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MINI-REVIEW

Developing fungal pigments for "painting" vascular plants

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Abstract The use of fungal pigments as color additives to wood as a method to increase forest revenue is a relatively new, but quickly developing field. Sugar maple (*Acer saccharum*) is currently the primary utilized hardwood for spalting and appears to be the best suited North American hardwood for such purposes. The combination of *Trametes versicolor* and *Bjerkandera adusta* has been identified in several instances as a strong fungal pairing for zone line production; however, *Xylaria polymorpha* is capable of creating zone lines without the antagonism of a secondary fungus. Few fungal pigments have been developed for reliable use; *Scytalidium cuboideum* is capable of producing a penetrating pink/red stain, as well as a blue pigment after extended incubation, and *Chlorociboria* sp. produces a blue/green pigment if grown on aspen (*Populus tremuloides*). Several opportunities exist for stimulation of fungal pigments including the use of copper sulfate and changes in wood pH.

Keywords *Bjerkandera adusta* · *Chlorociboria* sp. · Fungal pigments · *Scytalidium cuboideum* · *Trametes versicolor* · Spalting · *Xylaria polymorpha*

Introduction

The idea of a "value-added wood product" has become a recent popular method to increase revenue from commercial forests and place a value on otherwise economically stagnant wood species. One of the developing areas within the value-added category is spalted wood or wood that has been pigmented by fungi. This type of decorative wood has held a niche market with woodworkers and turners for decades, with spalted wood particularly preferred for small furniture items, like coffee tables (Donovan and Nicholls 2003) and wood turnings (Lindquist 1977).

Despite the commercial relevance of spalted wood, serious research into the induction of spalting under controlled conditions in order to minimize strength loss and maximize pigment production has only occurred within the past 5 years. Most of the current spalting research has been undertaken by a small group of researchers, with little additional information being produced outside of that group. However, the fundamental building blocks of spalting, such as the understanding of fungal antagonism, zone line components, and lignin degradation were developed in the last century and have been utilized as the building blocks of current spalting research. As consumer and industry interest in spalted wood continues to expand, the market and uses for this material should evolve, bringing with it new research areas and applications.

"Spalting" is not a word commonly found in usage outside woodworking circles, and to many its definition is somewhat vague. The word was specifically defined by Robinson et al. (2007a) to include all types of pigment, both melanin and otherwise, produced on wood by fungi. Pigments produced by surface molds are often excluded from this categorization, although surface zone lines are occasionally considered to be spalting (Robinson and Laks 2010a). The definition is further broken down into three categories based upon the mechanisms utilized. The first category, bleaching, includes the lightening of the wood due to colonization and lignin removal by white rot fungi. In association with these white rot fungi, but in its own

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category, are zone lines, produced due to inter- or intrafungal antagonism. The third category is defined simply as pigmentation and encompasses the colors produced by some fungi on wood, including the blue stain produced by Ophiostomatoid fungi.

Herein, we explore the development of spalting as a commercial resource and value-added process. We begin by looking at the history of spalted wood in ancient art, move through the twentieth century and the growing understanding of zone lines as a type of fungal antagonism, and finish with current research and a look at what the future might hold in terms of induced spalting in vascular plants.

History

Compared to the use of plant and mineral pigments, the time span over which fungal pigments have been utilized to color vascular plants, particularly wood from deciduous trees, is very short. While incidents no doubt occurred prior, the first noted use of fungal-pigmented wood is from the 1400 s in Renaissance Italy (Blanchette et al. 1992). During this time period, Italian artists utilized *Populus* sp. wood stained blue-green by *Chlorociboria* sp., in intarsia wood panels. Blanchette et al. also note that the blue-green wood was found in other inlay objects, such as book covers.

Unfortunately, little is known about the continued use of spalted wood in art and craft before or after this point, although the use no doubt persisted in some small amount. No widely distributed mention is made of its use until Mark Lindquist published on its use in woodturning in 1977 (Lindquist 1977). This and subsequent publications by Lindquist helped move spalted wood back into art and craft usage, although the type of spalting popularized by Lindquist, zone lines and bleaching, was not associated as a similar phenomenon to the blue-green-pigmented intarsia inlay pieces from centuries earlier. Spalted wood is currently still in use by woodworkers, although due to Lindquist's articles, woodturners appear to be the primary users of this material. Articles on spalted wood, from turning and finishing (Robinson 2010) to "secret recipes" for making it in your own backyard (Robinson 2008), persist in trade magazines and journals geared towards the crafter demographic.

Early research

The first research on spalted wood appears to have begun in the 1980s at Brigham Young University. Christensen (1982) conducted studies on the various physical properties of spalted wood and demonstrated a method of stabilizing spalted wood using an impregnation of methyl methacrylate. At the same university, Phillips (1987) conducted the first body of research specifically on the creation of zone lines for decorative purposes on both agar plates and wood—noting zone line formation and antagonistic reactions between six different white rot fungi. This work noted a difference in zone line production in media plates versus zone line production on wood (*Acer saccharinium* L.) and found some fungal pairings to produce zone lines more prolifically than others, including the pairing of *Trametes versicolor* (L.) Lloyd/*Bjerkandera adusta* (Willd.) P. Karst.

The work of Phillips drew heavily on the growing body of literature pertaining to zone line formation in wood. Investigations into the formation of zone lines are evident in scientific literature as far back as the late 1800 s to early 1900s, where the research of Hartig (1878), Weir (1915), White (1920), and Campbell (1933, 1934) associated zone line formation in wood as the result of fungal colonization, and in some cases, related zone line formation to specific fungi. However, it was not until the 1970s and 1980s that the nature of zone lines, including their formation due to inter- and intrafungal antagonism, was brought to light. Lopez-Real and Swift (1975) provided the first in-depth look at the type of hyphae present in zone lines, although Rayner and Todd later supplemented this information in 1979. This work was followed by Coates and Rayner in 1985 (1985a; b; c), describing the formation of zone lines in terms of fungal succession; the work of Sharland and Rayner in 1986 continued along similar lines, discussing zone line formation due to fungal colonization and genetic incompatibility.

Investigating the formation of zone lines

A great deal of research occurred in the 1970s and 1980s on the causes of zone line formation in woody tissue; many of which focused on zone lines and their role in fungal succession. Several types of "zone lines" were defined: those composed of pseudosclerotial plates (PSP) that incorporate non-fungal tissue (Lopez-Real and Swift 1975) and form from melanized hyphal tissue of competing fungi (Mallett and Hiratsuka 1986), those that form as a reaction zone between living and dead wood tissue colonized by fungi (Campbell 1933), and those formed as reaction zones between various decay columns and prematurely formed heartwood (Boddy and Rayner 1981).

In 1975, Lopez-Real and Swift found that *Armillaria novae-zelandia* (G. Stev.) Boesew and *Stereum hirsutum* (Willd.) Pers. preferentially produced PSP when exposed to 100% relative humidity and discounted the possibility that low moisture levels were responsible for the formation of PSP on wood, as hypothesized by Campbell in 1933. They again published on PSP formation in Lopez–Real and Swift (1977), stating that PSP formation by both fungi was not affected under oxygenless conditions. In addition, Lopez-Real and Swift noted that PSP formation did occur when fungi were grown in the presence of nitrogen or in conditions of low oxygen.

Rayner continued to investigate the genetics and formation of zone lines from the late 1970s through the 1980s. Of particular interest was the finding that zone lines could be produced due not only to interfungal antagonism but also due to intrafungal antagonism between antagonistic dikaryons of the same fungus (Rayner and Todd 1977). Rayner and Webber published an overview of the various fungal interaction studies to date in Rayner and Webber (1983), focusing on the importance of primary and secondary resource capture. In 1984, zone line formation in reference to somatic incompatibility within a single fungus was once again investigated, this time by Coates. This information would serve as the basic reasoning for single-culture spalting inoculations several decades later.

In 1981, Li began chemical investigations into zone lines, finding that various phenoloxidases and peroxidase isozymes occurred in zone lines of *Phellinus weirii* (Murrill) Gilb. Li hypothesized that several of the compounds may have been formed by the fungi in response to antagonism. Mallett and Hiratsuka found that the zone lines produced between competing strains of *A. novae-zelandia* were composed of melanized hyphae, surrounded by PSP plates (1986).

Developing methods and refining the process

Following the 1980s, no additional publications appeared directly on spalting until the work was again undertaken in the new century. In 2007 Robinson et al. (2007a), following the work of Phillips, tested 21 pairings of white rot fungi for zone line creation, both in malt agar plates and in maple blocks. While Phillips had tested only six white rot fungi, Robinson et al. tested 25 fungi, and unlike Phillips, include pigment-producing fungi as well. Of all the pairings tested, only two produced zone lines routinely in sugar maple (*Acer saccharum* Marsh), one of which was again the pairing of *T. versicolor*/*B. adusta*. The work of Robinson et al. was followed in 2011 by Qin et al., who determined that the formation of zone lines under controlled conditions did not differ from the formation of the lines under unregulated, natural conditions.

In 2007, Robinson et al. (2007b) also published on a method to assess the machinability of spalted wood, as relevant to woodturning, using a Universal Test Machine. The method focused on surface resistance to penetration, which the authors argue was a more relevant assessment of spalted wood's machinability than standard density testing. Unlike the work of Christensen, this study offered a nonsubjective method for evaluating the usefulness of spalted wood for its target demographic. Additional method papers were produced in 2009, which helped to define standard methods for testing and evaluating induced spalting. Robinson et al. 2009a established a method for evaluating external and internal pigment on spalted wood by coverage area, while Robinson et al. 2009b suggested the use of vermiculite instead of soil as an incubation substrate due to both the heterogeneity of soil and increased fungal pigmentation in vermiculite.

Stimulation

By the late 2000s, research focus moved away from chemical analysis and understanding how zone lines formed towards stimulation of zone line creation under controlled conditions utilizing known zone line-forming fungi. Substantial research was conducted using sublethal concentrations of copper sulphate, which was found to be stimulatory towards zone line production in *Xylaria polymorpha* (Pers.) Grev. (Robinson et al. 2011a), produced nonstandard decay pockets in *T. versicolor* (Robinson 2011), and positively affected pigment production during antagonistic reactions between *Scytalidium cuboideum* (Sacc. & Ellis) Sigler & Kang/*X. polymorpha* (Robinson and Laks 2011)—controlling the spread of the pink stain of *S. cuboideum* and in some instances causing pink zone lines to form.

Researchers also looked at nonchemical stimulation, utilizing either environmental control or naturally occurring melanin precursors in an attempt to increase fungal pigmentation. The effects of moisture content on melanin and other pigment production by fungi became a key area of interest. Tudor et al. 2011a found no significant effect of moisture available in the substrate in stimulating fungal pigment production with either *T. versicolor* or *X. polymorpha* on American beech (*Fagus grandifolia* Ehrh.). In addition, test block placement within incubation jars, whether above or below the wetted substrate, did affect fungal pigment production, although the effect did not appear to be from differences in block moisture content (Robinson et al. 2011b). Beech blocks left on top of the substrate had more pigment (black from *X. polymorpha* or pink from *S. cuboideum*) than those submerged, while sugar maple blocks had significantly more pigment from *X. polymorpha* when left above the substrate. However, blocks both above and below the substrate did not differ significantly in moisture content, leaving the cause for the increased pigmentation unknown.

Altering the pH of the wood test samples before fungal inoculation did appear to affect pigment formation, with pH levels near 4.5 and 5 causing both *X. polymorpha* and *T. versicolor* to produce additional brown/black pigment on beech wood, although the results were not consistent between multiple tested strains (Tudor et al. 2011b). In sugar maple, pigment was stimulated at pH 4.5 and 5.5 with *T.*

versicolor and pH 4.5 with *X. polymorpha*. The pressurized injection of catechol into wood test blocks did not affect the pigment production of *X. polymorpha* or *Inonotus hispidus* (Bull.) P. Karst. on either beech or sugar maple but stimulated melanin production in *T. versicolor* on beech at the 100-ppm concentration.

Studies on specific fungi

Despite the large number of fungus species that were initially tested for zone line or pigment production, only a small number appeared to routinely produce spalting under controlled conditions. In addition, relatively few wood species had been utilized in previous spalting trials. Hence, several fungi were the subjects of direct study in terms of pigment production under sterile, monoculture conditions, and several papers focused specifically on testing alternative wood species with pigment-producing fungi.

The ability of species within the *Xylaria* genus to produce zone lines without antagonism from a secondary fungus has been thoroughly studied, beginning with Campbell (1933), through Coates (1984), and Worrall et al. (1997). Robinson and Laks (2010a) looked specifically at the ability of *X. polymorpha* to produce zone lines under controlled conditions on varying wood species, with isolates of different ages. They found that sugar maple and aspen (*Populus tremuloides* Michx.) inoculated with *X. polymorpha* showed more zone lines than basswood (*Tilia americana* L.) or birch (*Betula alleghaniensis* Britt.). In addition, the age of the cultures significantly affected the number of zone lines produced on sugar maple, with older cultures producing fewer zone lines. However, culture age did not affect zone line production on aspen.

An additional fungus that was directly studied for induced pigment production was *Chlorociboria* sp., a genus well known for its production of the blue-green pigment xylindein (Maeda et al. 2003). Robinson and Laks (2010b) attempted to increase the amount of xylindein produced by a North American *Chlorociboria* spp. by growing the fungus on a variety of wood species, including those that had been previously colonized by white rot. The isolate produced significantly more xylindein on aspen than on birch or sugar maple; however, pretreatment by a white rot did not appear to affect pigment production.

Spalting with red/pink fungal pigments was explored in Robinson et al. (2011c). Within this study, the authors determined that *S. cuboideum*, regardless of strain, was best suited for red/pink pigment production on wood due to the deep penetration of the pigment, the low incubation time required for pigment penetration, and high reliability of the fungus to produce the pigment over replicate testing. The authors also noted the tendency of blue pigments to form on test blocks incubated longer than 8 weeks and the strong link between wood substrate sterility and amount of pigment produced, with unsterilized test wood showing significantly less pink/red stain than sterile or semisterile pieces.

Studies on specific wood species

Two studies have looked specifically at wood species effects on the pigment production of fungi. The first targeted noncommercial urban tree species in southern Ontario, Canada (Robinson et al. 2011d), while the other looked specifically at American beech (Robinson et al. 2011e). Of the urban tree species studied, the authors found that zone line producing fungi-favored American elm (*Ulmus americana* L.), while *S. cuboideum* (pink/red stain) favored tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle). The authors also reinforced the use of the hard maples as “control” species for induced spalting experiments, noting that all tested fungi readily produced a high amount of pigment on sugar maple and Norway maple (*Acer platanoides* L.).

American beech was found to be problematic when used in induced laboratory spalting experiments (Robinson et al. 2011e). Of the tested fungi (*X. polymorpha*, *T. versicolor*, *I. hispidus*, and *S. cuboideum*), only test blocks inoculated with *S. cuboideum* showed internal pigmentation. The authors determined the visibility of the internal pigmentation to be too low, due to the dark nature of the beech heartwood, and to combat this problem utilized *T. versicolor* as a white rot pretreatment to lighten the wood. The pretreatment significantly increased the red/pink saturation on the test blocks.

Implications and future areas of research

Despite the growing body of literature available on the potential of pigmenting wood with fungi, the high variability between fungal species indicates that there is no one “correct” method for spalting. In reality, the literature indicates that the method for optimal pigment production varies by both fungal and wood species to such a degree that the only “sure” wood species to use is sugar maple, and in addition that few fungal species are even suitable for spalting. Based upon the available literature, zone lines are best produced by either a pairing of *T. versicolor*/*B. adusta* or by solitary isolates of *X. polymorpha*, while the most reliable pigment fungi are *S. cuboideum* and *Chlorociboria* sp. Currently, the color palette available of fungal pigments includes zone lines, bleaching, pink/red stain, blue stain, and to some extent, the blue/green stain of *Chlorociboria* sp. Additional reliable colors will need to be developed in order to broaden both the use and appeal of spalted wood to consumers and industry.

Increasing the amount of pigment produced by fungi does appear to be possible with the application of copper sulfate. It remains unknown whether this method of induced spalting will be as commercially viable as nonadditive spalting, as the consumer draw for "natural" pigmentation may wane somewhat with the addition of an extra ingredient in the process. There is some evidence that wood pH may play a role in fungal pigment production; however, this evidence is preliminary and requires further study. Substrate moisture content does not appear to affect the amount of pigment produced by fungi, due to wood test block moisture equilibration; however, it remains unknown whether wood moisture content may play a role.

The development of fungal pigments for use as decorative color in wood holds considerable market potential; however, this research area is still developing, and several fundamental questions still need to be answered. If commercialization of spalted wood continues to develop, it will become important in the future to have a method for spalted wood stabilization that both insures color permanence (through coatings) and/or strength without brittleness (through impregnation of some type of polymer). In addition, it is likely that toxicity testing will eventually have to be conducted on functional spalted wood. Although there is currently no literature to indicate a toxic nature of any of the identified spalting fungi in this review, a recent abstract from the Mayo Clinic in Florida, USA, suggests a possible causal link between extended work with spalted wood and hypersensitivity pneumonitis (Soto et al. 2011). However, no actual fungi were identified as causal agents in the above study. This addition to the literature of any of the above-mentioned areas would be a substantial input into this developing field. It is possible that full commercialization of the spalting process, along with a full color palette, would help stimulate demand for North American hardwoods, particularly those of lower economic value.

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