Invasive Termites and Wood Protection

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ABSTRACT

Only about 1% of the 2,750 described termite species in the world are considered to be invasive species, but these 28 key termites create a constant need for research in the protection of wood from termite attack. Invasive termites are readily transported, since they all eat wood, are capable of nesting within their food, and easily produce secondary reproductives. Although Hawaii is the most isolated land mass in the world, it is also considered the invasive species capital of the world, with 24 new insects arriving annually. Seven of the eight termite species found in Hawaii are invasive. Both the subtropical Formosan subterranean termite and the tropical Asian subterranean termite occur in Hawaii, one of only three locations in the world where both are found. Largely due to the long-term presence of the destructive Formosan subterranean termite, Hawaii has led the nation in the adoption of termite prevention practices such as the requirement that all structural lumber in wood frame construction must be preservative-treated. Applied research on termite prevention and wood protection can productively range from simple observations, where all research projects begin, to more complex analysis and synthesis of results, to testing theories to determine the mechanisms behind complex questions. Examples from the author's experience that transgress research borders include examinations of the behavioral mode of action of borate wood preservatives in protecting wood from termite attack, and the relationship between termite tunneling patterns and their efficiency in locating food in the environments in which particular termite species evolved.

INTRODUCTION

Aloha oukou. I am grateful to the American Wood Protection Association for the opportunity to deliver this Colley / Hartford Memorial Lecture on "Invasive Termites and Wood Protection" at the 109th Annual Meeting of the AWPA in Honolulu, Hawaii. Hawaii is under constant threat from invasive insect species, and termites are the most economically important insect pests in the Hawaiian Islands. Hawaii has also led the nation in the adoption of termite prevention techniques in building construction and utility installations, including requiring preservative treatment of all structural lumber, sometimes referred to as "whole house treatment." Thus, it is particularly appropriate that we should be devoting quite a bit of the program to discussion of termites at this 109th AWPA conference in Waikiki.

Termites are consistent, and increasingly widely distributed, invasive pest species worldwide. In this paper, I will briefly discuss Hawaii's status as the invasive species capitol of the world, and review the termites found in Hawaii and the use of wood preservatives to deter their attack. Rather than focusing solely on Hawaii though, we will also examine the patterns of termite invasions worldwide, and discuss which termites are the most threatening invaders with the most rapidly growing worldwide distributions.

Finally, I am going to indulge in a little academic license, and discuss a rewarding personal approach to applied research, based around the theoretical model of a three-tiered "Research Space," and the stimulation to the researcher in the transition from the lower tier where *Observation* occurs to the space reserved for *Analysis*, and occasionally onward and upward into the *Theory* space. These theoretical spatial areas where researchers dwell (at least intellectually) overlap, of course, and most applied researchers spend the majority of our time in the border zone where *Observation* and *Analysis* overlap. Research projects that include a trip into the region of *Theory* tend to be very rewarding though, so long as the path remains open back through *Analysis* to the homeland of *Observation*. I hope that a few examples will help to ground this brief discussion of "Zen and the Art of Termite Research" in the real world of wood protection.

INVASIVE SPECIES CAPITAL OF THE WORLD

Hawaii has been referred to as the invasive species capital of the world, which is quite a distinction for a small archipelago of only 16,600 sq. m (6,420 sq. miles) located in the middle of the Pacific Ocean, and representing the most remote land mass in the world. However, it has generally been considered that 15-20 new insects arrive in Hawaii and become established every year (CGAPS 1997). In fact, a recent review of Hawaii Department of Agriculture records indicates that the actual number of new insect introductions each year is even higher than this, at about 24 insects each year (B. Kumashiro, Hawaii Dept. of Agriculture, personal communication). Many of these are significant pests of agricultural crops, such as the coffee berry borer discovered in Kona in 2010 (Burbano *et al.* 2011); human and animal health, such as the little fire ant first found near Hilo in 1999 (CTAHR 2010); or of structures and wood products. About 20 cockroaches have found their way to Hawaii, and over 50 ant species (Grace 2010).

It is likely to be of more significance to the members of AWPA that the number of termite species known to occur in Hawaii has doubled since the early 1990s from four to eight species (Grace 2010, Woodrow *et al.* 1999). Seven of these termites are among the 28 species of termites considered to be invasive worldwide (Evans *et al.* 2013). These termites share characteristics that allow them to be easily transported and readily establish in new locales. Hawaii has the distinction of having the two most widespread and destructive subterranean termites in the world, the Formosan and the Asian subterranean termites, *Coptotermes formosanus* and *Coptotermes gestroi*; and the most widespread drywood termite (living within wood above ground), the West Indian drywood termite, *Cryptotermes brevis*.

How could a small group of island in the middle of the Pacific Ocean, 4,000 km (2,500 miles) from the nearest continent, become so popular with invasive insects? Part of the explanation actually lies in that isolation. Prior to man discovering how to move rapidly around the globe, only a small number of insects were able to brave the ocean and air currents to reach Hawaii. Over time, these evolved into a much larger number of unique native species; but these species evolved without many natural enemies, and also left many ecological niches still unfilled. Thus, later invaders transported by the actions of man, were able to easily out-compete or prey upon the native species, and found unoccupied niches in which they could thrive. Like those hearty early insect colonists though, they also manage to outrun natural enemies left at home, and are able to increase in numbers in their new home without threat of parasitism or predation, at least initially.

And what a wonderful new home these invasive species find in Hawaii, where the temperature at sea level ranges from 22 to 25 ºC (72-78 F) year round. Rainfall can differ within a few miles from less than 500 mm per year to more than 7,600 mm (20 - 300 inches), creating diverse habitats. On the island of Kauai, the rainfall ranges from 500 mm to over 11,600 mm (460 inches) at Mt. Waialeale, the second wettest spot on earth, all within a distance of 20 miles. On the island of Hawaii, the climate ranges from tropical at sea level to temperate 64 km (40 miles) away at an elevation of 3,900 m (13,000 ft). Weather and vegetation patterns in the islands have combined to create tremendous soil diversity as well, with ten of the twelve soil orders recognized by USDA found in Hawaii (Deenik and McClellan 2007).

So, once the insect invaders arrive in Hawaii, there is a lot to welcome them. But, how do they travel 4,000 km over the Pacific Ocean? The answer lies with trade, tourism and military traffic. Hawaii is a major entry point for goods from Asia, and from parts of the Americas. Approximately 85% of the food, and about 98% of all goods, in Hawaii are imported, but only a small fraction of these imports and transient goods can be inspected, and cryptic insects are difficult to find under the best conditions. Commercial trade includes plant materials, food materials, lumber, furniture, and wooden shipping pallets, the latter of which are commonly infested by termites (Woodrow *et al.* 2006). Household effects of new residents are another source of insect infestation. Many of these new residents are part of Hawaii's large transient military population; and military traffic brings equipment and other materials that are difficult to inspect thoroughly for insect hitchhikers, particularly when there are large redeployments from the Philippines or other Pacific locations, or frequent exchange with war zones such as Vietnam in the 1960s, or regions needing immediate humanitarian relief, such as Southeast Asia following a typhoon. Incidences of successful insect transport and establishment have naturally increased as mankind has become more mobile. Distances that used to take months to traverse by ship are now bridged by air in less than two days.

TERMITES IN HAWAII

Prior to the 1860s, only three termite species were known to occur in Hawaii: the West Indian drywood termite (*Cr. brevis*), lowland tree termite (*Incisitermes immigrans*) and forest tree termite (*Neotermes connexus*). All three of these termites are members of the drywood termite family Kalotermitidae, meaning that they nest directly in wood (their food material) above the soil surface, and do not nest in or tunnel through the soil, as is the case with the subterranean termite family Rhinotermitidae.

The West Indian drywood termite is a very common pest worldwide of seasoned wood and wooden articles, but the latter two termite species generally occur in stumps or fallen wood, or in dead limbs on living trees. Like the West Indian drywood termite though, the lowland tree termite is considered to be an invasive termite that is expanding its range worldwide (Evans *et al.* 2013), and is occasionally (and perhaps more often than has been recognized) found infesting wood in structures, particularly rough-cut lumber or rustic trim in Hawaii. The forest tree termite, on the other hand, has only been found on Pacific islands, is considered endemic to the Pacific Basin, and has not been reported to attack seasoned wood.

Although the Formosan subterranean termite, the fourth termite species to reach Hawaii, was not officially reported to occur in Hawaii until 1913, when it was described as having been present for "considerable time" in damaged floor timbers in a Honolulu cathedral (Swezey 1914), it probably came to Hawaii from southern China in the mid-1800s, near the end of the sandlewood trade. An 1869 Honolulu newspaper article described damage to a fence by "white ants" that was clearly caused by subterranean termites (Yates and Tamashiro 1999).

In the 1990s, four additional termite species were found in Hawaii, doubling the number of established termites to eight (Grace *et al.* 2002, Grace 2010). One of these was the Pacific dampwood teremite, *Zootermopsis angusticollis*, native to the west coast of North America and a member of the rotten-wood family of termites (Termopsidae). As the name implies, this termite occurs in damp, rotting wood such as logs and stumps, and occasionally in structural lumber on or near the soil that is excessively damp. Although infestations have only been found at high elevation in Kula, Maui, winged reproductive dampwood termites (alates or swarmers) have been collected on other islands, suggesting that there may be undiscovered infestations. This is controversial, since winged termites often land on stacks of lumber and can be transported between islands or from the US west coast in this fashion.

The other three termite species discovered in Hawaii at the end of the 20th century were all found on the island of Oahu and all infest buildings, although their distribution in Hawaii is still very limited. These are the Indo-Malaysian drywood termite (*Cryptotermes cyanocephalus*), western drywood termite (*Incisitermes minor*), and Asian subterranean termite (*Co. gestroi*, first referred to in Hawaii under the synonym *Co. vastator*). The Asian subterranean termite is basically the tropical equivalent of the subtropical Formosan subterranean termite, and Hawaii is one of three locations in the world where the climate is suitable for both of these worldwide pests to occur simultaneously (Grace 2006, Hapukotuwa and Grace 2012).

INVASIVE TERMITES

Only 183 (7%) of the 2,750 described species of termites in the world have been recorded as pests of wood in service, trees, or agricultural crops; and only 80 of these (3% of the total number of described termites) damage buildings and furniture (Evans *et al.* 2013). Only 28, or about 1%, of the known termites are considered to be invasive species today, an increase from 17 termite species considered invasive in 1967. Invasive termite species are those that are capable of readily leaving their home region and moving to other parts of the globe, and they typically eat wood rather than grasses or other materials, are capable of nesting directly in their food source (wood), and can easily produce secondary reproductives so that a group of termites can thrive even if they are removed from their queen or she dies. These characteristics are most common in the drywood and subterranean termite families, which together make up 21 of the 28 species on the list of invasive termites. The most invasive species come from the tropical regions of South and Southeast Asia (seven species) and South America (six species) (Evans *et al.* 2013).

Termites are social insects, and live in colonies in which a king and queen produce all the offspring, and those offspring assist in the care of the young and distribute duties such as foraging for food and defense of the colony among various castes, or individuals with body forms specialized to carry out these different functions. For example, the soldier caste may have enlarged heads and protruding mandibles (jaws) that can bite an invading ant in half, but cannot chew wood, requiring these soldiers to be fed by members of the less modified worker caste that tunnels for food, shares that food by regurgitation, and takes on the day-to-day chores of colony maintenance. The winged reproductive caste are fully formed males and females that will fly in swarms to find and mate with termites from other colonies, and then settle down as king and queen of their own family, or colony. In invasive termite species, other individuals such as the workers are also capable of rapidly growing (or molting) into a secondary reproductive if the queen is dead or missing, facilitating both longevity of the original colony and also creation of new colonies by budding off from that parent colony.

Drywood termites are sometimes referred to as “one piece termites” because they live in colonies of 50 to several thousand individuals in a single piece of wood or several tightly connected pieces. By contrast, subterranean termites may nest temporarily within damp wood (in a cargo container or the hold of a ship, for example), but prefer to live in colonies of several thousand to several million in the soil, tunneling upward and outward to find wood to feed upon at or above the soil surface.

The cryptic habitat of drywood termites within a piece of wood makes them both very easy to transport unknowingly, and difficult to observe and control. Often the hard, six-sided, fecal pellets left in piles by the termites as they clean out their gallery systems are the only evidence of a drywood termite infestation. Termites are capable of ingesting and utilizing virtually all of the cellulose in the wood upon which they feed, and defecate the lignin and hemicellulose by producing 0.7-1.0 fecal pellets each day (Grace 2009, Grace and Yamamoto 2009), suggesting that if all the fecal pellets produced by a termite infestation could be collected over several successive periods, one could possible estimate both the size and age of the cryptic termite colony. Perhaps more practically, Haverty *et al.* (2005) demonstrated that these fecal pellets carried the same chemical signature (cuticular hydrocarbons) of the termite species producing them, and thus could be used as a survey tool, although the analyses required are neither simple nor inexpensive.

Their cryptic living habits within wood not only make detection difficult, but also make drywood termite control challenging, which is why whole-structure fumigation or heat treatment remain the preferable control options, since these will kill all termites anywhere in the structure, whether or not all infestations have actually been located. Local methods of treatment usually involve injecting an insecticide into holes drilled in the wood to reach the termite galleries and are effective only when they actually reach every termite colony. If a single termite colony has a large gallery system extending through several different connected boards, this may be no problem, but it is equally possible to have more than one drywood termite colony within a single board, with no connection between their gallery systems (Grace *et al.* 2009). Experiments injecting insecticides into boards where the termites appear to be most active have demonstrated that this approach to drywood termite control is literally hit or miss, with the average termite mortality ranging from 4-77% no matter what insecticide was used, and far more dependent on how many termites happen to be near the injection site than on the insecticide applied (Woodrow and Grace 2005, Woodrow *et al.* 2006).

In contrast to drywood termites, subterranean termites usually live in very large colonies in the soil, with gallery systems over an area potentially as large as a football field. The population size of these termite colonies, and the distances over which termites tunnel have been measured using mark-recapture methods where termites are captured, fed an indelible dye and returned to the soil (Grace *et al.* 1989); and genetic fingerprinting techniques that allow an individual termite to be assigned to its home colony (Husseneder and Grace 2001). Yet, despite these very large subterranean gallery systems, a small number of individuals broken off from the main colony, such as trapped while feeding in a piece of wood above ground, can persist and develop reproductive capabilities, and initiate a new gallery system when they once again come in contract with the soil. This flexibility explains how the Formosan subterranean termite has become distributed globally in the subtropics and warmer edges of the temperate regions; the Asian subterranean termite globally in the equatorial zone; and the eastern subterranean termite (*Reticulitermes flavipes*) in North America, Europe, and South America, including Easter Island (Evans *et al.* 2012).

The tropical distribution of the Asian subterranean termite (*Co. gestroi*, formally known as *Co. vastator* in the Pacific Basin) and subtropical territory of the Formosan subterranean termite (*Co. formosanus*) overlap only in southern Florida, Taiwan, and Hawaii. These two closely related species of the genus *Coptotermes* are superficially similar in appearance and feeding habits, but their tunneling patterns differ dramatically, as discussed below. Numerous comparative studies at the University of Hawaii have documented both the similarities (in wood preferences, for example, as shown by Hapukotuwa and Grace [2011]) and the many biological, ecological, and behavioral differences between these two termites. For example, the Asian subterranean termite prefers a warmer environment than the Formosan subterranean termite (Hapukotuwa and Grace 2012a) and is less susceptible to attack by certain insect-killing parasites (Mankowski *et al.* 2005), but feeds more slowly (Uchima and Grace 2003) and is 5-times more susceptible to desiccation under conditions of low humidity than its subtropical congener (Shelton and Grace 2003).

WOOD PRESERVATIVES IN HAWAII

In terms of protecting structures from these invasive termites, Hawaii has played a unique role in the development and application of wood preservatives, as has been reviewed by Wilcox (1984) and Grace (2002). The Hawaiian Islands have been a popular location for field testing of wood preservatives for many years (Preston *et al.* 1985, Morris *et al.* 2011), and the setting of quite a few technical, commercial and legal discussions and sometimes pointed disagreements over the efficacy and application of different preservatives for protection of structural lumber. Hawaii is unique among the 50 states in requiring (on a county basis, but statewide) that all structural lumber in wood frame construction must be pressure treated with a preservative system approved by the code authorities. This practice began in the early 1960s, with the "Hawaii Use Only" standard for CCA treatment of un-incised Douglas-fir to a target 0.25 pcf retention. An alternative provision in the building code specifying use of a sill plate incised and treated to 0.40 pcf ground contact retention without whole-house treatment was rarely used and was removed in the late 1980s. Soil treatment with an insecticide, and later the use of a gravel or stainless steel physical barrier were also required by the building code. Preservative systems have changed over the years, and today disodium octaborate tetrahydrate (DOT) is the most common preservative in Hawaii for structural lumber and plywood.

Attempts in 1999-2000 in the state of Louisiana to implement whole-house lumber treatment requirements modeled after those in use in Hawaii in order to address the enormous Formosan subterranean termite problem in that state unfortunately came to a halt amid local political turmoil. It appeared that many lumber suppliers and builders in Louisiana had either not had the first-hand experience with termite damage of their counterparts in Hawaii, or had managed to distance themselves further from the economic ramifications. In a public conference sponsored by the LSU Ag Center in mid-2000, it became clear that many local wood treaters and suppliers resisted treating to above-ground retentions and the need to keep both above-ground and ground-contact wood products in inventory, and the additional cost of treatment was strongly opposed by builders (McClain 2000). Thus, Hawaii remains the state with the most stringent building requirements with respect to termite control, although some counties in Florida have enacted similar code modifications.

TRANSCENDING THE BORDERS OF RESEARCH SPACE

In closing, I would like to briefly share some views on the rewards of applied research, with a couple of illustrations from my own experience. We can model the concept of "Research Space" as three overlapping spheres, linked together and rising from the ground upwards into the sky (Figure 1). The first sphere closest to the ground is labeled *Observation*, the second middle area is where *Analysis* (including synthesis) takes place, and the third and uppermost sphere in our model is reserved for *Theory*. The *Observation* space might be called the "What?" area, the *Analysis* sphere connected to it on top is the "Why?" area, and the uppermost *Theory* space is where we consider "What's it all mean?"

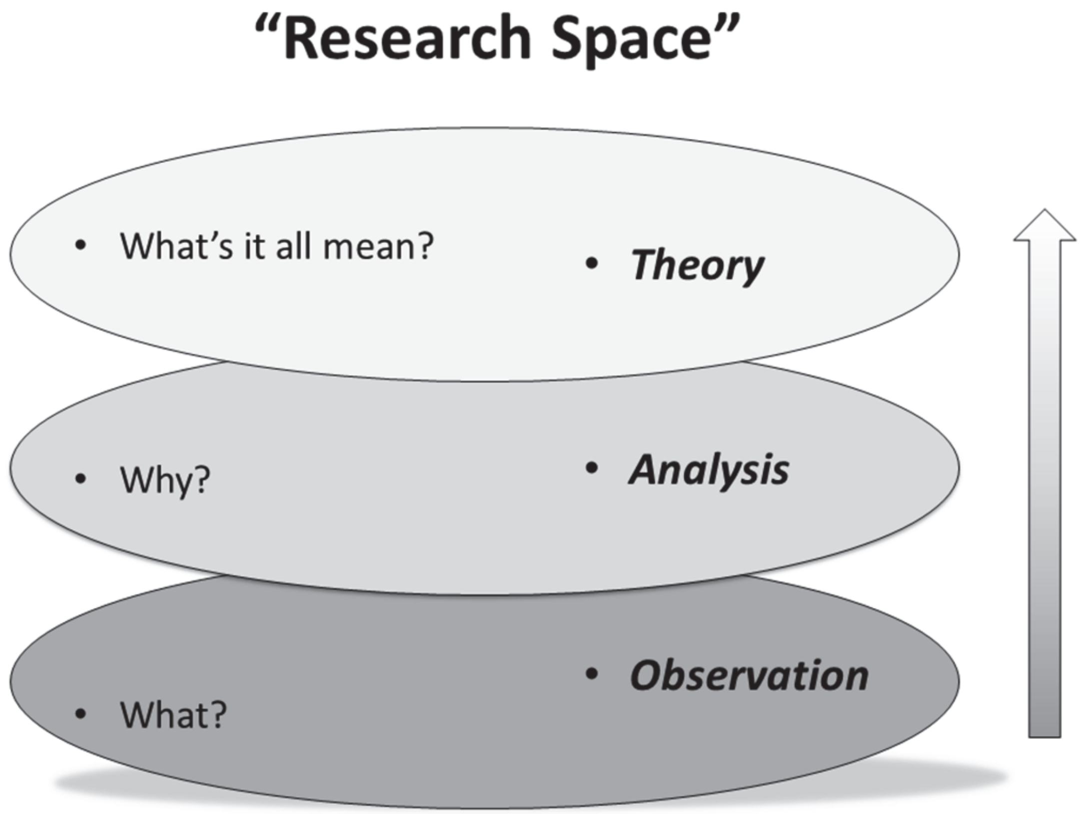
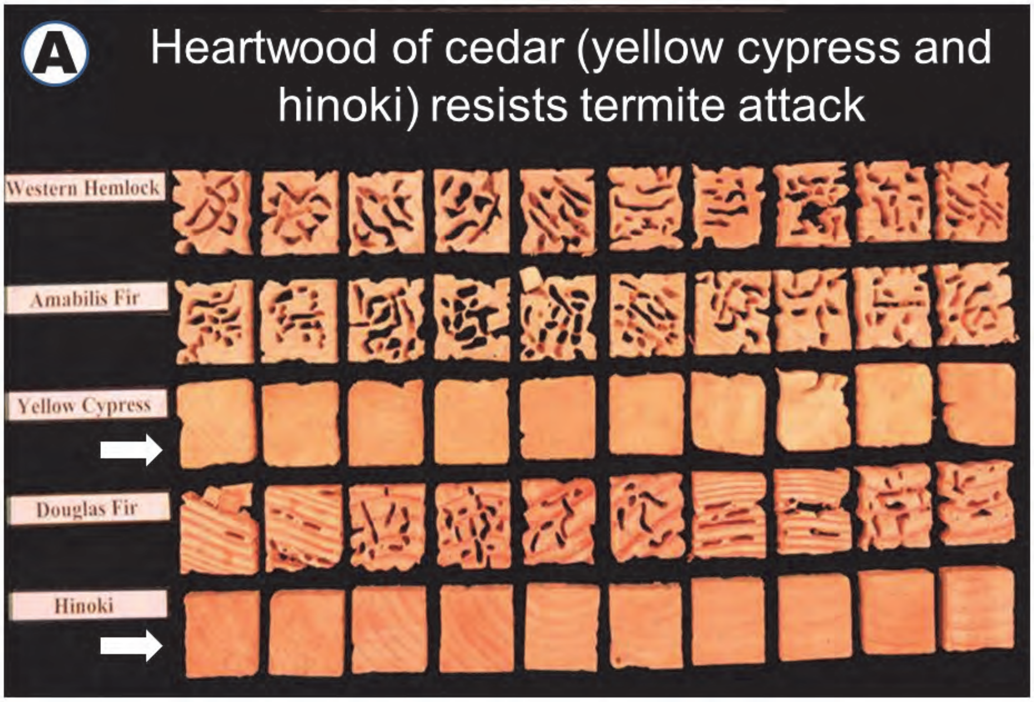


Figure 1: All research projects begin with observation, and each successive level of enquiry brings rewards

We applied researchers spend a great deal of our time in the *Observation* and *Analysis* regions of Research Space. For example, we may evaluate the efficacy of a particular wood preservative against termites, or the durability of different wood species. Figure 2 illustrates the results of a laboratory evaluation of the heartwood and sapwood of five Pacific Rim woods using a standard AWPA E1 protocol, in which a 25 X 25 X 6 mm wafer of each wood was exposed to 400 Formosan subterranean termites (360 workers, 40 soldiers) for 28 days. In this test, we observe that the heartwood of Yellow Cypress (also known as Alaskan Yellow Cedar) and the common Japanese timber Hinoki are resistant to termite attack. However the sapwood of each of these two durable species is completely susceptible to termites, as is both the heartwood and sapwood of the four nondurable wood species included in this test. As an observation, this demonstrates both that Yellow Cypress and Hinoki are durable (while the other species are not), but also that architects and builders must specify "heartwood only" to ensure that durability.

This more detailed *Analysis* and synthesis to address the question of "Why?" leads us to the edge of the third region of our Research Space, the area of *Theory*, or "What's it all mean?" Here we might hypothesize that species in the family Cupressaceae may be identified solely by characteristics of their extractive chemistry, that chemical titer or ratios may be influenced by stand and site conditions, or that evolutionary relationships within the Cupressaceae (or among durable tree species) may be revealed by a comparative meta-analysis of extractive similarities and diversity. On a practical side, development of novel extractive-based wood preservative systems might be investigated.

Every research project has to be grounded in *Observation*. No region in this model of Research Space is inherently better than any other, each region provides valuable information, and travel from one region to another is not necessarily a goal in every research project. But, speaking as a researcher, it is satisfying and potentially very rewarding when one is able to cross these borders.



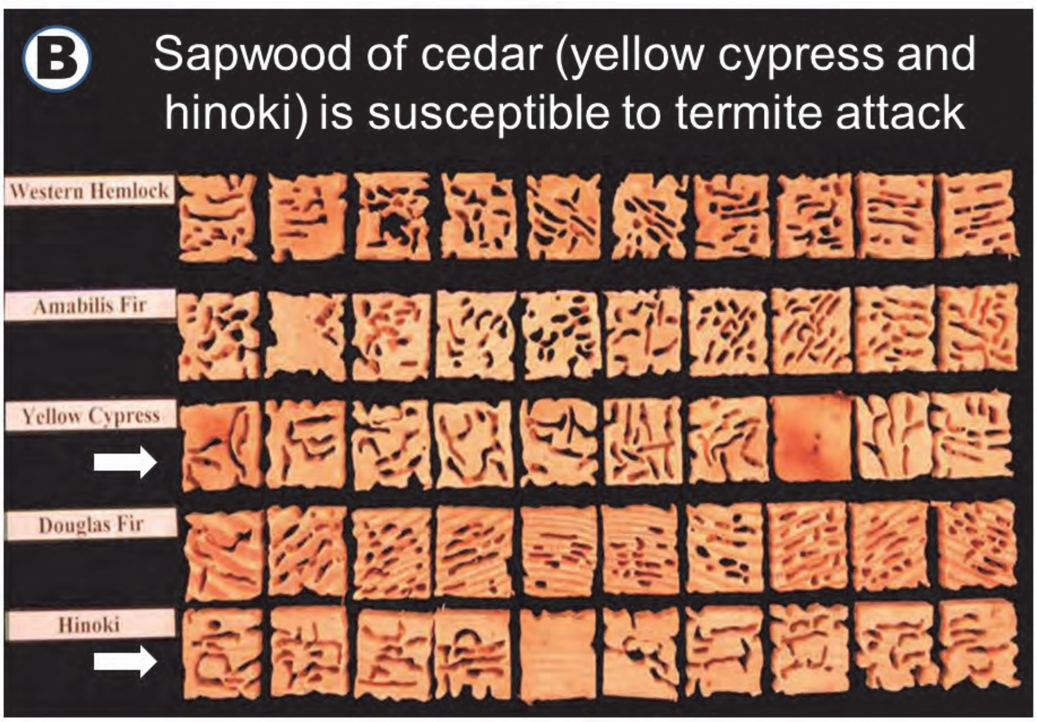


Figure 2: A comparison of the termite resistance of the heartwood (A) and sapwood (B) of five Pacific Rim wood species

These rewards from fully exploring the Research Space are illustrated in the continuing investigation of the mode of action of borates such as DOT in protecting treated wood from termite attack. We know from *Observation* in both laboratory (Grace *et al.* 1992) and field tests (Morris *et al.* 2011) that appropriate retentions of borates will protect the treated wood from significant damage. But how do borates protect the wood from termites? From further *Analysis*, we know that borates are neither strongly repellent nor rapidly toxic to termites, and that they can even recover from sublethal exposures (Gentz and Grace 2006, 2009). Some initial nibbling will always occur, but it ceases over time in relation to the boron concentration. To determine whether this minor surface feeding could threaten long-term protection of the treated wood in service, where several termite colonies might invade and investigate this wood over the life of the structure, we evaluated the cumulative damage to borate-treated wood sequentially exposed to termites at three different field sites. With each exposure to a new termite colony, there was initial nibbling, but the rapid cessation of feeding each time supported the conclusion that the wood mass loss resulting from a succession of termite infestations would never result in structural damage (Grace and Yamamoto 1994).

Analysis of the results of this sequential exposure study, coupled with further *Observation* through additional investigations of the efficacy of various borate compounds and treatment methods, also strongly suggested that termites were not leaving a chemical cue on the wood to deter future other foraging termites from feeding on it. If this had been the case, there would have been no successive tasting of the treated boards. This led to the *Theory* that perhaps a form of associative learning was involved in this gradual avoidance by termites of the borate-treated wood. Learning is controversial in insects, but has been previously demonstrated to occur at a much simpler level in termites (Grace 1989).

Hypothesizing that termites may be capable of mapping the woody resources that they encounter while creating their gallery systems in the soil and then selectively avoiding those resources with negative consequences, we tested this theory in large termite foraging arenas installed both in the laboratory, and at an active Formosan subterranean termite field site in order to ensure that the easier to interpret laboratory results were truly representative of naturally occurring termite behavior in the field (Campora and Grace 2007). Each foraging arena resembled a horizontally-oriented ant farm, with damp sand sandwiched between two acrylic sheets, and termites allowed to enter through a portal in the center of the arena. Termites tunneling outward from the center of the arena encountered smaller feeding portals in the arena, each containing a block of either borate-treated or untreated Douglas-fir wood. Each arena was divided into an east and west half, with the feeding portals in each half of the arena containing either all treated or all untreated wood. After the termites had thoroughly explored each arena (two weeks in the laboratory, one week in the field), the location of the treated and untreated wood was switched. Daily surface maps of the spatial distribution of live termites and cadavers in each arena were created from photographs to determine whether termites were avoiding areas of the arenas with both treated wood and termite cadavers present. Necrophobia is a known behavior in termites and has been suggested as a possible reason for avoidance of treated wood.

This was a large-scale experiment, with 1,500 termites in each laboratory arena, and a field colony with millions of termites allowed to tunnel up from the soil through plastic pipes into the field arenas. Interestingly, the spatial maps demonstrated that the impact of borate ingestion was slow, and no termites died in the immediate vicinity of the borate-treated wood blocks. Initially, termite tunnels radiated outward from the point of introduction in the center of the arenas, as demonstrated in other investigations of termite tunneling behavior (Campora and Grace 2001), and live termites were distributed throughout the arenas without regard to the location of the treated wood. However, after several days, termites began to avoid the side of the arena with borate-treated wood, and aggregate and feed on the side with untreated wood. When the location of the treated and untreated wood was switched, there was a lag period of several days before termites ceased all feeding on the new blocks of borate-treated wood placed in the locations originally containing untreated wood, and again completely shifted their feeding activity to the opposite side of the arena, now containing untreated wood. These same phenomena were observed in both laboratory and field arenas: no dead termites near the borate-treated wood, initial tasting of both the original and the “switched” borate treated wood, and a lag time of several days once the wood was switched before the termites refocused all of their feeding activities on the side of the arena now containing untreated wood.

These results (Campora and Grace 2007) clearly demonstrated associative learning in Formosan subterranean termites. Moreover, termites did not learn to recognize the borate treatment as undesirable, since they tasted the newly placed treated blocks when treated and untreated wood locations were switched. Rather, the foraging termites mapped the locations of both desirable and undesirable resources within their gallery network, creating a road map that took a bit of time for them to redraw when familiar objects were moved, as occurred when the treated and untreated wood blocks were switched. What specific cues are involved in drawing this map is another question to be addressed in future work.

A second, and final, example of the rewards of transgressing the borders between *Observation*, *Analysis*, and *Theory* in Research Space is offered by research on the comparative tunneling behavior of the Formosan and Asian subterranean termites. We first noticed that the tunneling patterns of these two species were very different in a laboratory test based on the AWPA E1 protocol (Grace *et al.* 2004). We saw that the tunnels created by the Asian subterranean termite were thin and highly branched, appearing overall like a mosaic or jigsaw puzzle. Formosan subterranean termite tunnels, on the other hand, were thicker and far less branched.

The next step was to move beyond simply recognizing that there were visual differences, and determine what measurable, quantitative differences (tunnel width, number of tunnels per unit area, number of branches per unit of tunnel length) contributed to this impression, using the foraging arenas described above. This *Analysis* established that the tunneling of the two termite species did indeed statistically differ in each of these variables (Hapukotuwa and Grace 2012b).

Why would these two related termite species exhibit such different tunneling patterns? Since subterranean termite tunneling patterns are a direct reflection of their foraging strategies, these differences give rise to the *Theory* that each species may have evolved to forage most efficiently in its particular ecological habitat. Perhaps vegetation is denser and more uniformly distributed near the equator, and trees become more widely distributed and woody resources more separated from each other and "clumped" as one moves further away from the equator. If trees are more densely and evenly distributed near the equator, then an equatorial termite like the Asian subterranean termite may find food (wood) more efficiently by an intensive search of the immediate area where food has already been found, rather than by moving further away from that location and searching for more distant food. Since termites forage for food by tunneling, an intensive local search would be facilitated by creating a highly branched network of short tunnels.

On the other hand, if fallen wood becomes a rarer occurrence as the distance from the equatorial zone increases, and trees tend to be separated rather than clustered tightly together, a more efficient method of finding food in subtropical and temperate regions might be to strike out in all directions with long and unbranched tunnels until one runs into a new piece of wood, rather than waste time and energy searching intensively in a single location for more wood. Such straight tunnels are characteristic of the Formosan subterranean termite, which lives in the subtropics and the warm temperate regions of the world.

To test this relationship between termite species tunneling patterns and increased foraging efficiency under specific environmental conditions, we mimicked the more widely separated, or clumped, distribution of woody resources that might occur in subtropical and temperate regions. We placed a single piece of wood at either end of a foraging arena, and released the termites in the center. Our hypothesis was that the highly branched tunnel network favored by the Asian subterranean termite would put it a disadvantage in this experiment, and that it might take longer to find the first piece of wood at one end of the arena then the Formosan subterranean termite, with its long, straight tunnels. Even if the two termite species did not differ in the time taken to find the first piece of wood, which was possible since the arenas were fairly small, the longer and straighter tunnels of the Formosan subterranean termite should give it a definite advantage in discovering the second piece of wood at the opposite end of the arena, since the Asian subterranean termite would likely start constructing a dense network of tunnels around the first piece of wood instead of immediately striking out across the arena. As it turned out, our predicted winner of this contest, the Formosan subterranean termite, did indeed find the first piece of wood in the arenas an average of 1 day faster than the Asian subterranean termite (2.5 vs. 3.5 days), and then discovered the second piece of wood at the opposite end of the arena an average of 2.5 days faster as well (6 vs. 8.5 days) (Hapukotuwa and Grace 2012c). These results were a satisfying affirmation of the *Theory* developed through *Analysis* of our initial *Observation* of termite tunneling behavior.

There is no question that invasive termites will continue to increase their global distribution, likely accelerated by climate change, and that wood protection will be a continuing need for mankind. Likewise, there is no question that the more we learn about termites, the more we will still want to know, and the more creative approaches we will need to develop to gain this knowledge. Again, I greatly appreciate this opportunity to share my thoughts with my colleagues in the American Wood Protection Association. A hui hou kakou.

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