International Biodeterioration & Biodegradation 65 (2011) 1145–1149

Contents lists available at SciVerse ScienceDirect

International Biodeterioration & Biodegradation

journal homepage: www.elsevier.com/locate/ibiod

Wood preference of spalting fungi in urban hardwood species

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ARTICLE INFO

Article history:
Received 23 May 2011
Received in revised form
11 July 2011
Accepted 11 July 2011
Available online 4 October 2011

Keywords:
Pigmentation
Spalting
Tree-of-heaven

ABSTRACT

Five fungal species representing the three major spalting categories were inoculated onto wood of five different urban tree species with low to moderate economic value. Sugar maple (*Acer saccharum*) was also inoculated to serve as a control. Test samples were evaluated both internally and externally for spalting. The tested fungi had significant preferences for different wood species, and the preferences appeared to be related to sucrose availability. Specifically, zone line producing fungi preferred American elm (*Ulmus americana*), while *Arthrographis cuboidea* (pink stain) preferred tree-of-heaven (*Ailanthus altissima*). Wood species preference was also significant by decay class, with decay fungi preferring American elm, silver maple (*Acer saccharinium*), and horse chestnut (*Aesculus hippocastanum*). Staining fungi showed a preference for tree-of-heaven, while both decay classes readily colonized sugar maple and Norway maple (*Acer platanoides*).

1. Introduction

Trees planted in urban settings hold considerable value for energy conservation and carbon sequestration. Unfortunately, once cut, these trees have little value and are often chipped for mulch or landfill disposal or burned. With the increasing emphasis being placed on the maximum utilization of all forest biomass, it is important not to overlook the potential value of wood produced from such trees. Urban tree species are particularly well suited for high-value, low-volume wood processes, as each individual species often does not occur in high enough numbers in a particular region to facilitate large-scale mill processing.

One value-added process that holds considerable potential for increasing the economic value of urban tree species is spalting. In this process, wood is inoculated with non-pathogenic pigment-producing fungi. The fungi are allowed a set amount of time for colonization such that pigmentation is maximized without a substantial loss in wood strength properties. Spalted wood is sold at a price premium at specialty lumber outlets regardless of species (Bell Forest Products, 2011) and is especially well suited for dense to moderately dense hardwood species with low natural decay resistance (Robinson and Laks, 2010a,b; Robinson et al., 2007).

Spalting is categorized into three types. The first two, bleaching and zone line formation, are generally associated with one another and are caused by inter- and intra-fungal antagonism in white-rot fungi (Rayner and Todd, 1977; Phillips, 1987; Robinson et al., 2007). The third category, pigmentation, is caused by a specific group of fungi, generally ascomycetes. While bleaching and zone line production via inter-fungal antagonism appears to be very common on hardwoods, preliminary spalting research in wood species preference by fungi (Robinson and Laks, 2010a,b) indicates that wood species plays a strong role in pigment production by fungi. In particular, previous work on penetrating pigment formation by fungi indicates that sugar maple and aspen allow for significantly more pigmentation formation than other comparable hardwoods (Robinson and Laks, 2010a; Robinson et al., 2011). The reasons for wood preference are currently unknown.

Over the past several years there has been an increase in the demand for value-added wood products (Donovan and Nicholls, 2003; Kozak et al., 2004), and spalting has become a simple, reliable method to increase the value of lumber. Unfortunately, research into controlled spalting has primarily focused on sugar maple (*Acer saccharum* Marsh.), basswood (*Tilia americana* L.), yellow birch (*Betula alleghaniensis* Britt.), and trembling aspen (*Populus tremuloides* Michx.), wood species that already hold considerable value (Robinson et al., 2007, 2009a; Robinson and Laks, 2010a,b). Previous work on spalting also indicates that some wood species may not be viable options for spalting in terms of pigmentation or intra-fungal formation of zone lines. Thus, it is necessary to test each new wood species against a range of spalting fungi to determine wood species suitability. Results from such testing can be compared against sugar maple, as this species is colonized by a wide variety of spalting fungi. Sugar maple has proven to be preferred by a wide variety of spalting fungi (Robinson et al., 2007; Robinson and

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doi:10.1016/j.ibiod.2011.07.012

Laks, 2010a,b), and is the only wood species that routinely allows for both zone line production via intra- and inter-fungal antagonism, and the formation of pigment staining.

The goal of this research was to determine if some of the common, non-commercial (or semi-commercial) urban wood species from Toronto, Ontario, Canada, could be spalted, and which types of spalting generally occurred on each wood species. The wood species were tested against a broad range of spalting fungi in order to maximize the possibility of creating penetrating zone lines, bleaching, and pigmentation. We also sought to elucidate potential reasons for fungal preference for certain wood species in terms of pigment production, especially in regard to sugar maple, which currently appears to be favored by both zone line and pigment-producing fungi.

2. Methods

2.1. Wood species selection

Five wood species were selected for testing, based on their prevalence as city shade trees in southern Ontario, and their low commercial value: Norway maple (*Acer platanoides* L.), silver maple (*Acer saccharinum* L.), tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle), American elm (*Ulmus americana* L.), and horse chestnut (*Aesculus hippocastanum* L.). Sugar maple (*A. saccharum*) was used as the control wood species. All wood species were harvested in the spring of 2010 within southern Ontario. The average oven-dry specific gravities of the wood species are as follows: Norway maple, SG = 0.73; silver maple, SG = 0.52; tree-of-heaven, SG = 0.57; American elm, SG = 0.66; horse chestnut, SG = 0.45; and sugar maple, SG = 0.68. Test blocks were cut from sapwood sections of the boards.

2.2. Fungus species selection

Trametes versicolor (L.) Lloyd (UAMH 11521, basidiomycete isolated from *A. saccharum* in Houghton, MI, USA); *Xylaria polymorpha* (Pers.) Grev. (UAMH 11520, ascomycete isolated from *A. saccharum* in Alberta, MI, USA); and *Arthrographis cuboidea* (Sacc. & Ellis) Sigler (UAMH 11517, ascomycete isolated from *Quercus* sp. in Memphis, TN, USA) were selected based upon their quick growth rate and successful utilization in previous spalting research. An additional fungus, *Inonotus hispidus* (Bull.) P. Karst (F2037, basidiomycete; isolation data unknown) was tested due to its yellow pigmentation (Nasser et al., 1996) and ability to form zone lines (Pearce, 1991). *Ophiostoma piceae* (Münch) (FTK 387T, ascomycete isolated from *Tsuga heterophylla* in Vancouver, BC, Canada) was chosen due to its production of a penetrating blue stain (Seifert, 1993). All fungi were grown and maintained at room temperature on 2% malt agar plates (95 × 15 mm petri plates).

2.3. Spalting procedure

Spalting tests were performed using a modified decay jar test with vermiculite instead of soil, as outlined in Robinson et al. (2009b). Canning jars with plastic screw-cap lids (250-ml jars) were sterilized in an autoclave for 30 min, then cooled overnight in a laminar flow hood prior to inoculation.

The wood test blocks were cut into 14-mm cubes, oven-dried overnight at 40 °C, and then weighed. Blocks were then steam-sterilized for 30 min, cooled, and buried in the jars just underneath the surface of the vermiculite. Three blocks were placed in each jar, and did not touch each other. Blocks inoculated with *T. versicolor* were placed with the transverse face upwards, while all other blocks were placed with the radial face pointing up. A roughly 2 × 2 cm strip of agar with actively growing mycelium was placed on the surface of the vermiculite between all three blocks, so that the three blocks were equidistant from the mycelium. Three jars were utilized per wood species per fungus, giving a total of nine replicate wood blocks per set. A total of 270 wood blocks were used during this test.

Inoculated jars were incubated in a temperature- and humidity-controlled chamber (27 °C ± 2 °C, 80% ± 5% relative humidity). Jars with *T. versicolor* were incubated for 8 weeks, jars with *A. cuboidea* were incubated for 10 weeks, and jars with *X. polymorpha*, *O. piceae,* and *I. hispidus* were incubated for 12 weeks. After incubation, blocks were removed from their jars, scrubbed with a soft-bristled bottle brush to remove mycelium and vermiculite, weighed to determine moisture content, oven-dried overnight, and then weighed again to determine mass loss.

Dried blocks were scanned with an Epson WorkForce 500 scanner at 2400 dpi. The side of the block with the most pigment (zone lines or color) was scanned. After external scanning, the blocks were cut in half to expose an internal radial face; the side with the most spalting was then scanned.

External and internal spalting amounts were measured using Scion Image software, following the protocol in Robinson et al. (2009b). Data were analyzed with a one-way ANOVA, followed by Tukey's HSD using SAS, version 9.2 (SAS 2009 system for Windows). An additional two-way ANOVA was run with wood species and decay class (ascomycete versus basidiomycete) as the independent variables. All data were transformed using arcsine square root to meet assumptions of normality and variance of the error term.

2.4. Wood analysis

Both spalted and unspalted wood samples were analyzed for simple sugar and nitrogen content to determine the use of these elements by the inoculated fungi. For sugar analysis, spalted and unspalted blocks were dried at 40 °C for 24 h, then ground and passed through a 20-mesh screen on a Wiley mill to prepare the wood for sugar and nitrogen analysis. Approximately 0.5 g of wood dust from each block was weighed and placed into centrifuge tubes. Ten milliliters of distilled water was added to each tube. The tubes were then placed in an ultrasonic bath for 1/2 h. After removal from the bath, the tubes were placed in a 70 °C water bath for 60 min. Tubes were then centrifuged and the water decanted for free sugar analysis by ion chromatography (Dionex DX 600) using pulsed amperometric detection ED50A. The pulsed amperometric detection was set with the system default with a repeating sequence of three potentials: $E1 = 0.05$ V, $E2 = 0.75$ V, and $E3 = 0.15$ V. Three durations were used: $t1 = 0.4$, $t2 = 0.6$, and $t3 = 1.0$ min. The analytical column used was a CarboPac® PA10 (2 × 250 mm). The eluent used for quantification for the monosaccharides was 150 mM NaOH, with a flow rate of 0.25 ml min^{-1} with an injection loop of 25 ul.

The simple sugars mannose, glucose, galactose, and xylose had elution times ranging from 2.9 to 3.3 min; therefore those sugars were not separated. Fructose, lactose, and sucrose had elution times of 3.4, 4.4, and 5.2 min, respectively. Subsequent runs with lower concentrations of eluent, i.e., 18 mM NaOH, were able to separate galactose and mannose from glucose and xylose.

Three randomly selected blocks of beech heartwood and sapwood were dried at 40 °C overnight, ground in a Wiley Mill with a 30-mesh screen, and analyzed for carbon and nitrogen concentration on a Leco TrueSpec model 630-100-400.

2.5. Large-scale testing

To determine if some results from the small block testing could be successfully scaled up to larger pieces, tree-of-heaven, horse

chestnut, sugar maple, and American elm boards measuring approximately 152 × 20 × 2.5 cm were inoculated with *T. versicolor*, *X. polymorpha*, or *S. cuboideum*. Boards were stacked directly on top of one another, with strips of agar with actively growing mycelium mashed between the boards. Strips of agar measured approximately 5 × 10 cm. Sugar maple boards were inoculated with *T. versicolor* and *X. polymorpha* (two boards, one fungus per board). The American elm board was inoculated with *X. polymorpha*, and the horse chestnut board and tree-of-heaven board were inoculated with *S. cuboideum*. Boards were incubated in the same chamber as listed above, for 12 weeks. After incubation the boards were air-dried for 3 weeks, then planed to half their thickness to assess color penetration.

3. Results

3.1. Weight loss and bleaching

T. versicolor was the only fungus that produced significant weight loss, which ranged between 18 and 31%, depending on wood species. Weight loss did not exceed 30% in any wood species, which is the highest amount of weight loss usually obtained with *T. versicolor* in vermiculite (Robinson et al., 2009b). Weight loss did not differ significantly between silver maple, sugar maple, horse chestnut, and American elm, with Norway maple having slightly less weight loss than silver or sugar maple (results not shown, difference significant at $\alpha = 0.05$). Tree-of-heaven had the least weight loss, at 18%. Tree-of-heaven also had the least amount of internal bleaching (60% ± 30% versus 95–100% in all other wood species). All wood species had 100% external bleaching.

3.2. Zone lines

Zone lines were not produced on any of the tested wood species when they were inoculated with *T. versicolor*, which is not unusual for this species in monoculture. *I. hispidus* produced external zone lines on all wood species, but failed to produce internal zone lines (Fig. 1). As with bleaching and weight loss, tree-of-heaven was the least affected. *X. polymorpha* colonized all of the wood species, producing the greatest amount of external zone lines on American elm and tree-of-heaven. Tree-of-heaven was also the only wood species other than sugar maple to have internal zone lines with *X. polymorpha*, and the differences between the two wood species were not statistically significant.

3.3. Pink and blue stain

A. cuboidea externally colonized all wood species with pink pigment, although some species were not consistently pigmented. Norway maple and tree-of-heaven had significantly more external pink stain than the other species (Fig. 2); however, tree-of-heaven had a much higher color saturation, giving a near magenta appearance instead of the pale pink color of Norway maple (Fig. 3). Norway maple and tree-of-heaven also had significantly more internal spalting than any other species, with the exception of silver maple, which had a high amount of internal pink stain without a correspondingly high amount of external pink stain.

A. cuboidea also produced external blue stain on some blocks, with Norway maple and tree-of-heaven having significantly more blue stain than American elm. Norway maple, silver maple, and tree-of-heaven had significantly more blue pigmentation than did horse chestnut, American elm, or sugar maple. This fungus is known to produce both blue and pink pigments under laboratory conditions; however, the reasons for this are unknown.

O. piceae failed to produce blue stain internally, and very little pigment was produced externally, with only horse chestnut blue stain exceeding 30% (results not shown).

3.4. Spalting by fungus class

With the exception of sugar maple and Norway maple, the tested fungi appear to show a wood species preference for one type of spalting over the other (lateral decay versus radial pigmentation). The fact that sugar maple does not appear to preferentially favor a specific type of fungus reaffirms its position as a key wood for spalting.

To further test the theory that wood species may play a role in preferential decay by decay class, a two-way ANOVA was run, with wood species and decay type (ascomycete versus basidiomycete) as the independent variables. Norway maple was the most similar to sugar maple in its lack of preference between ascomycete and basidiomycete colonization. All other wood species appeared to have a large difference in performance between the two decay classes. Interactions were significant within the means model ($P < 0.0001$).

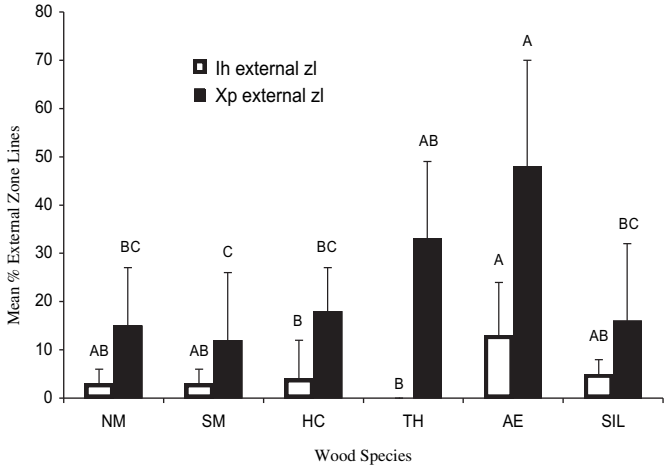

Fig. 1. External zone line production on sugar maple (SM), American elm (AE), horse chestnut (HC), Norway maple (NM), silver maple (SIL), and tree-of-heaven (TH) by *Inonotus hispidus* and *Xylaria polymorpha*. Error bars represent one standard deviation. Different letters represent significant differences between wood species within the same fungus. $N = 9$, $\alpha = 0.05$.

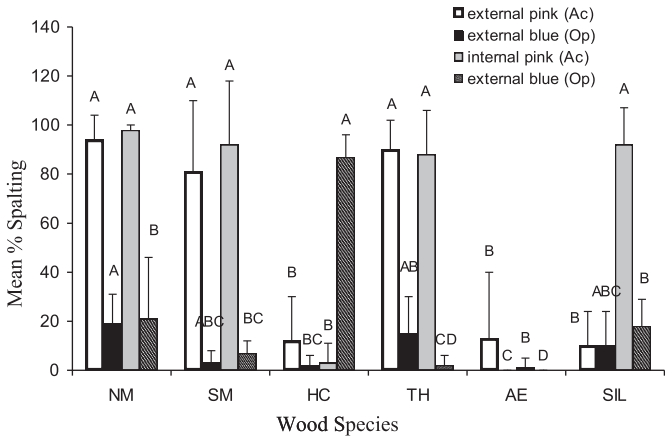

Fig. 2. Pink and blue stain production on sugar maple (SM), American elm (AE), horse chestnut (HC), Norway maple (NM), silver maple (SIL), and tree-of-heaven (TH) by *Arthrographis cuboidea* and *Ophiostoma piceae*. Error bars represent one standard deviation. Different letters represent significant differences between wood species within the same fungus. $N = 9$, $\alpha = 0.05$.

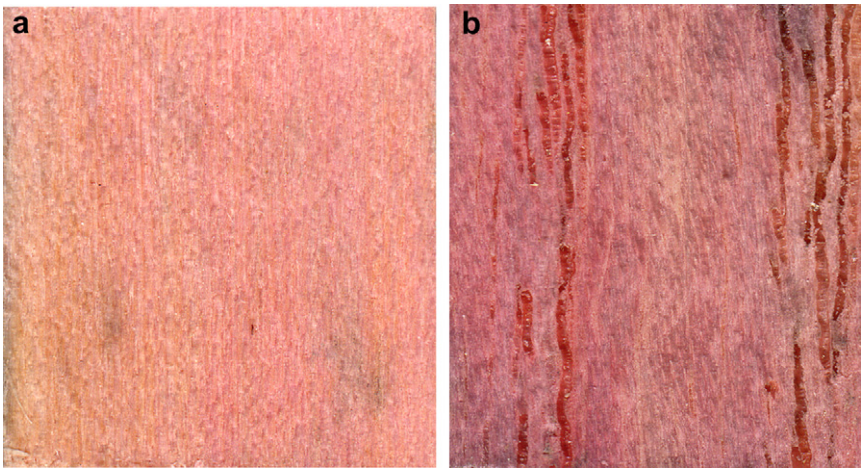

Fig. 3. External pink stain by *Arthrographis cuboidea* on (a) Norway maple and (b) tree-of-heaven. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

When broken down by wood species, the difference between ascomycete and basidiomycete colonization was statistically significant in all species except Norway maple. Of the wood species tested, basidiomycetes appear to prefer American elm, silver maple, and horse chestnut, while ascomycetes prefer tree-of-heaven.

3.5. Simple sugar content

Sugar maple and Norway maple, the two species readily spalted by all tested fungi, had higher amounts of sucrose than did the other wood species (0.04% and 0.02%, respectively, compared to <0.005% for all other species). No consistent differences in terms of total free sugar content were found among the basidiomycete-preferred wood species and tree-of-heaven, nor were any other differences found between basidiomycete-preferred wood species and the two wood species pigmented by both decay classes.

Based on sugar analysis after exposure to the fungi, no similarities were found in sugar use (or the production of simple sugars via the breakdown of complex sugars in terms of basidiomycete decay) between decay classes on their preferred wood species. There were also no differences in sugar consumption between fungi colonizing sugar maple/Norway maple and fungi colonizing the other wood species, with the exception of *A. cuboidea*. Sucrose was completely consumed on sugar maple and Norway maple by *A. cuboidea*, while the small amounts of sucrose from the other wood species were either untouched (American elm, silver maple), or showed a slight increase (tree-of-heaven and horse chestnut).

3.6. Nitrogen content

Nitrogen content of the wood species did not appear to play a role in pigment production by the tested fungi. Nitrogen content was highest in horse chestnut (0.32% N) and tree-of-heaven (0.30% N) with all other wood species having a nitrogen content lower than 0.26%. As with the sugar analysis, no difference was seen between the nitrogen content of basidiomycete-preferred species and ascomycete-preferred species. *O. piceae* was the only fungus to prefer horse chestnut in terms of pigment production, with significantly more blue stain produced on horse chestnut than on any other wood species.

3.7. Large-scale testing

Fungi performed identically in the large-scale testing to their performance in the inoculated jars. The coverage area of the pigments and zone lines within boards was similar to what they were in the small test blocks, and the type of pigmentation was consistent between the two types of tests.

4. Discussion

T. versicolor, a laboratory standard for white-rot decay testing, caused only moderate weight loss on most wood species, and did not produce zone lines. Tree-of-heaven was the least affected by *T. versicolor,* and it is possible that the poor colonization could be due to the numerous phytotoxic compounds produced by the tree (De Feo et al., 2003), which may have affected the growth of the fungus. As a similar inhibitory effect was not found with *X. polymorpha* or *A. cuboidea* on tree-of-heaven, it is possible that the phytotoxic compounds found in tree-of-heaven may only affect certain fungal species, such as the ones tested in this experiment.

In contrast to *T. versicolor*, *X. polymorpha* and *A. cuboidea* produced significant staining on tree-of-heaven. The surprising difference in pigment amounts in this wood species suggests several possible explanations: (1) The tested fungi that primarily colonize radially may have greater success than those that colonize laterally in colonizing high-extractive wood species, (2) high extractive contents in the wood are partially responsible for the increase in pigmentation due to either stress or antagonistic responses by the tested fungi. Various fungal species produce zone lines in reaction to environmental and substrate-level stress (Lopez-Real and Swift, 1975; Robinson et al., 2010), hence the toxicity of the tree-of-heaven (Heisey, 1990; Khattak and Ghazi, 2001) may be playing a role in the pigment production of the fungus. The high extractive content of American elm (Rowe et al., 1972) may also have stressed *X. polymorpha*, causing an increase in zone line production as compared to the sugar maple controls. In reference to the pink stain produced by *A. cuboidea*, previous spalting work with this fungus has found that, on sugar maple, *A. cuboidea* produces a penetrating pink stain within 10 weeks of incubation (Robinson et al., 2010). The heavy pink pigment found on tree-of-heaven may be due to the porous nature of the wood species enabling quick diffusion of the extracellular pigment throughout the wood. While chemical characterization of this pigment has been performed (Golinski et al., 1995), the water-solubility of this pigment is still unknown. If the pigment were water-soluble, this might also help explain its quick progression through a very porous, yet somewhat toxic, wood species.

Sorting the various wood species by decay type indicates that the fungi tested, within their decay groups, appear to better colonize certain wood species, and that the hard maples (sugar and Norway) appear to be favorable to all tested spalting fungi. It should be noted that *X. polymorpha*, an ascomycete that causes soft rot, also colonizes well on American elm (a preferred species of the other tested decay fungi). This could possibly be due to the moderate decay ability of *X. polymorpha*, antagonism of *X. polymorpha* by various extractives in American elm, or a combination of the two effects.

The preference of both stain and decay fungi for the hard maples may be due to the higher sucrose contents found in these trees, which may make them more attractive to a broad range of fungi. In regard to the increased sugar content of wood species after inoculation with *A. cuboidea,* this phenomenon has been reported before (Anagnost et al., 1994), although the increase was in galactose (sucrose was not measured). This increase was attributed to the presence of galactose within the fungal cell wall. The reason for the increase in sucrose from this study is unknown.

In contrast to the simple sugars, nitrogen did not appear to affect pigmentation in the tested fungi. Available nitrogen is usually a limiting factor in fungal growth, and increasing the availability of nitrogen can affect pigment production by certain fungi depending on the nitrogen source (Wong et al., 1981; Chen and Johns, 1993). Pigment production by the particular fungal species studied here does not appear to be affected by higher nitrogen levels. Potential reasons for this may include the inability of the tested fungi to access and utilize the nitrogen during the duration of the testing period, or that nitrogen availability is not directly related to pigment production of the tested fungi.

Final moisture contents for all tested blocks was recorded for this test, and were not found to differ significantly by inoculated fungus or between each separate wood species. Hence, it is unlikely that the small differences in moisture content within the blocks played a role in the pigmentation differences. However, it has been previously established that large differences in moisture content can change the amount of pigment produced (Robinson et al., in press).

This research indicates that, within this study, different fungal classes show a preference for pigment formation in different wood species. Within the tested fungi, stain fungi, generally the ascomycetes, tended to produce more pigmentation in tree-of-heaven, whereas decay fungi, generally the basidiomycetes, seemed to favor American elm, silver maple, and horse chestnut. Sugar maple continues to be the dominant wood species for controlled spalting due to its response to a broad range of fungi. However, this test indicates that Norway maple may also be a versatile wood for spalting.

American elm, horse chestnut, and silver maple are recommended for white-rot and zone line (via inter-fungal antagonism) spalting, as they appear to be preferred primarily by the tested decay fungi. Tree-of-heaven, a species very heavily favored by *A. cuboidea* and generally preferred by stain, is recommended for use in pigment production by spalting fungi. In addition, the very high saturation of pink present on tree-of-heaven, along with its ability to withstand decay by *T. versicolor*, could make spalted wood of this species a valuable commodity.

The results of this study also indicate that sucrose levels above 0.01% in wood may play a role in fungal preference in terms of spalting production. Sucrose levels above this threshold appear to be related to fungal preference (in terms of pigmentation output) for a wood species, regardless of whether the fungus is a basidiomycete or an ascomycete.

Acknowledgments

The authors would like to thank Tony Ung for his help with the monosaccharide sugar analysis.

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