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REVIEW

Heartwood Durability: The Quest for Natural Decay Resistance in a Changing Resource

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Abstract

Purpose of Review Fast-growing plantation resources will increasingly be relied upon to meet global demand for renewable timber products. Concerns exist regarding the quality of wood from plantations and second-growth forests; however, the heartwood quality of timber sourced from plantations and grown for its distinctive color and durability has received little attention. We examine the current status of selected species (in terms of research and development related to heartwood quality) known for their valuable heartwood and explore options that might maintain or improve heartwood quality of plantation grown trees.

Findings Plantation grown trees of all species examined had heartwood inferior to that sourced from natural forests. Management of plantation forests to maximize growth can unintentionally promote one process (growth) over other processes (heartwood formation) that may be detrimental to the management objectives related to heartwood durability and color. Heartwood characteristics can be targeted for improvement via breeding or by clonal forestry. Silvicultural interventions to induce a stress response may also improve heartwood quality.

Summary Failure to produce quality heartwood has manifold implications, both for plantation growers who may be unable to sell their products for the highest price, and retailers whose reputations depend on meeting customer performance expectations. Management decisions that deliberately cause a stress response (as opposed to maximizing growth) should be considered if plantations are being established using species valued for their heartwood properties. Advanced genetics and silvicultural strategies to promote heartwood formation on suitable sites are necessary to ensure that high value heartwood can be obtained from plantation forests.

Keywords Advanced genetics · Durability · Heartwood quality · Silvicultural interventions

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Introduction

Society has historically relied on native forests (either primary or secondary, where the first is a relatively undisturbed forest, and the latter a forest that has regrown after harvesting) to supply a multitude of fiber products. Recognition that forests are finite and provide society with a range of valuable ecosystem services has fostered a transition from harvesting native forests to an increased reliance on planted forests (see Payn et al. [1] for a definition of what constitutes a planted forest). Globally, the plantation estate has risen from 167.5 million ha in 1990 [1] to an estimated 312 million ha in 2025 [2] and investment in plantation establishment is ongoing. With fast-growing plantation resources playing an increasing role in meeting the global demand for renewable timber products, the quality of plantation-grown timber is of critical importance [3].

Concerns about the quality of wood sourced from plantations and second-growth forests date to the 1930s [4–12]. Research has primarily focused on density variation in response to growth acceleration and the application of various silvicultural practices (planting density, fertilization, competition control, precommercial thinning) in species such as loblolly pine (*Pinus taeda* L.), radiata pine (*Pinus radiata* D.Don) [13–16], and teak (*Tectona grandis* L.f.) [17, 18]. However, far less attention has been paid to the heartwood quality of timber sourced from plantations specifically grown for its distinctive color (which is darker than light colored sapwood), odor and resistance to biological decay.

The unique characteristics of durable heartwood rely on the presence of non-structural, low molecular weight secondary metabolites collectively referred to as extractives [19, 20]. Quantitative extractives determination is achieved using solvents with differing polarities to remove compounds of interest [20]. Typically, extractives content exhibits a radial increase from the pith reaching a maximum concentration at the heartwood - sapwood boundary, whereas concentration decreases with height [20–25].

Failure to produce heartwood lacking characteristics typically associated with a given species, has manifold implications, both for plantation growers who may be unable to sell their products for the highest price, and retailers whose reputations depend on meeting customer performance expectations. Many species known for their unique heartwood have significant cultural and ceremonial importance. These species have been traditionally used for producing high-value products including outdoor furniture [26], musical instruments [27–29], machine parts [30], dyes [31] and materials for exterior applications where inherent durability is required [30]. Maintaining wood supply of suitable quality is critical for these products.

Hillis [32] referred to the importance of an enhanced understanding of heartwood extractives in his preface of “Heartwood and Tree Exudates”. He stated “Greater understanding of their formation and their role in tree protection is needed if our remaining forests and the new plantations are to be maintained in a healthy and productive condition.” Looking to the future he concluded “Greater understanding of their biosynthesis should result in the enhancement of the consistent production of required compounds in the tree.” Almost four decades on, we are no closer to understanding how we can enhance heartwood properties of durable species rapidly grown in plantations. Therefore, we aim to review the current status of heartwood quality and related research for a selection of species recognized for their durability in native and plantation forests, and to explore options (tree improvement, silvicultural interventions, chemical treatments) that might maintain or improve heartwood quality of plantation grown trees.

Wood Quality of Species Producing High Value Heartwood and Grown in Plantations

Many species are recognized for their unique and valuable heartwood [20]. In the past, this material was sourced from primary forests but now this is transitioning to either naturally regenerated boreal and temperate forests (approximately 44% of industrial roundwood production) and planted forests (46% of industrial roundwood production) [3]. Here we provide information on the status of three species that are amongst the most important on global markets. Two of these species, sandalwood and teak, are advanced in terms of research and development, and another; mahogany, is less advanced. A brief review of selected species follows with a focus on the comparison of properties (including durability) of heartwood of trees from primary forests with that of heartwood from regrowth or planted forests. We recognize that several additional species valued for their heartwood and included in tree improvement programs could have been included. These include, but not limited to, black walnut (*Juglans nigra* L.), black locust (*Robinia pseudoacacia* L.), hinoki (*Chamaecyparis obtusa* (Siebold and Zucc.) Endl.), rosewood (*Dalbergia* species), Siberian larch (*Larix sibirica* Ledeb.), sugi (*Cryptomeria japonica* (L.f.) D.Don) and western red cedar (*Thuja plicata* Donn ex. D.Don). Finally, an example is provided of a successful breeding program in New Zealand focused on producing durable wood.

Sandalwood

Sandalwood is the scented heartwood of species in the genus *Santalum*. About seventeen species and one extinct species of sandalwood have been described, distributed naturally throughout India, Indonesia, Australia, and the Pacific Islands [33]. Indian sandalwood (*Santalum album* Linn) and Australian sandalwood (*Santalum spicatum* [R.Br.] A.DC.) are the main commercial species valued for their heartwood and oil. Heartwood harvested from native forests is being increasingly replaced by heartwood from plantation trees due to the overexploitation of the former [33, 34].

Sandalwood has traditionally been harvested from mature trees. Texeira da Silva et al. [35] and others note that heartwood is absent in young trees, and only trees older than 30 years have oil-rich heartwood. Plantation-grown sandalwood is harvested at much younger ages (Fig. 1), and there is concern that heartwood from fast-grown, immature trees will lack the properties that make the wood so valuable. Understanding heartwood formation, especially through increasing plantation productivity, is crucial for creating sustainable sandalwood resources.

Sandalwood grades depend on axial heartwood oil gradients. The oil consists primarily of terpenes, of which α-santalol and β-santalol (typically 50–60% and 20–25% respectively of total oil) are the most common [36]. The presence of the oil in the heartwood may contribute to the resistance of the living tree against pathogens and to the durability of wood [37]. Oil concentration and quality are greatest in the stump and major roots, declining upward through the stem and branches [38]. The production of large quantities of high-quality heartwood and oil is necessary for short-rotation financial feasibility.

Fig. 1 An example of heartwood development in 13-year-old Indian sandalwood trees established in Northern Australia (courtesy: Dan Firth, Apical Forest management)

There is no consensus on when sandalwood initiates heartwood formation, and little information is available on the factors that trigger the process or the rate at which it subsequently develops. However, tree age and size are most frequently cited [39–41]. For example, Brand and Norris [41] analyzed six families of Australian sandalwood at ages 10 and 18 from a Western Australian trial and found that the mean oil concentration increased from 0.8 to 1.3% with the mean α-santalol concentration increasing from 8.6 to 13.8% over that time. Mean tree diameter, which was measured 0.3 m from the ground, ranged from 84 to 99 mm at age 10 and increased to 113–135 mm by age 18. The authors did not report data on heartwood diameter, and the data did not suggest a relationship between tree diameters and oil yields. Similarly, Brand and Pronk [40] found that mean heartwood proportion and oil concentration significantly increased with age in Australian sandalwood trees planted in southwest Western Australia. Trees aged 8–26 years had oil and α-santalol concentrations that were high at the base of the trees and roots, but levels were lower in 8-11-year-old trees. Conversely, Arunkumar et al. [39] reported a weak positive correlation ($R^2=0.40$) between tree diameter measured at 0.6 m from the ground and heartwood diameter, for 20-year-old Indian sandalwood trees from a trial in Bangalore, India. However, no relationship between tree diameter and oil yield nor between heartwood proportion and oil content was observed. They also noticed that approximately 14% of trees sampled lacked visible heartwood.

Tree diameter at 0.2 m above ground was strongly correlated with merchantable mass ($R^2=0.92$), heartwood mass ($R^2=0.84$), and oil yield ($R^2=0.84$) for ninety Indian sandalwood trees (19 to 23 years) from a trial established in the Ord River Irrigation Area (Northern Territory, Australia) [42]. Tree diameter varied from 100 to 400 mm, heartwood from 19.8 to 70.5 kg per tree, and oil yield from 4.2 to 4.4%, while mean α-santalol concentration ranged from 46.4% to 48.0%. Similarly, Brand et al. [36] reported variable heartwood yields (5.8 to 43.7 kg/tree), partly due to tree size, for thirty-two 16-year-old Indian sandalwood trees growing in Kununurra, Western Australia, with the larger trees generally having more heartwood. At age 16, tree diameter at 0.3 m height (50–350 mm) was closely correlated with the air-dry mass of heartwood per tree ($R^2=0.87$).

One silvicultural approach to increase heartwood proportion is to use physical or chemical treatments. Li et al. [43] found that the mechanical damage of Indian sandalwood tree stems alone did not noticeably affect heartwood formation, while a combination of mechanical damage and chemical treatment with hydrogen peroxide could increase yield of heartwood and oil. Barbour [44] found that mechanical wounding of 10-year-old Vanuatu sandalwood (*Santalum austrocaledonicum* Vieill) stems induced lanceol rather than

Fig. 2 An example of teak sawlogs from an 18-year-old plantation in central Brazil. (Source: C. Mora)

santalol and that ethylene resulted in immediate santalol production during heartwood formation. Ethylene, as a foliage spray of ethrel, and the gibberellin-inhibitor, paclobutrazol, as a root drench, also positively affects oil production. These findings support the assumption that senescence regulates sandalwood oil production. Physical wounding has also been reported to significantly affect induction of oil production in Australian sandalwood, compared to chemical treatments. However, site variation had the greatest impact on oil production among the treatments studied [45].

Teak

Teak, which occurs naturally in forests of India, Laos, Myanmar, and Thailand [46, 47], is one of the most important globally traded tropical decorative species [48] and has been the subject of extensive research. Based on durability and heartwood color, four categories of wood are recognized [49]: (i) uniform golden yellow brown (typical), with high durability, (ii) darker yellow brown, of high durability, and (iii) uniform grey-brown (produced from pole sized trees), and (iv) light uniform yellow, both of lesser durability. Teak heartwood contains several quinones (desoxylapacho, tectoquinone, lapachol, isolapachol) [24, 50–54], which confer insect [55, 56], fungal [53] and marine borer resistance [57].

Teak is widely planted for sawlog production (Fig. 2) in tropical regions of Latin America, Asia, Africa and Oceania [48]. It is grown on short-rotations (harvest age approximately 18 years) [17] utilizing clonal forestry [58, 59], precision silviculture [60] and high intensity management [48]. Heartwood produced in trees from these plantations is recognized as being different to that of trees from native forests. It is light colored, has large color and quality variation and is less durable [17, 24, 53, 61–65]. Variable decay resistance in heartwood can be explained by the content of both non-structural carbohydrates and phenolic (quinone) compounds in the juvenile wood [65, 66], arising from variation in growing conditions [67] and soil fertility [68, 69]. In addition, the high proportion of juvenile wood results in mechanical properties inferior to trees from native forests [70]. Consequently, heartwood cannot be sold commercially according to the four categories defined by Bhat [49].

Several studies have examined the effect of precipitation levels or soil conditions and fertility on heartwood characteristics. Sites in the native teak range with low rainfall, or those cataloged as very dry, dry, or semi-dry (Fig. 3a), produce darker heartwood and higher heartwood proportions than moist and very moist sites (Fig. 3b) [71–73]. Soil fertility affected wood color [74], specifically CIElab color parameter b* (blue/yellow) which was significantly

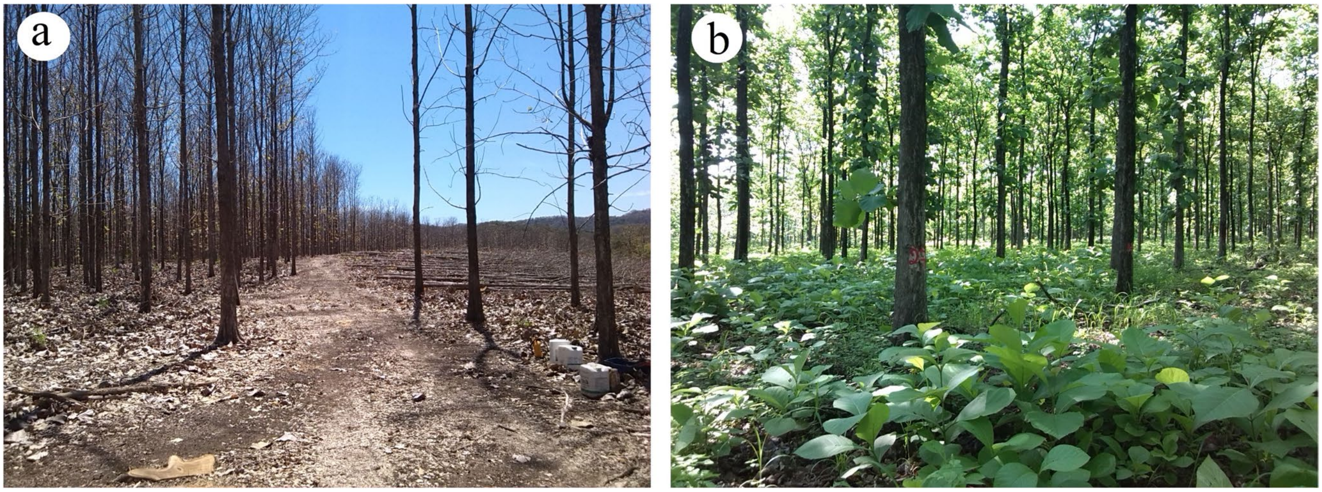

Fig. 3 Examples of teak plantations on dry sites (**a**) and humid sites (**b**). (Source: R. Moya)

correlated with climatic and edaphic variables. In summary, the proportion and color of teak heartwood improve in dry climates with deep, fertile soils [69].

Heartwood percent and wood color are moderately heritable. Solórzano et al. [75] reported broad-sense heritabilities of 0.27 for heartwood proportion (HWP) and values of 0.36, 0.57 and 0.48 for wood color parameters L*, a* and b*, respectively. Plus-tree selection has also been used to improve teak heartwood characteristics. For example, Kokutse et al. [76] considered HWP, wood color, and heartwood durability (amongst other properties) to determine which plus trees to select for future improvement on specific sites. They also indicated that plus trees should be selected after 15 years, when teak starts to produce mature wood [77]; however, trees are often harvested earlier.

Heartwood properties can be improved by clonal selection [78, 79]. For example, de Oliveira et al. [78] showed that clonal teak had superior HWP compared to trees propagated from seed. A study of 20 different 10-year-old clones at two sites in Costa Rica showed that L*, a* and b* and HWP were significantly influenced by clone (Fig. 4) and site [80, 81]. Clones were segregated into four groups (using multivariate analysis) according to color and five clones, uniformly dark and with high HWP, were identified. Arce and Moya [82] evaluated the same clones at 15-years and found that three clones had a desirable (in terms of end-user requirements) darker reddish color. Similarly, clones planted on the drier of two sites in Indonesia had a larger HWP that was more attractive in appearance [83]. While promising, variable results have been observed [84]. Kaosa-ard [85] reported that the color of teak wood was strongly controlled by planting site and that the effect of clone was small. Similarly, Solórzano et al. [75] studied four-year-old plantations of 36 clones at two sites in Costa Rica and found no difference in wood color or HWP, likely because of their young age.

Site or environmental conditions interact with the clone to influence heartwood properties [76]. Hidayati et al. [86] showed that color uniformity varied between three clones on two Indonesian sites. Similar findings were reported for heartwood L*, a* and b* and HWP for 20 10-year-old clones grown in Costa Rica [80, 81]. Hidayati et al. [87] suggested that specific clones might be used depending on site conditions and wood properties intended for improvement.

Mahogany

Mahogany (*Swietenia* spp) is native to the tropical forests of Mexico, Central America, and South America [88] and has been harvested from Neotropical forests since the arrival of Europeans [89]. It is one of the most important commercial tropical woods in international markets [88] owing to its excellent aesthetic qualities, good workability and high durability (owing to the presence of phenolic compounds) [90–92]. Native populations have become depleted with time, and in 1994 the Convention on International Trade in Endangered Species (CITES) designated it an Appendix II species [93].

Mahogany is grown in plantations in tropical regions of Asia, Oceania and Africa [92]. Production, establishment and management aspects of mahogany in plantations have been extensively described with rotation ages ranging from 20 to 60 years [88, 94]. Studies of plantation mahogany have considered general wood characterization [95–99], variations in wood properties [100–102], differences between pure and mixed wood plantations with wood from natural forest trees (Fig. 5) [103, 104], effects of growth rate [105], and age [106] on wood properties and industrial processing [107]. Studies are limited regarding the relationship between genetics and wood properties, especially heartwood formation and durability [108, 109]. Abarca-Alvarado et al. [99] reported that heritability was >0.30 for heartwood diameter in 9 eight-year-old mahogany clones in Costa Rica.

Fig. 4 Examples of wood color variations amongst different teak clones grown in Costa Rica. (Source: R. Moya)

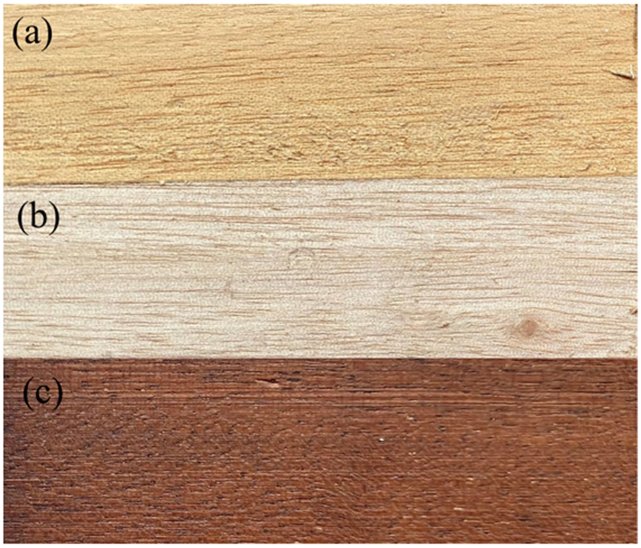

Fig. 5 Comparison of wood color between mahogany trees from fast growth plantation and natural forest: (**a**) heartwood and (**b**) sapwood from plantation tree and (**c**) heartwood from natural forest tree. (Source: R. Moya)

Examples of Other Species Reported to Have Lower Heartwood Quality for Plantation Sourced Wood

Redwood

Redwood (*Sequoia sempervirens* (D.Don) Endl) is native to a coastal strip in northern California but has been widely planted globally. Redwood heartwood is highly resistant to decay and commonly used for decking, garden beds and other exterior uses. While there are scattered pockets of old-growth redwood remaining, the majority of timber cut for this species is from second regrowth (coppice) or planted forests. Decay resistance of redwood heartwood has been related to color (darker heartwood is more resistant) and the concentration of ethanol soluble extractives [115]. Several authors [116–119] have reported that the heartwood of primary forest trees have higher extractive contents than that from trees of secondary forests.

Clark and Scheffer [120] evaluated the decay resistance of second growth redwood and concluded that it was moderately durable and highly variable, and Quarles and Valachovic [121] observed that regrowth redwood was less durable than old-growth. There are relatively recent reports of durable redwood. For example, redwood posts were classified as highly decay resistant in field trials [110] and Cabrera et al. [122] reported that untreated redwood was highly resistant to decay in a high decay hazard above ground exposure near Hilo, Hawaii. These studies did not specify the origin of the wood, and it is likely that it was not from regrowth forests.

Presently, heartwood quality is not considered for redwood tree improvement in the USA; however, in New Zealand heartwood quality is being evaluated with Jones et al. [123, 124] reporting that older trees had a higher proportion of durable heartwood and that heartwood percentage was influenced by tree age and size.

Port Orford Cedar

Port Orford cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl.) is native to a narrow band of forest along the coasts of California and Oregon. This species has a reputation for durability based upon post tests [110], and is highly prized in Japan as a substitute for hinoki [111]. Laboratory trials in the mid-1980s [112] of recently harvested, randomly selected samples, from a Northern California mill indicated heartwood resistant to fungal attack. Subsequently, Ajuong et al. [113] found wood from butts and tips of freshly harvested Port Orford cedar logs from Southern Oregon was far less resistant to attack by the brown rot fungus *Rhodonia placenta* (Fr.) Niemelä, K.H.Larss. & Schigel (moderate decay resistance) than previously reported for butt wood. Breeding programs have been initiated to develop varieties resistant to a root disease (*Phytophthora lateralis* Tucker and Milbrath) [114]. Incorporating decay resistance into this program may be challenging, but is important for maintaining the reputation of the species.

Dipteryx

Dipteryx species are native to South and Central America and are marketed under several commercial names including almendro (*Dipteryx panamensis* Benth.), baru (*Dipteryx alata* Vogel.) and cumaru (*Dipteryx odorata* (Aubl.) Willd.) [125]. Wood from natural forests is predominately used for flooring [126] due to its high specific gravity, attractive color and high durability [127]. Genetic improvement of some *Dipteryx* species has commenced [128, 129]; however, heartwood property data for baru and cumaru from plantation forests are limited. Almendro was introduced for commercial production in Costa Rica about 20 years ago [128, 129] and reports indicate wood is suitable for structural applications (high specific gravity, good mechanical properties) [130, 131]; however, heartwood percentage was lower and it was less durable and lighter in color than in native populations [130]. High heritability values were determined for heartwood proportion, L* and a*, suggesting provenance selection may improve heartwood quality [132, 133].

Eucalyptus

Over 700 *Eucalyptus* species are native to Oceania and many now have near global distributions because of extensive plantation establishment. Many species have heartwood with exceptional resistance to fungal, insect and marine borer attack. Durability classifications for over 200 species (codified in Australian Standard AS5604 [134]) were conducted over 50 years ago and based upon large field tests of native forest heartwood timbers. The sources for timber of these species are transitioning to either native forest regrowth or, increasingly, plantations managed using vegetation control, limited fertilizer application, and regular thinning to enhance growth rates. Francis et al. [135] examined decay resistance of plantation and native forest regrowth of Gympie messmate (*Eucalyptus cloeziana* F.Muell) heartwood (classified as very resistant, or Class 1, the category assigned to wood most resistant to biological decay [134]) and found that density and total extractives content were lower in the plantation resource and that these changes were associated with decreased resistance to white and brown rot fungi (*Pycnoporus coccineus* (Fr.) Bondartsev & Singer and *Fomitopsis ostreiformis* (Berkeley) Hattori, respectively). A limited number of trees were studied; however, trends were consistent, suggesting the need for caution in applying high yield silvicultural practices to these resources.

In contrast to previously discussed species in this section, there is research on *Eucalyptus* species in Australia and New Zealand focused on producing naturally durable roundwood, with initial work mostly aimed at replacing CCA-treated softwood vineyard posts [136, 137]. In 2008, the New Zealand Dryland Forests Initiative (NZDFI) commenced the domestication of five *Eucalyptus* species. We will focus on *Eucalyptus bosistoana* F.Muell., the main NZDFI durable species, which was selected not because of its appearance or high oil content, but for its class 1 natural durability [134]. The goal of the initiative is to domesticate the species targeting growth, form and, more importantly, early heartwood development.

As there were not enough stands available in New Zealand to start a breeding program, the NZDFI contracted the identification of superior trees and seed collection covering the natural range of the species in Australia. There were 3 collection series for *E. bosistoana* (starting with 40 open-pollinated families, later extended to over 200 families) established in provenance-progeny trials in 2009, 2010 and 2012.

Li et al. [138] reported on the first genetic analysis of heartwood diameter and extractive content across two environments at 7 years of age. It considered 40 families with 35 families in common, with a total of 1,665 assessed trees. Heritabilities for heartwood diameter ranged between 0.66 and 0.71, while those for extractive content were lower (0.16 and 0.25). There were statistically significant differences between site averages for both heartwood and extractive contents. However, there were only small changes to the heartwood diameter family rankings (genetic correlation 0.96), suggesting very low genotype-by-environment interaction. The situation for extractive contents was slightly different, with a weaker genetic correlation (0.6) and potentially significant ranking crossovers. Within-site genetic correlations between heartwood diameter and extractive contents ranged from non-significant in one environment to strongly negative in the other. Despite the low or negative correlations, it was possible to find families that had above average heartwood diameter and extractive contents. These analyses are currently being extended to cover a larger number of families and environments.

As the main interest of the breeding program is durability, not only heartwood presence, work was conducted to correlate extractive content with fungal decay resistance, measured as mass loss after exposure to brown-rot and white-rot fungi [139]. There were statistically significant negative correlations between extractive content (predicted using near infrared (NIR) spectroscopy) and mass loss for both white-rot ($r = -0.32$) and brown-rot ($r = -0.42$).

Options for Heartwood Improvement

Our review of selected species clearly shows reductions in heartwood quality of plantation sourced timber. Further, quality is species-dependent and can refer to several characteristics including durability of wood used in outdoor applications, color and oil content. It highlights the need for a consistent, knowledge-based approach to achieve high quality heartwood (as per industry standards), whether it is by silvicultural treatments, or utilization of selected genotypes (potentially at the family or clonal level), or a combination of both. Information we have compiled can potentially point to important areas on which to focus. In the following section we examine some of these areas and other important considerations with respect to the production of high-quality heartwood.

Genetic Improvement

Observed variability in breeding depends on genetic variability, environmental variability (changes in site and management), and their interaction. Breeding programs use trials with known experimental design and genetic relationships (families or clones, for example) to separate the different effects that contribute to the observed variability of, for example, heartwood.

Breeders make a clear distinction between objective traits (the characteristics that affect profit, usually at rotation age) and selection criteria (the variables that can be quickly and cheaply assessed in trials, often between 1/4 and 1/3 of rotation age) that are correlated with objective traits. As an example, breeders might be interested in increasing stem volume at 25 years of age, but they assess stem diameter and tree height at 8 years. Heartwood traits can be targeted using several selection criteria depending on the end-use: heartwood quantity (length of increment core showing heartwood), color variation using a colorimeter (for appearance), and extractive contents as an indication of heartwood durability.

Beyond differences in assessment age, programs must assess large numbers of trees to achieve high selection intensity and substantial genetic gain. This makes direct assessments of durability, in decades-long graveyard tests or even directly measuring extractive contents, infeasible. Instead, it is much more efficient to develop and use NIR spectroscopy calibrations to rapidly predict extractive contents [138, 140]. For heartwood quantity, heartwood diameter can be determined on increment cores using a pH indicator where applicable (such as methyl orange), though indicators are highly species specific.

Breeding trials established over multiple environments allow for the estimation of genetic variability, the degree of genetic control (heritability), the genetic correlation between heartwood diameter and other traits, and the degree of stability of the rankings of families or clones (genotype by environment interaction, GxE). There are examples of species in which there are both strong environmental effects and a moderate to high degree of genetic control. This is not a contradiction, as heritability is simply the proportion of the observed variance that's explained by genetic variance after accounting for other sources of variability, such as environmental effects. That is, the existence of strong site differences does not imply the presence of significant GxE interaction to explain the different heartwood averages across sites. However, there are examples of changes in the magnitude of differences or changes in the ranking of genetic entries (families or clones) across sites, which suggest the presence of G×E interactions. Extractive content in *E. bosistoana* appears to be more affected by G×E interaction than heartwood diameter.

Energy Balance in Plants

It is important to recognize that there are trade-offs in life-history characters (defined as traits related to survival, growth, reproduction, and longevity amongst others) that are ubiquitous across all forms of life [141]. Every aspect of tree growth involves trade-offs in energy utilization. Producing more wood permits the development of a larger, perhaps taller canopy that facilitates photosynthesis but comes at a cost of reducing, for example, energy directed to producing protective extractive compounds. At the same time, the tree must subsequently expend energy to retain the living cells in the additional wood. In nature, these trade-offs shape key aspects of life such as patterns of development and aging [142] as well as reproductive strategies [143]. These trade-offs are also known to shape characters like seed size, wood density, and production of chemical compounds associated with pathogen and herbivore defense [144–146] and are ultimately the result of fundamental energetic constraints (i.e. energy limitations prevent organisms from maximizing all life-history characters) [147]. Constraints and their potential benefits become a bit more distantly related in terms of heartwood extractives that contribute to color, odor, acoustic properties or durability since they are formed in dead or dying cells that continue to serve a structural function but play no physiological role. Despite the indirect connections, we suggest that heartwood characteristics should be considered when designing and maintaining tree breeding programs.

Efforts to maximize specific life-history traits may negatively impact other desirable characteristics in the short term, and increasingly so as populations adapt and evolve. For instance, trade-offs between growth and defense are well documented and characterized in plants [144, 145, 148], with growth (cell division and expansion) and differentiation (cell wall thickening and production of secondary metabolites, including extractives) representing opposing strategies to survival [149]. Plantation trees are grown in relatively low stress environments (compared to natural forests) to promote growth, and enhanced growth is potentially the product of shifts in energy allocation from defense to growth. As such, we suggest there may be considerable value in considering how growth conditions and selection interact with underlying trait architectures when breeding trees for specific wood characteristics.

Stress and Heartwood Formation

Appreciation that plants have a limited energy balance and that trade-offs exist in how that energy is allocated suggests that knowledge of how to shift the balance to favor a more defensive strategy could be beneficial for production of quality heartwood. Trade-offs are likely species-dependent and may manifest in some species but perhaps not in others, requiring specific trials for targeted species. Our review of teak and sandalwood indicates that biotic and abiotic stressors influence extractive production and concentration in heartwood. Management decisions that deliberately cause a stress response (as opposed to maximizing growth) should be considered for plantations of species valued for their heartwood properties. However, this would likely come at the expense of volume.

Perhaps the simplest approach for inducing stress appears to be growing trees on drier sites. As noted for teak, it is recognized that the proportion and color of heartwood improves in dry climates with deep, fertile soils. Growth responses (not described) can be expected, and research by Rudman and Da Costa [51] (cited by [20]) observed increases in ether- and methanol-soluble extractives for trees with slow growth rates; however, this was less evident in later research by Da Costa et al. [150] (cited by [20]). Hillis [20] observed that black walnut, sugi, and radiata pine plantation grown trees from drier locations all had more heartwood.

Further evidence for the importance of water stress in heartwood development is provided by Moreno Chan et al. [151]. This study examined functional changes in stem conductance and heartwood development in response to water stress in radiata pine from high-altitude sub-alpine and warm–dry inland sites in the Hume region of New South Wales, Australia. Trees at the warm-dry site had more rapid rates of heartwood development and mature stands (34.5–36.5 years old) at this location had 8–14% less sapwood. The authors suggested that inner sapwood cavitation preceded heartwood formation in water-limited environments and represented an adaptation to regulate water use and stem conductance. Hillis [20] also noted water loss from sapwood adjacent to the heartwood was commonly suggested to precede heartwood formation.

Another important management decision relates to better understanding the effects of planting density on crown size, heartwood and sapwood thickness and heartwood characteristics [152–154]. Identifying an appropriate spacing for a given species that optimally balances resource allocation to growth and defense across a variety of site qualities would require a long-term research effort, but an understanding of how such decisions influence heartwood quality is a critical question. Another important decision that may be implemented later in the rotation is pruning, since controlling crown size may have important effects on heartwood development [154].

Silvicultural interventions such as wounding and chemical treatment were noted for sandalwood and have also been employed in previous attempts to enhance heartwood production [20]. A brief review of recent literature indicates considerable recent activity in chemical treatments of high value species, such as Indian sandalwood [155], the agar wood producing species, *Gyrinops versteegii* (Gilg.) Domke [156], and *Dalbergia odorifera* T. Chen [157]. Identifying the types and timing of specific treatments to achieve desired outcomes appears potentially costly and problematic, especially in hardwood species where color is important.

The large body of literature on interactions between plants and insect pests/fungal pathogens exemplifies the potential complexities and challenges involved with eliciting a desired protective response. Focusing on Pinaceae species, interaction between insect pests like bark beetles, pine processionary caterpillars, and pine weevils, and various pathogenic fungi have been well characterized [158–161]. Analysis of phloem resin chemistry post treatment in greenhouse [162], forest [158, 163, 164] and in natural forest trials following an attack [159] all indicate a rapid induced response. However, the nature of the response can be heavily dependent on how the response is induced (e.g. mechanical damage versus chemical elicitor, chemical elicitor versus fungal exposure, etc.) [165]. With respect to fungal inoculation, dosage [158] and exposure history can be major factors with “naive” species (those not previously exposed to a pathogen or insect) often showing elevated susceptibility [166–169]. Lastly, responses can vary between species [158, 163, 170, 171] and within species due to genetic variation between and within regions [172, 173].

Anatomical responses to stressors include formation of traumatic resin canals in the xylem and activation and production of polyphenolic parenchyma cells in the phloem [174]. Traumatic resin canals, which are much larger than constitutive canals, allow for enhanced resin flow, accumulation of resin, and compartmentalization of tissue where treatment (wound to xylem / phloem, fungal inoculation, fire) directly impact the tree with the size and number of canals decreasing with increasing distance from the attack site [174, 175]. These responses are consistent with the compartmentalization of decay in trees (CODIT) model developed by Shigo [176].

It is unclear how directly applicable these plant and pest/pathogen dynamics are to heartwood formation. However, the body of work described above can serve as a blueprint to address their relevance. Such understanding could inform efforts to pair appropriate treatment programs with the “right” genotypes of a given species to elicit desired responses.

An interesting line of research relates to defense priming, essentially exposure to a stimulus that subsequently enables a quicker or stronger response when attacked. Mageroy et al. [177] applied sublethal inoculation with *Endoconidiophora polonica* (Siemaszko) de Beer, Duong & Wingfield, and / or spraying with methyl jasmonate to 48-year-old Norway spruce (*Picea abies* (L.) H. Karst.). Five weeks after priming, pheromone dispenser tape was used to attract spruce bark beetles (*Ips typographus* L.) and bark landing rates were monitored as was subsequent colonization. Treated trees were largely avoided, whereas untreated trees were heavily infested and killed [177].

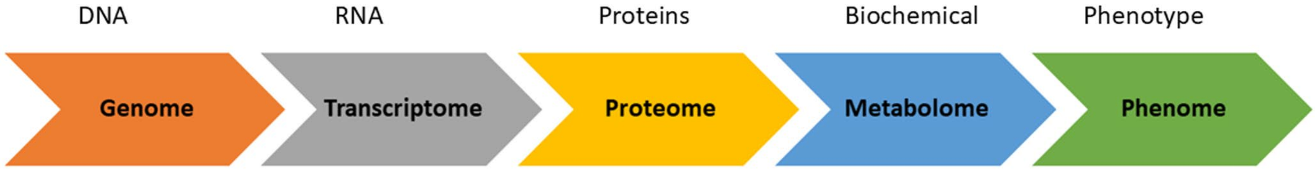

Fig. 6 A visual representation of the hierarchy of levels of biological organization going from the genome to the phenome

Another example of defense priming is fire in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests. Hood et al. [178] found that regular, low-severity fires have an important role in increasing tree defense against bark beetle attack. Fire induced an increase in resin canal size and frequency, allowing for the transport of greater volumes of resin, the primary mode of insect defense in pines [179]. The effect was long lasting, but resin canal production decreased in the long-term absence of fire rendering the trees more vulnerable to beetle attack. Effectively, "previous responses can affect the subsequent responses", improving resistance to abiotic and biotic stresses [180]. Responses to repeated stimuli can be positive ("sensitization") where the response is reinforced or negative ("familiarization") where the response is weakened [180]. Practicing these concepts in future plantations may provide a pathway to producing desirable heartwood.

An undesirable outcome of exposing trees to stress is reduced growth. For example, Cui et al. [181] subjected *D. odorifera* to different levels of water stress (heavy drought, light drought and irrigation in the dry season) and observed that trees from the drought treatments had a higher HWP. However, trees grown under heavy drought were significantly smaller than those from the other treatments. The economic viability of growing trees on stressful sites or subjecting them to chemical treatments, which can also reduce growth, requires investigation. Conversely, failure to produce high quality heartwood may also have large economic implications.

Multi-Omic Approaches for Understanding Heartwood Formation

Given the complexities involved in characterizing the relationships that determine heartwood properties, we suggest adopting a systems biology approach. Collecting and integrating data across multiple omics layers (Fig. 6) can provide deeper insight into the mechanisms governing phenotypic traits and reveal opportunities for targeted manipulation. These approaches are already widely used in other areas of biology to investigate complex phenomena such as disease, e.g. Hasin et al. [182] and Kaczenski et al. [183], and are gaining momentum in forestry and plant breeding [184–186]. Recent studies report the use of comparative metabolomics to examine differences between the heartwood and sapwood of *Taxus chinensis* (Pilger) Rehd [187] and *Cunninghamia lanceolata* (Lamb.) Hook [188]. We believe that applying such strategies will make current challenges more tractable and help pave the way toward sustainable, long-term solutions.

Conclusions

Wood of naturally durable species has been highly valued for centuries. Demand remains high and will only increase as we shift to plantation grown wood to meet our fiber needs, while also seeking natural alternatives to wood treated with preservatives (that confer durability to non-durable wood). We contend that management of plantation forests can unintentionally promote one process (growth) over other processes (heartwood production) that may be detrimental to the management objectives for end-products from the plantation, e.g. teak grown for heartwood production failing to have an acceptable color. Recognition that energy balance tradeoffs exist, and the utilization of advanced genetics and silvicultural strategies to promote heartwood formation on suitable sites are all required in the future to ensure that high value heartwood can be obtained from plantation forests.

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  - ○ A more technical overview (than Wang et al. 2023) emphasizing how advances in high-throughput sequencing, single-cell and spatial transcriptomics, and genome editing are being integrated into forest genetics programs. They make the case that these approaches are essential to identifying and understanding the regulatory networks that shape traits like growth, wood formation, and stress resposnes.

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    - ○ Stress events can alter the response of a plants when similar conditions are encountered in the future. Potentially plant repsonses can be manipulated to achieve desired outcomes, i.e. production of secondary metabolites.
- Herms DA, Mattson WJ. The dilemma of plants: to grow or defend. Q Rev Biol. 1992;67(3):283–335
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    - ○ Provides a big picture overview of how multi omics can be used to enhance our understanding of complex trait variation, e.g. growth, responses to abiotic stresses etc., in trees. They argue that this knowledge can then be applied to improve forest-tree breeding programs.
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Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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