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Relative In Vitro Wood Decay Resistance of Sapwood from Landscape Trees of Southern Temperate Regions

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Abstract. **The development of wood decay caused by 12 major root-rot and trunk-rot fungi was investigated in vitro with sapwood extracted from nine ornamental and landscape hardwood and conifer species native to southern temperate regions of North America, Europe, and the lower Mississippi Delta. Wood decay rates based on dry weight loss for 108 host tree–wood decay fungi combinations were compared at 21 °C over 1-year and 2-year incubation periods in the absence of tree-resistance mechanisms. Strains of *Armillaria mellea, Ganoderma lucidum*, and *Heterobasidion annosum* exhibited the highest decay potential in most tree species tested. The order of fungi causing the greatest decay varied over time as a result of temporal changes in decay-rate curves. Relative wood durability or resistance to decay generally was greater in gymnosperm than in angiosperm wood types. *Quercus nuttallii*, *Fraxinus pennsylvanica*, and *Quercus lyrata* sustained the highest levels of decay by all fungi. Northern white cedar (*Thuja occidentalis*) sapwood was most resistant to decay by all rot-fungi tested, sustaining only limited weight loss after 1 and 2 years of decay, although sapwood of *Pinus taeda*, *Liquidambar styraciflua*, and *Platanus occidentalis* had relatively low levels of decay after 2 years. These results in combination with data from portable decay-detection devices provide useful information for the management of tree breakages or failures resulting from wood decay fungi in hazardous landscape trees. Some potential landscaping applications for tree evaluations, risk assessments, and selections for tree-replacement plantings are discussed.**

Landscape trees are becoming increasingly important in urban and suburban environments as a result of the values and benefits they provide by virtue of their aesthetic nature, ability to purify ambient air, use in providing shade, and service as effective wind breaks (Dwyer et al., 1992; McPherson and Biedenbender, 1991; McPherson and Rowntree, 1993). For these reasons, urban forestry is rapidly gaining in importance relative to commercial forestry as urban trees continue to appreciate in value. A single large urban tree can add tens of thousands of dollars to urban and residential property values in terms of aesthetic (social), environmental, utility, and monetary benefits (Nowak, 1993; Nowak et al., 2002; Scott and Betters, 2000). Thus, tree mortality resulting from diseases, wood decay, and insects causes significant economic losses in many different ways. Despite the importance and valuable roles that landscape trees play in the enhancement of our quality of life, urban trees are often subjected to considerable abuse and must endure adverse and inadequate growing conditions that preclude normal development and increase susceptibility to further damage by biotic and abiotic factors. Many anthropogenic activities such as wounding, soil compaction, tree planting in adverse locations, and water pollution cause serious damage to roots and the lower trunk; retard tree growth; and open up infection courts for pathogen entry. Damage to tree roots may reduce structural stability and result in an inadequate nutrient supply to sustain a healthy crown (Jokela et al., 1996).

Many adverse conditions present in the urban setting reduce tree vigor and subject trees to stresses that predispose them to attack by various pathogens, particularly wood-rotting fungi that decay living sapwood. Common root-rot fungal pathogens in the southern United States such as *Armillaria* and *Ganoderma* species are often particularly damaging in cities because they compromise the stability of urban trees resulting in potentially dangerous consequences when trees fail, i.e., when limb or trunk breakages occur (Guglielmo et al., 2007). Devastating injuries to people and damage to property may result from falling trees and limbs. Wood decay is the most crucial risk factor that increases the probability that urban trees will fail, but environmental stresses, competition, anthropogenic disturbance, and the activities of other organisms are contributing factors considered in risk assessments (Ossenbruggen et al., 1986). Nevertheless, wood decay fungi are the primary and most common cause of decreases in mechanical strength of wood in standing trees (Råberg et al., 2005).

Studies of wood decay development in forest and urban trees have involved many different aspects of decay processes, including detailed descriptions of effects on wood microscopic anatomy (Barnett and Bonham, 2004; Schwarze and Fink, 1998), different decay types (Greig, 1989; Luna et al., 2004; Otjen and Blanchette, 1985; Schwarze et al., 2000, 2003), possible mechanisms of infection (Despot, 1998; Schwarze and Baum, 2000; Sturrock et al., 2007), and the role of enzymes involved in degradation (Cullen and Kersten, 2004; Eichlerová et al., 2000; Hatakka, 1994, 2001; Tuor et al., 1995). Investigations of host–pathogen interactions have focused on the capability of wood decay fungi to overcome host-tree defenses (Schwarze and Baum, 2000; Schwarze and Fink, 1997) and the ability of trees to form chemical and structural barriers to restrict wood colonization by various decay fungi (Shigo and Shortle, 1979; Shortle, 1979). The most comprehensive in vitro wood decay study on decay mechanisms was done by Worral et al. (1997), who reported mean weight losses for birch (*Betula alleghaniensis* Britton) and loblolly pine (*Pinus taeda* L.) artificially inoculated with 79 wood decay fungi. Nevertheless, there is a dearth of comprehensive studies on the relative decay potential of different wood decay fungi on diverse urban tree hosts, particularly the most commonly destructive pathogenic fungi on ornamental and landscape tree species, and the relative decay resistance of wood from these species.

The objectives of this study were to investigate the in vitro development of decay caused by 12 major rot-rot and trunk-rot fungi in sapwood extracted from nine ornamental and landscape tree species native to southern temperate forests in the lower Mississippi alluvial valley (Mississippi Delta region), to compare the relative wood decay potential and host specificity of damage associated with these wood-rotting fungi, and to determine the relative in vitro susceptibility or resistance of sapwood from each tree species to decay over 1-year and 2-year incubation periods in the absence of active tree-resistance mechanisms. This information is prerequisite for the development of improved management guidelines for city foresters, urban arborists, and other tree-care specialists to facilitate urban forestry planning decisions and strategies. Urban tree management activities involve tree plantings,

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tree maintenance, and occasional tree removals to minimize property damage and personal injuries attributed to landscape tree failures, including limb breaks, stem breaks, and windthrow associated with root breaks.

Materials and Methods

Collection and preparation of sapwood blocks. Nine species were selected as representative ornamental and landscape trees considered most common in urban and natural forest stands of temperate forests and the lower Mississippi Delta region: *Fraxinus pennsylvanica* Marsh., *Liquidambar styraciflua* L., *Platanus occidentalis* L., *Populus deltoides* Bartr. ex Marsh., *Quercus lyrata* Walt., *Quercus nuttallii* Palmer, *Pinus taeda* L., *Taxodium distichum* (L.) Rich., and *Thuja occidentalis* L. One young healthy tree, ≈15 to 25 cm diameter at breast height of each species, was cut down and 1- to 2-m trunk sections from each stem were placed in a drying room for 24 h at 60 °C. Each trunk section was peeled to remove the bark and cut tangentially into 1.5-cm-thick sapwood sections that were subsequently cut into small wood blocks (approximate dimensions 1.5 × 1.5 × 8.0 cm). A minimum of 150 wood blocks were prepared from boards of each tree species, each labeled on the end with wood-type codes using a waterproof felt-tipped marker. The wood blocks were dried in an oven for 15 h at 105 °C and weighed to within 0.01 g by means of a Sartorius balance (Sartorius Corp., Edgewood, NY) to record initial dry weight. All wood blocks were placed on aluminum foil sheets within shallow metal trays and sterilized by autoclaving for 40 min at 121 °C and 15 psi and rehydrated to fiber saturation by soaking in sterile distilled water for 10 min immediately before inoculations.

Collection and culture of wood decay fungi. Twelve species of wood decay fungi, considered major root-rot and trunk-rot fungi that attack native trees in temperate regions of North America and Europe, were selected as the most common pathogenic species that contribute most frequently to the decline and failure of landscape trees in urban and suburban areas. Pathogenic strains of *Armillaria gallica* Marxmüller & Romagnesi, *Armillaria mellea* (Vahl) P. Kumm., *Armillaria ostoyae* (Romagn.) Herink, *Armillaria tabescens* (Scop.) Emel., *Daedalea quercina* (L.) Pers., *Fomitopsis pinicola* (Swartz) P. Karst., *Ganoderma lucidum* (Curtis) P. Karst., *Heterobasidion annosum* (Fr.) Bref., *Inonotus dryadeus* (Pers.) Murrill, *Laetiporus sulphureus* (Bull.) Murrill., *Phellinus pini* (Brot.) Bondartsev & Singer, and *Stereum hirsutum* (Willd.) S. F. Gray were selected for use in this study. All strains tested were in the dikaryotic somatic phase and no test comparisons were done with monokaryons. Most strains were obtained from the fungal culture collection of Dr. A. Dan Wilson (USDA, Forest Service, Southern Hardwoods Laboratory, Stoneville, MS). Other strains were obtained from the American Type Culture Collection in Manassas, VA. Three strains were used per fungal species and two replications for each treatment (wood type–fungal strain) combination.

The isolates were previously preserved in sterile distilled water as mycelial plugs in 1.8-mL cryotubes (Nunc A/S, Roskilde, Denmark) stored at 5 °C using methods described by Burdsall and Dorworth (1994). Two mycelial plugs were transferred from cryotubes to sterile petri plates on 4.5% w/v malt agar (Sigma M9802, Sigma-Aldrich Corp., St. Louis, MO) substrate (MA). The substrate was previously sterilized for 40 min in an autoclave at 121 °C and 15 psi and poured into 9.0-cm diameter petri plates. All physical transfers of inoculum were done using aseptic techniques on a sterile surface within a laminar flow hood (Nuaire Laminar Flow Products, Plymouth, MN). To assure the purity of cultures and avoid contamination, all isolates were transferred twice onto sterile petri dishes on 4.5% w/v MA substrates. After 1 to 3 weeks, cultures were transferred to the same growth medium within the decay culture tubes.

Mycelia used for inoculation of wood blocks were prepared in liquid broth cultures. Approximately eight mycelial plugs from each petri dish culture were transferred into 250-mL Pyrex sterile glass flasks (Fisher Scientific Co., Pittsburgh, PA) containing 150 mL of 3.0% w/v sterile malt extract (Merck KGaA, Darmstadt, Germany) broth medium (MEB). The flasks were plugged with sterile cotton and gently shaken to distribute the plugs throughout the broth. After 3 weeks, a large mass of mycelium was formed in the flasks. A handheld stainless steel Polytron Kinematica tissue macerator (Brinkmann Instruments, Mississauga, ON, Canada), previously sterilized with 10% Clorox® and 95% ethanol and rinsed with sterile distilled water, was used to shred the mycelial masses into very small fragments within the liquid broth culture to produce an inoculum suspension. The inoculum concentration within the suspension, measured in cfu/mL, was determined using a Spencer improved Neubauer hemocytometer (American Optical Corp., Buffalo, NY) immediately after maceration. The inoculum suspension was vortexed thoroughly just before inoculations because the hyphal fragments tended to float to the surface of the suspension after vortexing.

Decay culture preparation. Approximately 25 mL of 4.5% w/v MA medium was poured into Duran 25 × 200-mm glass decay culture tubes (Kimble Glass Inc., Vineland, NJ), plugged with cotton, sterilized, and placed in a 20° incline position to solidify. The next day, a single mycelium plug grown for 1 to 3 weeks in petri dishes, as previously described, was transferred to each culture tube. Decay culture tubes were inoculated separately with one of three strains of each of the 12 wood decay fungal species for each wood type. Two replicate culture tubes were prepared for each treatment combination. After 1 to 2 weeks, the fungal mycelium had covered the entire surface of the substrate, and the tubes were filled with inoculated wood blocks. Wood samples of each species were sterilized by autoclaving before being inoculated. The sterile wood blocks were dipped into an inoculum suspension (3.7 to 4.3 × 10^6 cfu/mL) of 3.0% MEB with the appropriate wood decay fungus to inoculate the wood blocks and aseptically transferred with large sterile forceps to a glass decay culture tube. Two wood block samples were placed into each tube. Uninoculated wood blocks were prepared as controls for each wood type. All decay tubes were firmly covered with plastic caps, sealed with Parafilm® (Pechiney Plastic Packaging Company, Chicago, IL), placed in plastic test tube racks, and incubated in the dark within a large Model 815 incubator (Precision Scientific Inc., Winchester, VA) at 21 °C for 1-year and 2-year incubation periods.

Data collection. After 1 year of incubation, one wood block from each tube was gently pulled out, rinsed with tap water, brushed to remove every visible trace of fungal mycelium, and blotted onto tissue paper. The samples were dried for 15 h in a 105 °C oven and weighed by means of the laboratory balance to record final dry weight. The remaining wood block in each tube was given additional moisture, ≈5 mL of sterile distilled water to the bottom of the culture tube, and put back into the incubator for an additional year of incubation at 21 °C. The second wood block was removed at the end of the second year of incubation and subsequently dried and weighed using the same procedure describe thus far.

Data analysis. The quantification of wood decay for each fungus–wood species combination was determined by loss in dry weight and statistically compared with control wood blocks that had not been subject to decay. Mean values and SEs were calculated, and analysis of variance (ANOVA) was performed to test for treatment effects on mean dry weight loss after 1- and 2- year incubation periods. When ANOVAs indicated statistically significant treatments effects on dry weight, differences between means were determined using Fisher's protected least significant difference tests at the $\alpha \leq 0.01$ level of significance. All analyses were performed using SigmaStat statistical software Version 15.0 (SPSS Inc., Chicago, IL).

Results

The ability of 12 major root-rot and trunk-rot fungi to decay sapwood of nine landscape tree species, common to the lower Mississippi Valley and certain southern temperate forests of North America and Europe, was highly variable depending on the fungus–host wood combination and the duration of decay (Tables 1, 2, and 3). Some wood decay fungi caused the highest levels of decay with the majority of wood types tested, regardless of decay duration, whereas the effects of other decay fungi were much more dependent on decay duration. The trunk-rot fungi tested in this study tended to cause higher weight loss

Table 1. Mean dry weight loss % ± SE resulting from decay of sapwood from nine landscape tree species after in vitro inoculations with 12 major root-rot and trunk-rot fungi and incubation for 1 year at 21 °C.

	Dry wt loss[z]									
Species[y]	*P. deltoides*	*F. pennsylvanica*	*L. styraciflua*	*Q. nuttallii*	*Q. lyrata*	*P. occidentalis*	*T. occidentalis*	*P. taeda*	*T. distichum*	Total
A. gallica	3.0 ± 0.5 abc	3.6 ± 0.2 abcd	0.0 ± 0.0 d	3.5 ± 0.3 e	4.6 ± 0.8 bc	2.4 ± 0.4 ab	0.0 ± 0.0 a	1.3 ± 0.4 abc	1.1 ± 0.5 cd	2.2 ± 0.3 de
A. mellea	2.4 ± 0.2 bcd	4.3 ± 0.5 abc	2.2 ± 0.4 abc	7.3 ± 1.1 ab	5.4 ± 0.5 abc	2.9 ± 0.9 ab	0.3 ± 0.2 a	0.9 ± 0.3 bc	3.1 ± 0.9 abc	3.2 ± 0.3 bc
A. ostoyae	2.4 ± 0.3 bcd	1.9 ± 0.3 de	0.8 ± 0.3 cd	6.9 ± 0.6 abc	2.9 ± 0.1 e	2.6 ± 0.3 ab	0.0 ± 0.0 a	0.8 ± 0.4 bc	3.0 ± 0.7 abc	2.4 ± 0.4 cde
A. tabescens	2.1 ± 0.3 cd	2.9 ± 0.6 cd	1.3 ± 0.3 bcd	4.0 ± 0.6 de	3.0 ± 0.5 de	1.0 ± 0.7 bc	0.1 ± 0.1 a	0.6 ± 0.4 ab	1.4 ± 0.7 bc	1.8 ± 0.3 e
D. quercina	1.8 ± 0.5 cd	5.1 ± 1.0 ab	1.6 ± 0.3 bcd	4.9 ± 0.7 bcde	6.4 ± 0.8 a	2.6 ± 1.3 ab	0.1 ± 0.1 a	4.0 ± 1.6 ab	4.1 ± 1.6 a	3.4 ± 0.5 abc
F. pinicola	2.6 ± 0.2 bcd	5.7 ± 0.4 a	1.6 ± 1.2 bcd	4.9 ± 1.2 bcde	5.7 ± 0.5 abc	2.6 ± 0.9 ab	0.1 ± 0.1 a	4.3 ± 2.3 a	2.2 ± 0.6 abc	3.3 ± 0.5 abc
G. lucidum	5.2 ± 1.6 a	5.4 ± 1.0 a	4.0 ± 1.2 a	6.0 ± 0.7 abcd	4.6 ± 0.4 bcd	3.6 ± 0.9 a	2.0 ± 1.1 a	3.5 ± 1.5 ab	3.1 ± 0.8 abc	4.1 ± 0.4 a
H. annosum	2.6 ± 0.6 abc	4.5 ± 0.3 abc	4.1 ± 0.6 a	5.3 ± 0.3 bcde	4.1 ± 0.6 cde	2.2 ± 0.5 ab	1.3 ± 0.9 a	2.6 ± 1.0 abc	4.0 ± 0.6 a	3.4 ± 0.3 abc
I. dryadeus	1.6 ± 0.5 cd	3.2 ± 0.5 bcd	1.6 ± 0.3 bc	5.7 ± 0.7 abcde	4.3 ± 0.5 bcde	2.2 ± 0.6 ab	0.0 ± 0.0 a	0.0 ± 0.0 c	2.3 ± 0.8 abc	2.3 ± 0.4 cde
L. sulphureus	2.4 ± 0.7 bcd	3.4 ± 1.3 bcd	2.0 ± 0.4 a	4.2 ± 1.3 cde	5.3 ± 0.5 abc	3.8 ± 0.4 a	0.0 ± 0.0 a	1.6 ± 0.3 abc	3.6 ± 0.5 ab	2.9 ± 0.4 bcd
P. pini	3.1 ± 0.3 abc	3.3 ± 0.9 bcd	2.1 ± 0.4 abcd	6.5 ± 1.0 abcd	6.0 ± 0.3 ab	0.9 ± 0.4 bc	0.1 ± 0.1 a	1.5 ± 0.2 abc	3.2 ± 0.8 abc	3.0 ± 0.4 bcd
S. hirsutum	5.1 ± 2.0 ab	4.1 ± 0.5 abcd	3.2 ± 1.2 ab	8.3 ± 1.8 a	5.4 ± 1.2 abc	2.8 ± 0.4 ab	0.7 ± 0.4 a	1.8 ± 0.2 abc	3.8 ± 0.4 ab	3.9 ± 0.5 ab
Control[x]	0.0 ± 0.0 d	0.0 ± 0.0 e	0.0 ± 0.0 d	0.0 ± 0.0 f	0.0 ± 0.0 f	0.0 ± 0.0 c	0.0 ± 0.0 a	0.0 ± 0.0 c	0.0 ± 0.0 d	0.0 ± 0.0 f
F	2.772	6.292	3.681	6.834	12.903	2.595	1.243	2.135	2.848	11.661
P	0.009	<0.001	0.001	<0.001	<0.001	0.014	0.298	0.040	<0.001	<0.001

[z]Means within columns followed by the same letter are not significantly different according to Fisher's protected least significant difference tests ($P < 0.01$).
[y]Two sapwood blocks (1.5 × 1.5 × 8.0 cm) of each tree species were placed into separate glass vials per fungal strain and a minimum of two to three fungal strains and three replications per strain were prepared for each treatment.
[x]Control wood blocks received identical treatment except that no inoculum of a wood decay fungus was applied before incubations.

Table 2. Mean dry weight loss % ± SE resulting from decay of sapwood from nine landscape tree species after in vitro inoculations with twelve major root-rot and trunk-rot fungi and incubation for 2 years at 21 °C.

	Dry wt loss[z]									
Species[y]	*P. deltoides*	*F. pennsylvanica*	*L. styraciflua*	*Q. nuttallii*	*Q. lyrata*	*P. occidentalis*	*T. occidentalis*	*P. taeda*	*T. distichum*	Total
A. mellea	11.1 ± 3.2 a	12.2 ± 2.9 a	5.9 ± 1.9 abcd	14.1 ± 3.3 a	11.6 ± 1.5 a	4.9 ± 1.0 ab	2.5 ± 1.6 a	5.2 ± 1.7 abcd	18.0 ± 3.0 a	9.5 ± 1.0 a
A. gallica	3.2 ± 0.8 bcd	4.8 ± 0.3 bcd	1.3 ± 0.1 de	6.1 ± 0.4 b	7.9 ± 0.2 bcde	3.2 ± 0.4 bc	0.0 ± 0.0 a	1.9 ± 0.6 cde	3.6 ± 1.5 cd	3.6 ± 0.5 ef
A. ostoyae	2.4 ± 0.7 cd	4.8 ± 0.7 bcd	1.8 ± 0.1 cde	7.2 ± 0.7 b	4.4 ± 0.4 e	4.8 ± 1.4 ab	0.9 ± 0.6 a	1.0 ± 0.5 de	4.1 ± 0.9 cd	3.5 ± 0.4 ef
A. tabescens	2.2 ± 0.3 cd	5.1 ± 0.6 bcd	2.8 ± 0.2 bcde	5.7 ± 0.3 bc	4.6 ± 1.0 de	3.7 ± 0.6 ab	0.6 ± 0.6 a	1.2 ± 0.1 de	3.6 ± 0.4 cd	3.3 ± 0.4 f
D. quercina	7.7 ± 1.8 abc	6.5 ± 0.4 bc	6.6 ± 1.5 abcd	6.1 ± 0.5 b	6.4 ± 1.9 de	7.2 ± 2.5 ab	1.5 ± 1.0 a	6.9 ± 2.9 ab	12.0 ± 3.0 b	6.8 ± 0.7 bcd
F. pinicola	5.1 ± 1.0 bcd	8.4 ± 1.4 abc	2.4 ± 0.6 bcde	5.2 ± 0.6 bc	5.6 ± 1.2 de	5.4 ± 0.9 ab	0.4 ± 0.2 a	5.5 ± 1.2 abcd	5.2 ± 0.3 cd	4.8 ± 0.5 def
G. lucidum	11.0 ± 2.2 a	7.5 ± 1.2 abc	10.0 ± 1.9 a	10.8 ± 1.4 ab	6.5 ± 0.5 de	6.7 ± 1.4 ab	4.5 ± 1.9 a	6.0 ± 1.5 abc	6.1 ± 1.6 bc	7.7 ± 0.6 b
H. annosum	9.5 ± 0.9 ab	9.4 ± 1.0 abc	10.5 ± 1.2 a	11.7 ± 1.3 ab	10.1 ± 1.5 abc	3.8 ± 1.1 ab	6.2 ± 2.9 a	3.6 ± 0.6 bcde	8.6 ± 2.6 bc	8.2 ± 0.7 ab
I. dryadeus	7.3 ± 2.1 abc	10.9 ± 2.4 ab	7.6 ± 3.0 ab	15.6 ± 3.8 a	6.0 ± 0.5 de	7.5 ± 0.7 a	0.0 ± 0.0 a	8.9 ± 1.6 a	2.6 ± 1.8 cd	7.4 ± 1.0 bc
L. sulphureus	3.8 ± 0.7 bcd	7.0 ± 0.4 abc	7.2 ± 2.8 abc	11.5 ± 1.5 ab	7.2 ± 0.9 cde	4.2 ± 1.4 ab	0.0 ± 0.0 a	6.0 ± 2.4 abc	7.0 ± 3.1 bc	6.0 ± 0.8 bcd
P. pini	4.0 ± 0.3 bcd	4.2 ± 0.3 cd	3.6 ± 0.6 bcde	12.1 ± 3.0 ab	8.2 ± 1.8 bcd	4.8 ± 2.3 ab	2.6 ± 0.5 a	5.0 ± 1.5 abcd	5.7 ± 0.2 bc	5.6 ± 0.7 cde
S. hirsutum	7.2 ± 1.1 abc	11.9 ± 4.7 ab	7.0 ± 3.0 abc	11.7 ± 3.3 ab	11.0 ± 1.7 ab	5.6 ± 1.2 ab	1.6 ± 1.1 a	3.7 ± 1.0 bcde	4.6 ± 0.6 cd	7.1 ± 0.9 bc
Control[x]	0.0 ± 0.0 d	0.0 ± 0.0 d	0.0 ± 0.0 e	0.0 ± 0.0 c	0.0 ± 0.0 f	0.0 ± 0.0 c	0.0 ± 0.0 a	0.0 ± 0.0 e	0.0 ± 0.0 d	0.0 ± 0.0 g
F	4.034	4.038	4.110	4.783	9.178	3.033	1.931	3.139	6.936	17.343
P	<0.001	<0.001	<0.001	<0.001	<0.001	0.005	0.064	0.004	<0.001	<0.001

[z]Means within columns followed by the same letter are not significantly different according to Fisher's protected least significant difference tests ($P < 0.01$).
[y]Two sapwood blocks (1.5 × 1.5 × 8.0 cm) of each tree species were placed into separate glass vials per fungal strain and a minimum of two to three fungal strains and three replications per strain were prepared for each treatment.
[x]Control wood blocks received identical treatment except that no inoculum of a wood decay fungus was applied before incubations.

Table 3. Mean dry weight loss % ± SE resulting from decay of sapwood from nine landscape hardwood and conifer species after in vitro inoculations with 12 major root-rot and trunk-rot fungi after incubation for 1 and 2 years at 21 °C.

	Dry wt loss[z]			
	Yr 1		Yr 2	
Species[y]	Hardwoods	Conifers	Hardwoods	Conifers
A. gallica	2.8 ± 0.4 cd	0.8 ± 0.3 cd	4.4 ± 0.5 cd	1.8 ± 0.7 cd
A. mellea	4.1 ± 0.4 ab	1.4 ± 0.4 bc	10.0 ± 1.1 a	8.6 ± 2.0 a
A. ostoyae	2.9 ± 0.5 cd	1.3 ± 0.5 bcd	4.2 ± 0.5 d	2.0 ± 0.6 cd
A. tabescens	2.4 ± 0.3 d	0.7 ± 0.3 c	4.0 ± 0.4 d	1.8 ± 0.5 cd
D. quercina	3.8 ± 0.5 abc	2.7 ± 0.9 ab	6.8 ± 0.6 bc	6.8 ± 2.0 a
F. pinicola	3.8 ± 0.5 abc	2.2 ± 0.9 abc	5.4 ± 0.5 cd	3.7 ± 0.9 bc
G. lucidum	4.8 ± 0.4 a	2.8 ± 0.7 a	8.8 ± 0.7 ab	5.5 ± 0.9 b
H. annosum	3.8 ± 0.3 abc	2.6 ± 0.6 ab	9.2 ± 0.7 ab	6.1 ± 1.4 ab
I. dryadeus	3.1 ± 0.4 bcd	0.8 ± 0.5 c	9.1 ± 1.1 ab	3.8 ± 1.5 bc
L. sulphureus	3.5 ± 0.4 bcd	1.7 ± 0.5 abc	6.8 ± 0.8 bc	4.3 ± 1.6 bc
P. pini	3.7 ± 0.5 abc	1.6 ± 0.5 abc	6.1 ± 1.0 cd	4.4 ± 0.7 bc
S. hirsutum	4.8 ± 0.6 a	2.1 ± 0.5 abc	9.1 ± 1.1 ab	3.3 ± 0.6 bcd
Control[x]	0.0 ± 0.0 e	0.0 ± 0.0 d	0.0 ± 0.0 e	0.0 ± 0.0 d
F	12.598	3.044	16.728	4.189
P	<0.001	<0.001	<0.001	<0.001

[z]Means within columns followed by the same letter are not significantly different according to Fisher's protected least significant difference tests ($P < 0.001$).
[y]Two sapwood blocks (1.5 × 1.5 × 8.0 cm) of each tree species were placed into separate glass vials per fungal strain and a minimum of two to three fungal strains and three replications per strain were prepared for each treatment.
[x]Control wood blocks received identical treatment except that no inoculum of a wood decay fungus was applied before incubations.

percentages as a result of decay than the root-rot fungi with few exceptions. The resistance of woods to decay by both root-rot and trunk-rot fungi were usually species-specific, although *T. occidentalis* (northern white-cedar) exhibited universally high levels of resistance to decay by all 12 rot fungi tested over both 1-year and 2-year decay periods. Greater rates of decay generally occurred on sapwoods of angiosperm species (hardwoods) than on conifer species (gymnosperms) during the first and to a lesser extent in the second year of decay. Treatment effects on mean percent dry weight loss of wood blocks (the measure of decay) were highly significant for both Year 1 and Year 2 decay periods ($P < 0.001$).

Wood decay progress of fungi. The mean decay amounts, measured as percent dry weight loss of wood caused by the 12 decay fungi in sapwood of the nine landscape tree species, ranged from 0.0% to 8.3% at the end of 1 year of incubation at 21 °C (Table 1). The highest levels of decay, caused by the rot fungi in all wood types collectively after 1-year incubation, were attributed to the following six species (in order from highest to

lowest magnitude): *G. lucidum*, *S. hirsutum*, *H. annosum*, *D. quercina*, *F. pinicola*, and *A. mellea*. Intermediate levels of decay were caused by *P. pini*, *L. sulphureus*, *A. ostoyae*, and *I. dryadeus*. The lowest levels of decay in all wood types were attributed to *A. gallica* and *A. tabescens*. Most treatment means were significantly different from controls for all wood types except for *T. occidentalis*.

The effects of individual decay fungi on each wood type were host species-specific for most fungus–host wood combinations tested. *G. lucidum* caused the greatest decay in sapwood of (in order) *Q. nuttallii*, *F. pennsylvanica*, and *P. deltoides*, whereas *D. quercina* and *A. gallica* caused the most decay in sapwood of (in order) *Q. lyrata*, *F. pennsylvanica*, and *Q. nuttallii* (Table 1). *F. pinicola* caused equal levels of decay in *F. pennsylvanica* and *Q. lyrata* sapwood, and slightly lower levels in *P. taeda* sapwood. *L. sulphureus* caused the most decay of (in order) *Q. lyrata*, *P. occidentalis*, and *T. distichum. Phellinus pini* caused high levels of decay in *Q. nuttallii* and *Q. lyrata* and intermediate levels of decay in *F. pennsylvanica*, *T. distichum*, and *P. deltoides*.

The highest rates of decay caused by all decay fungi for each wood type occurred in *Q. nuttallii*, *Q. lyrata*, and *F. pennsylvanica* sapwoods. Intermediate ranges of decay for all decay fungi occurred in *T. distichum*, *P. deltoides*, and *L. styraciflua*. Very little differences between mean decay rates, caused by all decay fungi, were found for *P. occidentalis*, and no significant differences between treatment means relative to controls occurred for *T. occidentalis* during the first year of decay ($P = 0.298$).

The mean amount of decay, caused by all 12 rot fungi, was mostly greater in the five hardwood species than in the four conifer species during the first year of decay. Some notable exceptions include the relatively high level of decay caused by *H. annosum* in *T. distichum*, *D. quercina* in *T. distichum*, and *P. taeda* and *F. pinicola* in *P. taeda*. All 12 wood decay fungi caused the greatest decay of *Q. nuttallii* sapwood and the least decay of *T. occidentalis* sapwood after incubation for 1 year.

Significantly greater decay (6.5% ± 0.2% versus 3.1% ± 0.1% dry weight loss) occurred for all wood types collectively in the second year of decay than in the first year of decay ($F = 152.9$, $P < 0.001$). Mean dry weight loss of sapwood caused by the decay fungi ranged from 0% to 18% at the end of 2 years of incubation at 21 °C (Table 2). The highest levels of percent dry weight loss, caused by the rot fungi on all wood types collectively after 2 years of decay, were attributed to the following six species (in order from highest to lowest): *A. mellea*, *H. annosum*, *G. lucidum*, *I. dryadeus*, *S. hirsutum*, and *D. quercina*. Intermediate levels of decay were caused by *L. sulphureus*, *P. pini*, *P. pinicola*, and *A. gallica*. The lowest levels of decay accrued in Year 2 for all wood types were the result of *A. ostoyae* and *A. tabescens*. Similar to Year 1 results, the treatment effects of the decay fungi on dry weight loss were highly significant in Year 2 and the decay rates caused by individual fungal species on most wood types were significantly different from controls ($P < 0.001$) for all wood types except for *T. occidentalis* ($F = 1.9$, $P = 0.064$).

Comparisons of wood decay by wood type category (hardwoods versus conifers) showed significantly higher decay rates at the end of Year 2 than in Year 1 for all fungi collectively in both hardwood (7.3% ± 0.3% versus 3.7% ± 0.1% dry weight loss) and conifer (4.7% ± 0.4% versus 1.8% ± 0.2% dry weight loss) wood types ($F = 78.1$, $P < 0.001$). The host specificity of decay by rot fungi on individual wood types was again prevalent in decay Year 2, but the order of decay rates and combinations of host woods most severely decayed by individual fungi changed from the first year of decay. *Armillaria mellea* (Table 2) caused the greatest decay of sapwood in (order from highest to lowest): *T. distichum*, *Q. nuttallii*, *F. pennsylvanica*, *Q. lyrata*, and *P. deltoides*, whereas *H. annosum* caused the most decay in sapwood of *Q. nuttallii*, *L. styraciflua*, and *Q. lyrata. Ganoderma lucidum* caused the highest dry weight loss in *P. deltoides* and slightly lower rates of decay in *Q. nuttallii* and *L. styraciflua. Inonotus dryadeus* caused the highest amount of decay of *Q. nuttallii* and *F. pennsylvanica. Stereum hirsutum* was equally most damaging to *F. pennsylvanica*, *Q. nuttalli*, and *Q. lyrata*; and *L. sulphureus* produced the highest percent of decay in *Q. nuttallii*, and lesser rates in *L. styraciflua* and *Q. lyrata. Quercus nuttallii* consistently sustained the highest amounts of sapwood decay by most rot fungi in the second year of decay.

The highest levels of decay in Year 2 for all decay fungi by wood type occurred in *Q. lyrata*, *P. taeda*, and *L. styraciflua* sapwoods. Intermediate ranges of decay by wood type occurred in *T. distichum*, *P. deltoides*, and *F. pennsylvanica*. The lowest levels of decay occurred in wood of *P. occidentalis and Q. nuttallii*, and no significant differences between treatment means relative to controls occurred for *T. occidentalis* during the second year of decay ($P = 0.064$).

The five angiosperm wood types showed generally higher weight losses than the four conifer wood types after 2 years of decay. However, certain rot fungi–coniferous host wood combinations had the highest decay rates of all host wood types tested. For example, *A. mellea* and *D. quercina* caused exceptionally severe decays in *T. distichum* relative to angiosperm and other conifer wood types. All 12 wood decay fungi caused the greatest decay of *Q. nuttallii* sapwood and the least decay of *T. occidentalis* sapwood during Year 2 decay.

The relative decay potentials of all 12 rot fungi, based on mean dry weight loss resulting from decay of all wood types combined, were compared for the first and second years of decay. Relatively small differences in decay potential among the rot fungi occurred during the first year of decay (Fig. 1). However, a well-defined gradation of decay potentials was apparent among the rot fungi in the second year of decay. The fungi with the highest decay potentials of all wood types combined were (in order): *A. mellea*, *G. lucidum*, *H. annosum*, *S. hirsutum*, *D. quercina*, and *I. dryadeus*. Those species with intermediate decay potential were *L. sulphureus*, *F. pinicola*, and *P. pini*. The three *Armillaria* species, *A. ostoyae*, *A. gallica*, and *A. tabescens*, exhibited the lowest decay potentials among the fungi tested. There were overlaps in decay ranges for fungi within each decay category in Year 2, but a clear

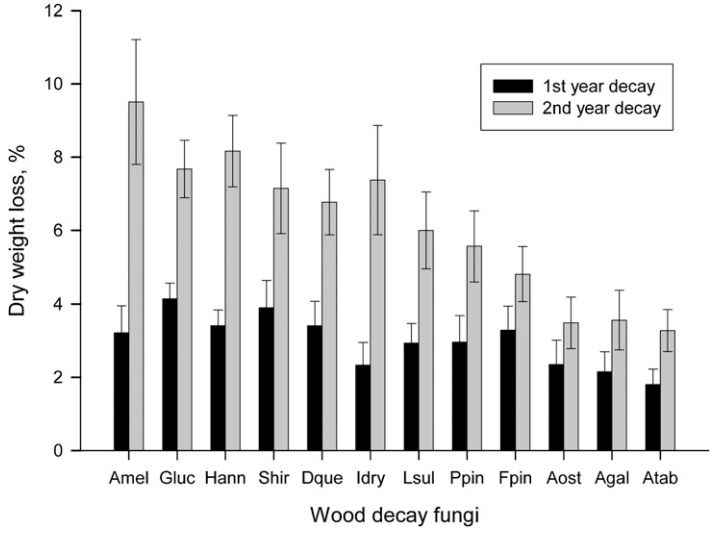

Fig. 1. Relative wood decay potential of 12 major root-rot and trunk-rot fungi determined from nine host wood types after 1- and 2-year incubation periods at 21 °C. Abbreviations for wood decay fungi tested include: *Armillaria mellea* (Amel), *Ganoderma lucidum* (Gluc), *Heterobasidion annosum* (Hann), *Stereum hirsutum* (Shir), *Daedalea quercina* (Dque), *Inonotus dryadeus* (Idry), *Laetiporus sulphureus* (Lsul), *Phellinus pini* (Ppin), *Fomitopsis pinicola* (Fpin), *Armillaria ostoyae* (Aost), *Armillaria gallica* (Agal), and *Armillaria tabescens* (Atab). Indicated rankings of wood decay potential (in order from most to least decay potential, left to right) are based on mean dry weight loss (%) of all host sapwoods tested. Error bars indicate SES of the mean.

cline or continuum of decay potentials was established for the collective wood types included in this analysis. Dry weight losses resulting from decay of all wood types in Year 2 were significantly greater than weight loss in Year 1 for all rot fungi except *A. ostoyae*.

Analyses of decay rates for each rot fungus, based on dry weight losses of wood types grouped into angiosperm (hardwood) and conifer (gymnosperm) wood-type groups, provided more detailed information of decay effects relative to differences between these two major wood categories (Table 3). The most damaging decay fungi of both hardwood and conifer wood types for both years of decay were (in decreasing order): *A. mellea*, *G. lucidum*, *H. annosum*, *D. quercina*, *S. hirsutum*, and *I. dryadeus*. These results were very similar to analyses of all wood types combined for those fungal species causing high, intermediate, and low dry weight losses. All of the rot fungi caused greater rates of decay in the hardwood wood types than in the conifer wood types in both Year 1 and Year 2 of decay ($F = 78.1$, $P < 0.001$). *Armillaria mellea* caused a higher rate of decay of hardwood and conifer wood types in Year 2 than decay rates for most other fungus–wood group combinations. The only exceptions were Year 2 decay of hardwood wood types by *H. annosum*, *S. hirsutum*, and *I. dryadeus*. Nevertheless, *A. ostoyae*, *A. gallica*, and *A. tabescens* consistently caused the lowest rates of decay among the rot fungi for both wood-type groups.

Resistance of wood types to decay. The relative resistance of the nine wood types to decay by all 12 rot fungi similarly was determined based on dry weight loss over 1-year and 2-year incubation periods (Fig. 2). Mean dry weight losses were significantly greater at the end of the second year of decay compared with the first year of decay for all wood types. A continuum of decay rates for different wood types was observed for both Year 1 and Year 2 incubation periods as a result of differential effects of the decay fungi. Significant differences in decay by wood type were greater near the extremes of the decay-resistance continuum than at intermediate levels of decay resistance. Decay rates of individual wood types ranged from less than 1% dry weight loss to more than 5% in Year 1 and nearly 2% to almost 10% weight loss in Year 2. The wood types with the greatest resistance to decay were (in order from the highest): *T. occidentalis*, *P. taeda*, and *L. styraciflua* (Fig. 2). Intermediate levels of decay resistance were found in *P. occidentalis*, *P. deltoides*, and *T. distichum*. Wood types with the lowest resistance to decay included *F. pennsylvanica*, *Q. lyrata*, and *Q. nuttallii*. The sapwood of *T. occidentalis* was by far the most resistant to decay by all of the rot fungi tested (0% dry weight loss after 2 years of decay by *A. gallica*, *I. dryadeus*, *L. sulphureus*). *Q. nuttallii* exhibited the greatest weight loss (up to 15.6% after 2 years of decay by *I. dryadeus*) among the wood types tested with all of the rot-fungi.

Discussion

The effective management of damage caused by wood decay fungi in landscape trees of urban and suburban forests requires knowledge of the wood decay potentials of the most common and important fungi responsible for decay of wood in these areas and the inherent susceptibility and resistance of the woods of common landscape trees to decay by these fungi. Relatively few publications with specific information of this type are available to urban foresters, city arborists and tree-care specialists to help guide their ability to make assessments and management decisions necessary to effectively mitigate wood decay damage to landscape trees to minimize economic losses associated with tree failures. Most wood decay studies have reported in vitro decay data for relatively few combinations of rot fungi and tree species (Čermák et al., 2004; Elissetche et al., 2001; Fernandes et al., 2005; Ferraz et al., 2000; Krekling et al., 2004; Luna et al., 2004; Pandey and Pitman, 2003) and with very limited data from field studies on decay potentials in living trees with actively operating host-defense mechanisms. Swift (1978) investigated the developmental growth of *Stereum hirsutum* on 15 branches of *Quercus robur* L. Other studies have examined the growth potential of artificially or naturally inoculated *Armillaria* species in forest stands (Bruhn et al., 1994, 1996; Dobbertin et al., 2001; Lung-Escarmant and Guyon, 2004). Klein-Gebinck et al. (1991) and Kodrik (2001) assessed the progress of decay and succession of wood decay fungi in *Fagus sylvatica* L. artificially inoculated with *Pleurotus ostreatus* (Jacq.) P. Kumm. Čermák and Strejĉek (2007) studied the progressive rate of rot spreading vertically in the stems of *Picea abies* (L.) H. Karst. infected with *Stereum sanguinolentum* (Albertini & Schwein.) Fr. The effects of various decay fungi on the wound responses of *Eucalyptus* species were studied by Barry et al. (2002) and Deflorio et al. (2007). The host responses and decay development resulting from wound inoculations of sapwood in coniferous and deciduous trees with six wood decay fungi were compared by Deflorio et al. (2008, 2009).

Our results indicate that the most important wood-rot fungi responsible for the greatest damage to the tree species tested here were similar after 1-year and 2-year decay periods. Five of the six most damaging fungi found as the top decay producers for both years included *A. mellea*, *H. annosum*, *G. lucidum*, *S. hirsutum*, and *D. quercina*. In the second year of decay, *I. dryadeus* replaced *F. pinicola* among the top six decay fungi. However, the level of damage (decay) or dry weight loss attributed to individual wood decay fungi changed between Year 1 and Year 2. The relative order of importance of individual decay fungi, based on decay potential, changed from Year 1 to Year 2 largely as a result of differences in decay-rate curves relative to time or duration of decay. These results suggest that differences in inherent host-wood resistance to decay by different fungi include several important variables that affect the decay-rate curves of individual wood decay fungi over time. The most important variables associated with the decay of nonliving sapwood include both chemical and structural resistance of the host wood, fungal growth rates, wood colonization, and the mechanisms of decay associated with each fungal species (DeGroot et al., 2000; Hennon et al., 2002).

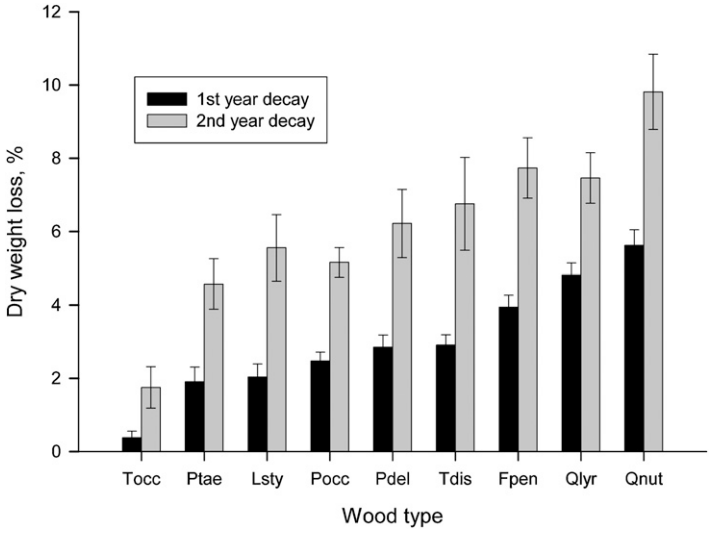

Fig. 2. Relative resistance of nine host wood types to wood decay by 12 major root-rot and trunk-rot fungi after 1- and 2-year incubation periods at 21 °C. Abbreviations for host woods include: *Thuja occidentalis* (Tocc), *Pinus taeda* (Ptae), *Liquidambar styraciflua* (Lsty), *Platanus occidentalis* (Pocc), *Populus deltoides* (Pdel), *Taxodium distichum* (Tdis), *Fraxinus pennsylvanica* (Fpen), *Quercus lyrata* (Qlyr), and *Quercus nuttallii* (Qnut). Indicated rankings of host wood resistance to decay (in order from most to least resistance, left to right) are based on mean dry weight loss (%) caused by all wood decay fungi tested. Error bars indicate SES of the mean.

Armillaria mellea and *G. lucidum* had the greatest overall potential to decay wood among the nine common urban landscape trees after 2 years of decay. The mean dry weight losses caused by *H. annosum* were only slightly lower for the same wood types. Results of the present study suggest that these three rot fungi are among the most damaging fungi common to southern temperate landscape trees within urban and suburban forests of the Northern Hemisphere. Tree care professionals should pay particular attention to these fungi because of their ability to rapidly colonize and decay wood, overcome natural active host defenses, cause root and butt rot that increase susceptibility to windthrow, and because of their progressive development in urban forests as a result of human activity, especially wounding as a result of pruning tools and mechanical cutting machines (Wilson et al., 2004a). Bark wounds on the lower trunk provide effective infection courts for these fungi and potential sites for the formation of fruiting bodies and subsequent dispersal to surrounding trees.

The list of wood decay fungi most important in one location may be quite different from the list in another location as a consequence of differences in environmental conditions, climatic factors, and host–pathogen interactions. For example, Terho et al. (2007) determined that *Armillaria* species and other common facultatively saprotrophic agarics (*Hypholoma*, *Pholiota*, and *Pleurotus*) may be only weak pathogens with low potential for causing stem breakage in Finland. Thus, the management of potentially hazardous trees in urban environments must necessarily be specialized to some extent for each locality based on the unique conditions (host variation, pathogen type, aggressiveness, and ambient factors) that prevail in each locality. Nevertheless, certain biological factors such as the wood decay potential of specific rot fungi and resistance of specific wood types to decay tend to largely govern the outcome of host–pathogen interactions in most localities because significant variation in decay resistance between individual trees of the same species mainly is controlled genetically and rarely attributed to differences in site factors (Scheffer and Cowling, 1966).

Effect of environmental factors on wood decay. Many environmental variables influence the process of infection, colonization, and decay development within different tree species (Vitanen and Ritschkoff, 1991). The physical factors that most limit wood decay development are air and wood moisture content and oxygen concentration. The optimal wood moisture content that supports decay by most fungi is near the fiber-saturation point, between 25% and 30% for most woods (Schmidt, 2007). The microclimate that surrounds the host can influence plant growth, host defense activity, and disease development within the temperature optima for fungal growth, usually between 20 and 30 °C for most fungi (Schwarze et al., 2000). We conducted the current study at 21 °C, close to the mean optimum growth temperature for the rot fungi tested, to minimize moisture loss from the wood blocks. Many fungi can survive a broad range of temperatures well outside of their optimum, although the optimal temperatures for wood decay may be very different from the range of temperatures that support maximum mycelial growth (Grinda, 1976). A multitude of resident microbes associated with decaying wood also can significantly affect, either inhibit or promote, fungal growth and wood decay (Folman et al., 2008).

Decay in vitro relative to decay in living trees. A study of the progress of wood decay is very difficult to achieve under field conditions as a result of a myriad of factors that influence all aspects of host–pathogen interactions during the many complex stages of infection, colonization, and decay. The inability to control the numerous variables that affect these processes often leads to results that are conflicting or difficult to interpret. Although in vitro wood-decay tests do not provide absolute definitive evidence of the activity of xylophagous fungi in living sapwood or decay progress under urban or forest environment conditions, they are useful for determining relative decay potentials of fungi and relative decay resistance of wood types in the absence of host-resistance factors.

Decay results associated with host–pathogen interactions in vitro are not necessarily representative of results that will occur in living trees. For example, *Armillaria mellea* was most damaging to *T. distichum*, *Q. nuttallii, F. pennsylvanica*, and *Q. lyrata* in the present study. Sapwood of *Taxodium distichum* (bald cypress) showed the greatest damage (18% dry weight loss) from decay by *Armillaria mellea* after 2 years. However, *T. distichum* is not likely to sustain this high rate of decay under natural conditions because of the tendency of this species to grow predominantly in wet, swampy soils of floodplain lakes and along riparian corridors. Although the root system is the preferred penetration site of *Armillaria* species (Morrison et al., 1991), roots of *T. distichum* are often submerged where oxygen levels usually are too low for these fungi to grow (Garraway et al., 1991).

Recent studies have provided indirect evidence that the natural inherent chemical resistance of wood to decay may be more important that active host-defense mechanisms (e.g., compartmentalization of decay, reaction and barrier zone formation in response to wounding) in inhibiting or preventing wood decay. Deflorio et al. (2008) found that wood decay (indicated by weight loss) was influenced significantly by the fungal species and host species (wood type) being attacked, but the amount of decay was less influenced by host resistance mechanisms (reaction and barrier zone formation) because strongly invasive pathogenic fungi often were able to overcome barrier zones associated with wounding. In a separate study, Deflorio et al. (2009) showed that although strongly invasive wood-decay fungi sometimes triggered a higher magnitude of host response than weakly invasive fungi, host response to wounding often appeared to be nonspecific and the degree of fungal invasiveness did not influence the magnitude of the host response within sapwood xylem. Data in the current study support the hypothesis that inherent wood resistance to decay determined from in vitro studies may provide a more effective indicator of relative decay resistance of wood than in vivo inoculations that often tend to be masked by nonspecific host responses and variable wood-weight changes associated with inoculations and host–wound responses.

Results of the present study provide useful comparative in vitro wood decay data for 108 host tree–wood decay fungi combinations among 12 common temperate landscape trees inoculated with nine important root-rot and trunk-rot fungi in North America and Europe. An understanding of the relative decay potential of individual rot fungi to decay wood of specific landscape tree species in the absence and presence of active host-resistance mechanisms is essential to predict the probability and extent of future decay damage and to determine the most prudent and effective course of action to take after individual tree assessments. Information on wood decay potentials of fungi combined with data from noninvasive decay-detection devices such as electronic noses (Baietto, 2008; Wilson et al., 2004b, 2005), damage risk assessments or hazard analyses of living trees, and decay pattern analyses (Terho et al., 2007) allow for more informed decisions about whether to leave living decayed trees untreated or to remove parts or all of the tree.

The peculiarities of host wood types are some of the main factors that can impact the development of decay. These factors include host species, the age of the tree, wood anatomy, and the biological and pathological condition of the wood. For example, young trees tend to be more susceptible to fungal attack than older trees because younger trees are relatively rich in sapwood, whereas older trees are richer in more decay-resistant heartwood (Scheffer and Cowling, 1966). However, older trees tend to respond less vigorously to attack, particularly as a result of the decreased ability to react to the disease through the compartmentalization of the decay or to the depletion of antifungal compounds in sapwood over time (Eisner et al., 2002; Scheffer and Cowling, 1966).

Resistance of wood types to decay. Sapwood of *Thuja occidentalis* (northern white-cedar) exhibited very good resistance to decay by all 12 wood-rotting fungi tested here. Decay rates for all of the fungi in this wood type were mostly less than 2% at the end of Year 1 and rarely more than 4% after 2 years of decay. Only *H. annosum* caused slightly greater decay (6.2% weight loss) in this wood species at the end of the second year. These results indicate that *Thuja occidentalis* is inherently quite resistant to decay in vitro

and probably even more resistant to decay with the addition of active host-defense responses in living trees. Fengel and Wegener (1984) recognized that weight loss of 2% can be considered the threshold for decay because fungi may consume several low-molecular-weight wood constituents without decaying cell wall polymers. The identification of landscape tree species with such remarkably high resistance to decay by a diversity of rot fungi is advantageous to landscape designers in several ways. *Thuja occidentalis* is a good candidate for urban greening designers and arboriculturists as an important alternative ornamental tree species that could be used in initial plantings for long-term aesthetic benefits and to replace highly hazardous decayed or dead trees in the landscape. Nondeciduous conifers provide aesthetic value year-round, serve as effective wind breaks, and reduce snow drifts during winter months.

The chemical basis of wood decay resistance in *T. occidentalis* will likely provide useful information for identifying other ornamental coniferous tree species that may have similar chemical defenses and perhaps new classes of compounds that are useful for controlling wood decay either through wood treatments or through molecular transfer of resistance genes (responsible for producing these compounds) to other tree species. There may be a commonality in the chemical basis of wood decay resistance (wood durability) in *T. occidentialis* to the occurrence of high concentrations of lignans such as plicatic acid derivatives (Maclean and Macdonald, 1967) present in the wood of *Thuja plicata* D. Don (western red-cedar), a closely related species known to have high resistance to wood decay. In the absence of active host-defense mechanisms operative in living sapwood (e.g., decay compartmentalization, phytoalexins, and other secondary metabolites), resistance to wood decay by dead sapwood is largely limited to the presence of fungistatic compounds in the wood that either inhibit fungal growth or block enzymatic access to structural components of wood fibers.

Three other species that sustained relatively low damage after 2 years of decay in the present study were *P. taeda* (loblolly pine), *P. occidentalis* (sycamore or planetree), and *L. styraciflua* (sweetgum). These species could be useful choices for tree replacements in landscape tree plantings after removal of hazardous trees. London plane is widely planted as an urban landscape species throughout the world, although it can be susceptible to certain deforming and lethal diseases such as crown gall, caused by *Agrobacterium tumefaciens*, and canker-stain, caused by *Ceratocystis fimbriata* Ellis & Halst. f. sp. *platani* J. Walter.

Potential applications to landscape tree management. The data reported here on the wood decay potentials of common root-rot and trunk-rot fungi, and the inherent decay resistance of specific wood types to these fungi, are useful in making general assessments of the hazard status of individual urban trees. This information may be combined with empirical data from urban tree assessment surveys using various decay-detection devices to predict the probabilities of future tree failures, estimating timing scenarios (temporal risk assessments) for the likely occurrence of damage resulting from falling tree parts, and for developing individual tree inspections and maintenance schedules to avoid personal and property damage resulting from structural failures of landscape trees. The monitoring of landscape trees on an individual basis is necessary to determine effective treatments of appropriate magnitude necessary to avoid failures. This may involve removal of only parts of the tree or complete tree removal depending on the extent to which the tree is colonized by the decay fungus.

The extent of accrued decay damage in individual trees is dependent on the duration of tree colonization after infection, the decay fungus involved, the tree species, and ambient microclimatic (environmental) conditions. Ultimately, the accretion of wood decay volume within a decay column is highly dependent on the decay fungus–host wood combination and resulting interactions. However, the risk or hazard severity of the decay, i.e., the likelihood that catastrophic failure will occur in the near future, must be judged in terms of the location of the decay relative to gravitational and wind stress points and the distribution of the decay. The key stress point for individual limbs of the tree usually is at the point of greatest leverage at the limb axle or point of attachment to the trunk. For the trunk of the tree, the greatest stress point is at the ground level near the base of the stem, particularly when root- or trunk-rot fungi compromise the structural strength of the roots or lower trunk. The existence of wood decay at any of these key stress points greatly increases the probability of tree failures. Terho et al. (2007) found that the extensiveness of horizontal decay in the stem is more important than the vertical extensiveness of the decay column in determining breakage hazard. Their results suggest that certain fungal species such as *Cerrena unicolor* (Bull.) Murrill, *Ganoderma applanatum* (Pers.) Pat., *Inonotus obliquus* (Pers.) Pilát, *Kretzchmaria deusta* (Hoffm.) P. Martin, and *Phellinus igniarius* (L.) Quél that cause extensive horizontal decay, especially when it extended into the cambium, had the greatest potential for causing stem breakage. Extensive horizontal decay of the roots and butt log are especially hazardous because of the high potential for windthrow to occur during high-wind events, particularly straight-line winds associated with orographic, cyclonic, or convectional thunderstorms.

Management decisions concerning the disposition of hazardous trees can be serious because of the potentially dire consequences that may result if preventable stem breaks or tree failures result in catastrophic damage to property or human life. On the other hand, unnecessary removal of large valuable landscape trees may also be costly in terms of all of the long-term benefits that are lost. Biological information about decay fungi and host woods also is useful for determining which alternative tree species are appropriate choices for replanting to replace hazardous trees that have been removed. To avoid future wood decay damage by specific rot fungi common to a particular locality, the choices of initial plantings and replacement trees in a given area should include species that are nonhosts, resistant to decay by resident rot fungi, have low susceptibility to infections, or sustain minimal decay damage resulting from resident fungi over prolonged periods of time. Because the prevalent decay fungi and principal tree species can vary considerably in different locations, specific information should be acquired empirically to determine the probable outcomes of host–fungus interactions associated with each combination.

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