtropical with monthly average rainfall ranging from 8.0 cm (May) to 12.5 cm (August) and average daily temperatures ranging from 5.9°C (January) to 26.3°C (July) (National Oceanic and Atmospheric Administration 2021). The CEF is split into the North Forest, which is considered part of the southeastern inner Piedmont region and contains mixed pine-hardwood forests including various tree species such as *Pinus, Carya* and *Quercus*, and shrub species such as *Oxydendrum* (sourwood) and *Callicarpa americana* (American beautyberry). The steeper slopes and well-drained soils of the North Forest are also ideal for sassafras growth, which is where we identified four independent (i.e., not connected via roots) sites with sassafras of varying densities. Each site contained at least two mature (> 2 m height) sassafras trees (also referred to as 'source trees' herein), which were connected to surrounding sassafras sprouts at each respective site and which served as inoculation trees. Due to the distance between source trees, and the lack of sassafras root sprouts between sites, we assumed that these mature, source trees were not, however, connected to each other.

2.2 | Inoculations

On 6 May 2020, we inoculated the largest dia. tree (i.e., source tree) at each site according to methods used by Fraedrich et al. (2008). Briefly, inoculation sites were created by using a 2.75 mm (7/64″) bit to drill 1-cm deep into each inoculation tree at each cardinal direction, resulting in four holes total, into the base of each source tree, sterilizing the drill bit between inoculations. Next, 100 µL of cultured *H. lauricola* spores (approx. 100,000 spores/hole) were aseptically pipetted into each hole and each hole was covered with parafilm and duct tape to maintain moisture and prevent secondary infection (Figure 1). At the time of inoculations, height (m) and diameter at breast height (DBH; ~1.37 m) were recorded of each source tree, as well as its crown condition (i.e., damage) rating on a scale of 0 (no damage symptoms) to 5 (completely dead or wilted). All live trees were identified and tallied up to 13.7 m away from inoculated source trees. At plots 1–3, every sassafras tree was categorized by height (i.e., Class A < 0.3 m ft., B ≥ 0.3 m > 1.5 m, C ≥ 1.5 m > 2.1 m, and D ≥ 2.1 m), the distance of each labelled tree from the inoculated source tree (Distance From Inoculated = DFI; m) was measured, and crown condition (scale described above) and azimuth were recorded. The fourth site had such a high density of sassafras that we were unable to label and measure every tree, so instead we counted the number of trees within each size class and estimated an overall crown condition for trees by size class.

FIGURE 1 | *Harringtonia lauricola* inoculation. (a) Stephen Fraedrich using a sterile pipette tip to insert a *H. lauricola* spore suspension into the drilled hole on a sassafras tree selected for inoculation. This was completed four times—once at each of the sassafras cluster sites. (b) After inoculation, each tree base was wrapped first with parafilm and then with duct tape to keep in the spore suspension and keep out secondary infection.

Following inoculations, the crown condition of every labelled tree at plots 1–3 was recorded, and the number of sassafras individuals per crown condition category was tallied for each size class at site 4 every 2 weeks until October 2020. Sites were also surveyed with the same methodology in April 2021 and May 2024, after leaf out. To ensure that no RAB were present at any of the sites, one 6-funnel Lindgren trap was placed at each site, baited with an α-copaene 50 redbay kairomone lure (Synergy Semiochemicals Corp., Burnaby, BC, Canada) that was replaced monthly, and traps were checked weekly from May to October 2020, to ensure that no RAB were present at any site. Trapping was not continued during the 2021 or 2024 surveys, but trees were examined for signs of beetle attack, and none were found at any site. Furthermore, laurel wilt had never been reported in the county (Pickens) or any adjacent counties at any time during the study period (Georgia Forestry Commission 2026).

To confirm inoculation success and measure *H. lauricola* movement, a 2.5 cm (1″) arch punch and hand shears were used to collect xylem tissue from inoculated trees and surrounding sassafras trees within each cluster, 2 weeks following inoculation, noting whether each tree was symptomatic or asymptomatic. To isolate fungi from vascular tissues, the methods detailed in Fraedrich et al. (2008) were followed. Briefly, each sample was surface sterilized by dipping into 95% ethyl alcohol followed by flaming. Each sample section was then cross-sectioned into ~1 mm thick discs and plated on cycloheximide-streptomycin malt agar (CSMA; 1% malt extract, 1.5% agar, with 200 ppm of cycloheximide and 100 ppm of streptomycin sulfate added after autoclaving). Plates were evaluated daily for up to 14 days. Once a colony growth resembling *H. lauricola* was present, a small amount of the colony was collected and transferred to a drop of water on a glass microscope slide, covered with a cover slip, and examined with a compound microscope (Laxco, Bothell, WA, USA) to morphologically confirm its identity as *H. lauricola*.

2.3 | Root Excavation

On April 26, 2021, 1 year after *H. lauricola* inoculations, root systems were excavated between the inoculated source tree and surrounding symptomatic seedlings at plots 1 and 2 using an air spade (Bartlett Trees Experts, Charlotte, NC), which allowed the removal of the soil surrounding roots while keeping them intact. Due to difficulty accessing all sites with the air spade equipment, roots were not excavated at Sites 3 or 4. After roots were exposed, whole root samples were cut and removed starting at the inoculated source tree root flare and following each root as far as possible, including connected trees if possible. After removing roots, samples were collected every 0.5 m along the length of each root, using the same methods as described above, to test for the presence of *H. lauricola*, noting the presence of any fungal staining as well as the DFI and root dia. (cm). The same sites were visited 4 years post-inoculation, and the number of dead and live sassafras trees was tallied in each category as described above.

2.4 | Statistical Analyses

To test for an effect of Site on sassafras mortality and crown damage, we compared the number of sassafras trees in each size class, as well as crown damage of all trees at each site, across all four sites at pre-inoculation, 1-year, and 4-year post-inoculation using a Chi square test of independence (χ^2). Because the number of sassafras was significantly different across sites at 4-year post-inoculation, we then compared the number of sassafras over time with Site and size class as our independent variables,

using a PERMANOVA with 999 iterations. Pairwise comparisons were then conducted for Site and size class using the RRPP package in R (Collyer and Adams 2018). Finally, using binomial regression, we compared pathogen presence and staining presence to root diameter (mm) and DFI (m). All statistics were completed in R v4.5.1 (R Core Team 2025).

3 | Results

Prior to inoculation, 454 sassafras trees were identified across the four sites in the CEF with most individuals ($n = 355$; 78%) occurring at Site 4. Most trees were classified as either size class A (i.e., < 0.3 m tall; $n = 199$; 44%) or B (i.e., 0.3–1.5 m tall; $n = 163$; 36%), and the distribution of size classes was not significantly different across the four Sites ($\chi^2 = 37.922$, df = 36, $p = 0.3818$). Crown condition of trees at pre-inoculation also did not significantly differ by Site ($\chi^2 = 75.005$, df = 60, p-value = 0.0918) as all trees had a condition rating of '3' or less (i.e., all were alive) and no wilt symptoms were present at any Site. *Harringtonia lauricola* was isolated from trees at all four sites, confirming that inoculations were successful, and no RAB, or any other ambrosia beetles, were collected at any of the four sites during the study period.

Abundance of sassafras did not significantly decrease 1-year post-inoculation at any site ($\chi^2 = 13.385$, df = 10, $p = 0.2029$) but did significantly decrease 4-year post-inoculation ($\chi^2 = 25.534$, df = 12, $p = 0.0125$), with a final count of 226 sassafras individuals across the four sites (a loss of 51% of all sassafras trees). Again, most individuals recorded ($n = 152$; 67%) were at Site 4. The only significant pairwise differences in mortality were between size classes D (i.e., largest) and A (i.e., smallest) ($z = 2.2513$, $p = 0.003$) and D:B ($z = 1.6135$, $p = 0.044$), with class D trees experiencing 100% mortality at all sites by 4-year post-inoculation.

Post-inoculation, crown condition of sassafras differed by size class ($F = 1.751$, df = 3, $p = 0.033$), Site ($F = 0.353$, df = 1, $p < 0.001$), and over time ($F = 1.670$, df = 4, $p = 0.028$). Pairwise comparisons showed that trees in size class B had the lowest crown condition rating (i.e., least symptomatic) while both smaller trees and larger, mature trees had higher ratings (i.e., most symptomatic). Trees at Site 3 had the highest crown condition rating while Site 1 had the lowest, and all sites were significantly different from each other with respect to tree mortality ($p < 0.0001$ for all pairwise Site comparisons) (Figure 3). DFI also significantly affected crown damage at 1-year post-inoculation (t-value = −2.43; df = 98; p-value = 0.01) with trees closest to the inoculated source tree having the highest crown damage rating (Figure 2).

Roots collected via air spading were examined for vascular staining and also plated to confirm the presence of *H. lauricola*. Both staining and *H. lauricola* were present in roots excavated from both sites (Sites 1 and 2). Not all roots that had vascular staining tested positive for *H. lauricola* and not all roots which tested positive for *H. lauricola* showed vascular staining. Out of the 45 root samples, staining was noted on 19 (42.2%) and *H. lauricola* was confirmed in 11 (24.4%). The largest root sample collected, which showed staining and had confirmed *H. lauricola*, was 51.2 mm dia. and was attached to the Site 2 inoculated source tree (ST2). The smallest root sample collected was 1.9 mm dia. and was a secondary branched root off of inoculated source tree at Site 1 (ST1), but contained neither vascular staining nor *H. lauricola*. The smallest root sample which contained *H. lauricola* was 7.5 mm in dia. and was a first branch off the main root of ST2, 1.5 m from the inoculated tree. Despite the observed trend of confirmed *H. lauricola* in larger roots, there was no significant relationship between root diameter and pathogen presence (z-value = 1.837; p-value = 0.066); however, there was a significant relationship between root diameter and the presence of staining (z-value = 2.613; p-value = 0.009). DFI had a significant effect on both pathogen presence (z-value = −2.787; p-value = 0.005) as well as root staining (z-value = −3.313; p-value = 0.0009) with both staining and pathogen presence being more likely the closer the root was to the inoculated tree. The furthest DFI with confirmed *H. lauricola* was 3.6 m from the inoculated ST2 and 2.0 m from the inoculated ST1.

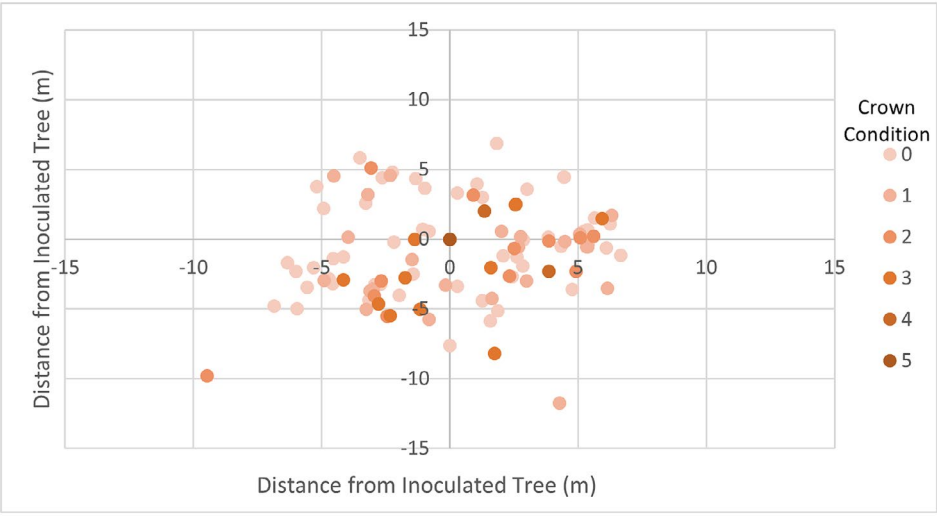

FIGURE 2 | Crown damage (0 = no damage to 5 = completely wilted) of all sassafras trees from Sites 1–3 and across all size classes at 1-year post-inoculation. Darker brown represents higher crown damage (i.e., higher damage or wilting). The center point of (0,0) indicates the inoculated tree at each site. Positive integers indicate cardinal directions of N and E while negative integers refer to cardinal directions of S and W.

FIGURE 3 | Average crown condition (0 = no wilt symptoms to 5 = dead or completely wilted) for each size class of trees (A < 0.3 m ft., B ≥ 0.3 m > 1.5 m, C ≥ 1.5 m > 2.1 m and D ≥ 2.1 m) across Sites 1–3 from 5 May 2020 to 7 October 2020.

4 | Discussion

Our study was the first to experimentally demonstrate the spread of *H. lauricola* through the roots of sassafras in the absence of its primary vector, RAB. We were able to confirm the spread of the pathogen through sassafras root systems at two independent sites, with the pathogen being collected up to 3.6 m from the inoculated source tree 1-year post-inoculation. Prior studies that have estimated rate of spread for *H. lauricola* did so on a macroscale and included aboveground spread by RAB (e.g., Cameron et al. 2015; Ward and Riggins 2023). Our study is the first to demonstrate the rate of spread of *H. lauricola* via roots up to 3.6 m in a single year in the absence of its beetle vector. Although studies have shown that various species of ambrosia beetles are capable of transmitting *H. lauricola* into live avocado trees in Florida orchards (Carrillo et al. 2014), no ambrosia beetles were collected at any site during the duration of the study, and we found no evidence of other ambrosia beetles on the trees themselves. When taken together, our results demonstrate that the laurel wilt pathogen is capable of killing sassafras trees several metres from the inoculation point, independent of ambrosia beetle vectors.

Understanding the belowground rate of pathogen spread is important for determining appropriate management of diseases like laurel wilt. Similar diseases, such as oak wilt (caused by *Bretziella fagacearum*), are also able to spread aboveground via beetle vectors and belowground through root systems and are able to kill whole stands of oaks, although mortality differs depending on the host species involved (Juzwik et al. 2011). In cases such as oak wilt, management is done by severing root systems using heavy equipment and blades that cut several feet below ground, preventing pathogen spread through root grafts (Koch et al. 2010). This kind of management could also be appropriate for laurel wilt but, considering the required time and expense involved, may only be feasible in commercial situations such as avocado management (Olatinwo et al. 2021).

Crown condition and mortality were significantly different across size classes, with class D trees (i.e., the largest, source, trees) experiencing 100% mortality at all four sites, although it's important to note that these source trees were directly inoculated. Trees in size class A (< 0.3 m tall) and size class B (0.3–1.5 m tall) also experienced high mortality, 56% and 58% respectively, but were also the most abundant prior to inoculation, thus they were still the most abundant size classes at 4-year post-inoculation (Figure 3). Even 4-year post-inoculation, every site had sassafras trees present, and young trees (i.e., size class C) experienced the least amount of decline (−20.5%) compared to all other size classes. While larger trees may be thought to have more rapid underground pathogen spread due to their larger roots containing more tissue available for infection, other root-spreading pathogens, like oak wilt, have shown 'sporadic and unpredictable' spread via root suckers and root grafts (Blaedow and Juzwik 2010). Importantly, root structure and chemical composition changes over time, and primary roots have been found to be less susceptible to pathogens compared to fine roots (Emmett et al. 2014), thus future studies should investigate structural and chemical differences of sassafras that may contribute to, or inhibit, the spread of laurel wilt.

Crown condition also varied by site, a stochastic variable that is influenced by many other variables, such as sassafras density, density of other plant species, soil types, elevation, slope, aspect, and more. In fact, Choudhury et al. (2021) found that disease incidence varied significantly with environmental variables such as relative humidity and wind speed, suggesting that site characteristics may have played an important role in the movement of the pathogen in our sites. It is unknown which site variables specifically impacted the difference in crown condition between the first and last measurement and more research is needed to better understand the impact of site characteristics on *H. lauricola* movement in the absence of RAB.

Crown condition, as well as confirmed pathogen presence, was also significantly affected by the distance of the sample from the inoculated source tree (DFI). Sassafras of all size classes experienced more wilting the closer they were to the inoculated source tree (Figure 2). Trees that were 9 m or more from the inoculated tree actually improved after initial symptoms, and many recovered to a crown condition rating of 0 (i.e., no wilt symptoms) by the end of the study. Similarly, confirmed *H. lauricola* plates were more likely to occur closer to inoculated source trees, as was vascular staining. Pathogen presence and staining were also more likely in larger diameter roots, although this could be a byproduct of the short distance from the source trees, which were all larger mature trees.

Laurel wilt is a serious disease of Lauraceae that includes many ecologically, economically, and culturally significant species. Our study is the first to document the movement of the laurel wilt pathogen, *H. lauricola*, from stem to stem in the absence of its associated beetle vector (RAB). We were able to confirm *H. lauricola* more than 3.5 m from inoculated source trees in a single year. Efforts to manage laurel wilt in clusters of sassafras trees, where individual stems are likely to be connected belowground, should consider this potential mode of pathogen transmission. Research on the efficacy of techniques that prevent belowground spread of laurel wilt (such as trenching to sever root connections) could help expand the number of management options for this disease.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data will be made available upon request.

Peer Review

For transparency, the peer review documents associated with this article are available at https://doi.org/10.1111/efp.70095.

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