

A Review of the Factors Influencing Variations in the Heartwood Proportion for Solid Wood

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ABSTRACT

Using 146 journals, 6 chapters, 4 reports, 2 books, and a proceeding, this research seeks to investigate the factors that influence variations in the proportion of heartwood. The data were collected through an online search in databases such as Scopus, Science Citation Index, Science Direct, Google Scholar, and ResearchGate with seven search queries, namely heartwood variability, heartwood proportion, tree age of heartwood, growth rate of heartwood, silvicultural treatment of heartwood, as well as genetic and environmental effects of heartwood. By eliminating papers that were out of topic or title, purpose and year of publication, 67 journal articles, 4 chapters, 3 reports, a book, and a proceeding were selected. The review results showed that the amount of heartwood was influenced by its position in the tree, tree variations, such as age, growth rate, and species/genera, as well as the growing conditions, including location and environmental factors. It is also affected by various silvicultural treatments, namely spacing, thinning, pruning, fertilization, and irrigation. These findings indicate that the amount of heartwood is more controlled by the diameter of the wood than the age. Furthermore, several studies reported that the growth rate of sapwood rings was significantly higher than the heartwood rings, which can reduce the quality of solid wood used for construction. Therefore, it is necessary to control the proportion of heartwood through genetics and environmental factors, especially genetics, which has more effects on the growth rate of tree diameter than environmental factors. Previous studies revealed that tree diameter has a weak or negative correlation with other wood properties, such as basic density, color, and wood stiffness, which are generally important in global markets. It is important for breeders to concentrate on using species with superior genetic variations as well, especially the highly demanded traits in further studies.

Keywords: heartwood formation; heartwood variation; silvicultural treatment; genetic effect; environmental effect

INTRODUCTION

The majority of tree species have two histologically similar, but physiologically different xylem zones, namely sapwood and heartwood. Sapwood contains living cells that are physiologically active as well as reserve materials located in the outer zone. The outer ring allows the transport of water and minerals from the roots to the cambium and leaves. Meanwhile, heartwood is located in the inner zone of the xylem, and it is physiologically inactive in terms of water conduction (Pinto et al. 2004).

Piqueras et al. (2020) revealed that the formation of heartwood is the final step in the life cycle of ray cells. Furthermore, these cells undergo metabolic changes in the transition zone between sapwood and heartwood before

death, which leads to increased synthesis of secondary metabolic compounds, such as extractives. Pande (2013) also stated that the formation process is a natural growth regulation mechanism that is associated with tree development. The process also helps to maintain optimal sapwood volume (Taylor et al. 2002).

Heartwood and sapwood have different properties and proportions in the trunk, which have a significant effect on wood utilization. The presence of heartwood is often used to determine the wood value (Yang et al. 2020). In pulping, it has a negative effect because its extractives can affect the process and properties of the final product. Meanwhile, for solid wood applications, the properties of heartwood and sapwood affect the drying, durability, and aesthetic value of panels and furniture. Although there is a large

color difference between the two zones of the xylem, the selection of wood components based on color also plays an important role in some applications (Pinto et al. 2004).

Meunpong et al. (2021) revealed that differences in humidity, wind exposure, climate area, elevation, and aspect are closely associated with the width of heartwood. Silvicultural practices can also affect its formation and quality, for example, proper thinning and fertilization promote stem growth, which accelerates the formation (Yang et al. 2020). The content of heartwood and sapwood varies between and within species. It is also associated with growth rates, stands, individual tree biometric features, site conditions, and genetic control (Pinto et al. 2004). A better understanding of the heartwood formation process helps to control and maintain its production (Taylor et al. 2002). Therefore, this study aims to review the factors that cause variation in heartwood proportion. The results are expected to help foresters and farmers plan or control its formation based on the end-use of wood, especially in construction.

MATERIALS AND METHODS

While conducting this review, we performed a semi-systematic or narrative review. We explored several databases such as Scopus, Science Citation Index, Science direct, Google Scholar, and ResearchGate, to identify and to download the abstracts, chapters, reports, books, proceedings, review articles and research papers related to the factors influencing variations in the heartwood proportion for solid wood. The search queries used during searching of information were: “heartwood variability”, “heartwood proportion”, “tree age

of heartwood”, “growth rate of heartwood”, “silvicultural treatment of heartwood”, “genetic effect of heartwood”, and “environmental effect of heartwood”. The publication years were restricted from 1970 to 2022. Subsequently, a total of 159 documents (146 journals, 6 chapters, 4 reports, 2 books, and a proceeding) were found from the databases, but they were reduced to 67 journal articles, 4 chapters, 3 reports, a book, and a proceeding, based on the criteria of topic or title, objectiveness, and year of the publication. Both published and unpublished articles, such as journal articles, chapters, reports, books, and proceedings related to the heartwood formation and heartwood variation were grouped (Table 1). They were then analysed using qualitative analysis to identify, analyse and report patterns in the form of themes in a text.

RESULTS AND DISCUSSION

Figure 1 shows the various factors that affect the proportion of heartwood based on the review, namely 1) within tree variation (position), among tree variation, such as age, growth rate, and species/genera/family; 2) growing conditions, namely site and environment, and 3) silvicultural treatment, including spacing, thinning, pruning, irrigation, and fertilization. Furthermore, they can be divided into two groups based on their effect, namely into direct, and indirect categories. Direct factors affect the proportion of heartwood directly, while the indirect variants affect heartwood through other intermediaries. The results showed that all the aforementioned influential factors were controlled by genetic and environmental factors, as shown in Table 2.

Table 1. Reviewed publications.

Theme	Number of publications	References
Heartwood, sapwood, heartwood formation, positive and negative impacts of heartwood	6	Meunpong et al. 2021, Pande 2013, Pinto et al. 2004, Piqueras et al. 2020, Taylor et al. 2002, Yang et al. 2020
Within tree variation	24	Bamber 1976, Björklund 1999, Brix and Mitchell 1983, Climent et al. 1993, 2003, Fernandez-Solis et al. 2018, Gominho et al. 2001, Gominho and Pereira 2000, 2005, Hillis 1987, Knapic et al. 2006, Knapic and Pereira 2005, Miranda et al. 2006, Morais and Pereira 2007, Moya et al. 2014, Pinto et al. 2003, 2004, Rink and Phelps 1989, Sellin 1994, 1996, Stokes and Berthier 2000, Wilkins 1991, Wilkes 1991, Yang and Murchison 1992
Among tree variation	31	Anish et al. 2015, Anoop et al. 2014, Bamber 1976, Bamber and Fukazawa 1985, Bhat 1995, Bradbury et al. 2005, 2011, Climent et al. 2002, Fernandez-Solis et al. 2018, Gominho et al. 2001, Gominho and Pereira 2000, 2005, Hazenberg and Yang 1991, Hillis 1987, 1972, 1987, Karkkainen 1972, Miranda et al. 2006, 2014, Morais and Pereira 2007, Moya and Munoz 2010, Nicholas et al. 1994, 2007, Pillai et al. 2013, Pinto et al. 2004, Sotelo Montes et al. 2008, Wadsworth and Gonzales 2008, Wilkins 1991, Woeste 2002, Yang and Hazenberg 1991, Yang and Murchison 1992
Growing condition	7	Bhat 2000, Bhat et al. 2004, Crespo et al. 2008, Kjær et al. 1999, Kokutse et al. 2004, Perez and Kanninen 2003, Thulasidas and Bhat 2009
Silvicultural treatment (site and environmental)	14	Bergstrom et al. 2004, Gominho and Pereira 2005, Langstrom and Hellqvist 1991, Miranda et al. 2003, 2006, Morling and Vallinger 1999, Moya and Perez 2008, O'Hara 2012, Pérez and Kanninen 2005, Pimentel et al. 2008, Ramanan et al. 2018, Santos et al. 2020, Vallejos et al. 2015, Viquez and Perez 2005
Genetic x environmental	13	Bradbury et al. 2011, Bush 2011, Ericsson and Fries 1999, Freitas et al. 2019, Harrison 1975a, 1975b, Kurinobu et al. 1992, Miyamoto et al. 2016, Nakada 2007, Nicholas et al. 2007, Rodríguez-Pérez et al. 2022, Searle and Owen 2005, Zobel and Jett 1995

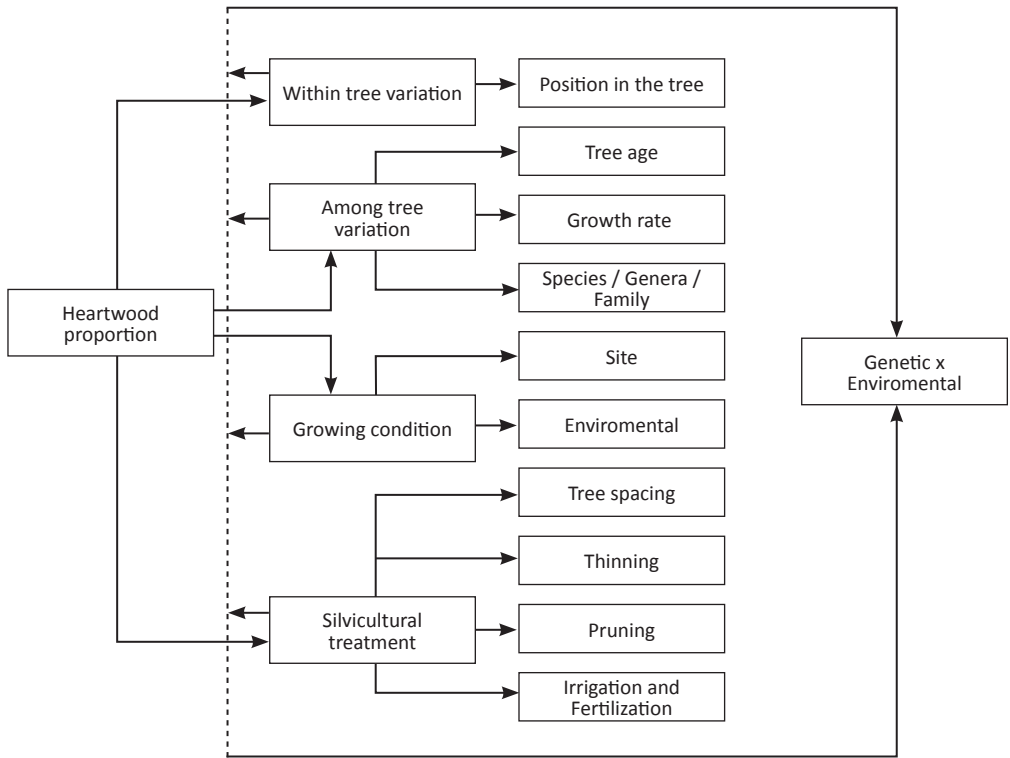


Figure 1. Factors that affect the proportion of heartwood.

The heartwood percentage has significantly decreased from base of the stem to top of the stem, with the highest value at the base part. This is a general trend of within-tree variation in heartwood proportion and has been reported for many hardwood and softwood species, such as *Picea abies* (L.) Karst (Sellin 1994, 1996), *Juglans nigra* L. (Rink and Phelps 1989), *Acacia melanoxylon* R.Br. (Knapic et al. 2006), *Pinus pinaster* Aiton (Stokes and Berthier 2000, Pinto et al. 2003, 2004, Knapic and Pereira 2005), and *Pinus canariensis* C.Sm. ex DC. (Climent et al. 1993, 2003). In addition, it was also found in *Eucalyptus globulus* Labill. wood from Chamusca, Penamacor, Odemira, Quinta do Paço, Crato, Sertã, V. F.Xira, Azambuja, and Obidos in Portugal (Gominho and Pereira 2000, 2005, Morais and Pereira 2007, Miranda et al. 2006), *Eucalyptus hybrid urograndis* (Gominho et al. 2001), *Eucalyptus grandis* W.Hill. (Wilkins 1991), and *Tectona grandis* L.f. (Fernandes-Solis et al. 2018).

Corresponding to the fact that the development of the inner heartwood of trees in the lower part correlates with tree growth, the greater part is larger in the lower trunks of large trees (Gominho and Pereira 2005). In previous studies, some authors also reported that there were positive or negative correlations with regard to the impact of growth rate and size on heartwood formation (Hillis 1987, Wilkes 1991, Wilkins 1991, Pinto et al. 2004). In addition, the distribution of heartwood at a certain height and age is not present. Gominho and Pereira (2000) observed that the proportion

of *E. globulus* heartwood at the age of nine had disappeared by about 60% of the total tree height in Penamacor and by 74% in Chamusca and Odemira. Heartwood content was also absent in the relative height levels at 65% in *E. hybrid urograndis* (5.6 years old) from Brazil (Gominho et al. 2001) and 90% of the total tree height in *E. globulus* (12 to 15 years old) from Central Portugal (Morais and Pereira 2007).

Furthermore, the thickness of sapwood increased from bottom to top and at a certain height sapwood thickness is the same or stable. Moya et al. (2014) assumed that the thickness of sapwood for different tree ages of *T. grandis* is stable with height, varying from 2 to 5 cm in thickness. Miranda et al. (2006) reported that the area and width of the sapwood showed little variation due to the small thickness of the sapwood at the bottom of the trunk which contains a lot of heartwood. The opposite pattern was found at the end of the trunk, where the thickness of the sapwood was greater, which made the variation of the sapwood greater than at the base of the tree. This variation trend in the tree was also previously obtained in *E. globulus* (Gominho and Pereira 2000, 2005), *E. grandis* (Bamber 1976, Wilkins 1991), *A. melanoxylon* (Knapic et al. 2006), *Pinus contorta* Dougl. ex Loud. (Yang and Murchison 1992), *P. pinaster* (Knapic and Pereira 2005, Pinto et al. 2003, 2004), *Pinus silvestris* L. (Björklund 1999), and *Pseudotsuga menziesii* Mirb (Brix and Mitchell 1983). Fernandez-Solis et al. (2018) stated that a tree regulates its physiological processes to

Table 2. List of research related to the factors causing variation in the proportion of heartwood in several wood species.

Factors		Effect on the heartwood	Relationship	Species	References
Within tree variation	Position in the tree (bottom to top of the tree)	Direct	Negative	<i>Acacia melanoxylon</i> R.Br., <i>Eucalyptus globulus</i> Labill., <i>Eucalyptus grandis</i> W.Hill., <i>Eucalyptus hybrid urograndis</i> , <i>Juglans nigra</i> L., <i>Picea abies</i> (L.) Karst., <i>Pinus canariensis</i> C.Sm. ex DC., <i>Pinus pinaster</i> Aiton, <i>Tectona grandis</i> L.f.	Climent et al. 1993, 2003, Fernandes-Solis et al. 2018, Gominho and Pereira 2000, 2005, Gominho et al. 2001, Knapic and Pereira 2005, Knapic et al. 2006, Miranda et al. 2006, Morais and Pereira 2007, Pinto et al. 2003, 2004, Rink and Phelps 1989, Sellin 1994, 1996, Stokes and Berthier 2000, Wilkins 1991
	Tree age	Direct	Positive	<i>Picea abies</i> , <i>Populus tremuloides</i> Michx., <i>Tectona grandis</i>	Fernandez-Solis et al. 2018, Sellin 1994, 1996, Yang and Hazenberg 1991a, 1991b
Among tree variation	Growth rate	Direct	Positive	<i>E. globulus</i> , <i>E. grandis</i> , <i>Eucalyptus tereticornis</i> J.E.Sm., <i>J. nigra</i> , <i>P. canariensis</i> , <i>Pinus contorta</i> Dougl. ex Loud., <i>T. grandis</i>	Bhat 1995, Climent et al. 2002, Gominho and Pereira 2000, 2005, Miranda et al. 2006, Morais and Pereira 2007, Pillai et al. 2013, Wilkins 1991, Woeste 2002, Yang and Murchison 1992
			Negative	<i>Cryptomeria japonica</i> (L.f.) D.Don., <i>Picea abies</i> , <i>Pinus sylvestris</i> L.	Hillis 1987, Karkkainen 1972
	Species/ Genera/ Family	Direct	Positive	<i>E. globulus</i>	Miranda et al. 2014
Growing condition	Site	Direct	Positive	<i>T. grandis</i>	Anish et al. 2015, Kjær et al. 1999
		No effect		<i>T. grandis</i>	Bhat 2000, 2009, Bhat et al. 2004
	Environmental	Direct	Positive	<i>T. grandis</i>	Crespo et al. 2008, Kokutse et al. 2004, Perez and Kanninen 2003
Silvicultural treatment	Tree spacing	Direct	Positive	<i>E. globulus</i> , <i>T. grandis</i>	Gominho and Pereira 2005, Miranda et al. 2003, Pimentel et al. 2008
		No effect		<i>Eucalyptus grandis</i> × <i>E. urophylla</i> hybrid	Santos et al. 2020
	Thinning	Direct	Positive	<i>Gmelina arborea</i> Roxb.	Vallejos et al. 2015
		Indirect	Positive	<i>Acacia mangium</i> Willd., <i>T. grandis</i>	Pérez dan Kanninen 2005, Ramanan et al. 2018
	Pruning	Direct	Positive	<i>P. sylvestris</i> , <i>T. grandis</i>	Langstrom and Hellqvist 1991, Viquez and Perez 2005
		No effect		<i>P. sylvestris</i> , <i>Sequoia sempervirens</i> (D.Don) Endl.	Bergstrom et al. 2004, O'Hara 2012
Fertilization and irrigation	Direct	Positive	<i>E. globulus</i>	Miranda et al. 2006	
	No effect		<i>P. sylvestris</i>	Morling and Valinger 1999	

keep the sapwood area, holding the formation of heartwood during the first years of growth, because the tree uses its physiological processes to achieve a greater height quickly. Miranda et al. (2006) stated that in several species, sapwood width increased with tree age in absolute measurements and declined in relative measurements.

Among Tree Variation

Among trees, heartwood variation occurs partly because of the age of the wood and the rate of growth. The heartwood proportion increases with the increasing age of tree (Fernandez-Solis et al. 2018). Moya and Munoz (2010) reported that heartwood percentage at diameter and breast height (DBH) of a 14-year-old *Swietenia macrophylla* King, grown in Costa Rica was 41.2%. The values of heartwood

percentages were lower compared to *S. macrophylla* (the total height ranged from 13 to 20 m), with a heartwood content of 89% at the bottom area from the Olavakkode Research Range, India (Anoop et al. 2014). In addition, Wadsworth and Gonzales (2008) also observed that 40-year-old *S. macrophylla* trees obtained heartwood volumes ranging from 70 to 80%. In *Eucalyptus* species, Gominho and Pereira (2000) reported that the heartwood percentage of a 9-year-old *E. globulus* was 43% of the cross-sectional area at breast height. This value was lower than the percentage of heartwood reported by Morais and Pereira (2007) of 12-15-year-old *E. globulus* trees amounting to 54%, and by Miranda et al. (2006), of 18-year-old *E. globulus* trees amounting to 77% of the cross-sectional area of the tree. Gominho et al. (2001) also reported that heartwood content

is related to the tree's age. Furthermore, heartwood growth increased with the age of the tree until a maximum tree height was reached (Anish et al. 2015, Fernandez-Solis et al. 2018). This suggests the role of tree age in increasing the proportion of heartwood, as already mentioned for *E. grandis* (Bamber 1976), *P. menziesii* (Hillis 1987), *Pinus tremuloides* Michx (Yang and Hazenberg 1991), *P. pinaster* (Pinto et al. 2004), and *Abies balsamea* (L.) Mill. (Hazenberg and Yang 1991). It seems clear that heartwood develops with tree ageing, as has been shown in several reviews of heartwood formation (Hillis 1972, 1987, Bamber and Fukazawa 1985).

On the other hand, Gominho and Pereira (2005) stated that heartwood proportion increased with tree diameter. Pillai et al. (2013) also reported that growth rate affected heartwood proportion due to increased radial growth. Miranda et al. (2006) reported that the heartwood area of *E. globulus* was positively correlated with the radial growth of the stem. As reported by Gominho and Pereira (2000), a positive correlation was found between heartwood content and growth for 9-year-old *E. globulus* trees. Wilkins (1991) found that the percentage of heartwood in *E. grandis* was higher in the faster growing trees. Similar results were also obtained for other species, i.e., *T. grandis* (Bhat 1995), *P. contorta* (Yang and Murchison 1992), *J. nigra* (Woeste 2002), and *P. canariensis* (Climent et al. 2002). However, some authors have reported reverse correlations for species such as *P. silvestris*, *P. abies*, and *Cryptomeria japonica* (L.f.) D.Don. (Karkkainen 1972, Hillis 1987). In several previous studies, the proportion of heartwood was more influenced by tree diameter than tree age, as reported by Miranda et al. (2006) in *E. globulus* wood and by Bradbury et al. (2011), Nicholas et al. (1994), and Nicholas et al. (2007) in *A. melanoxylon*. This is very beneficial for tree breeding programs to select bigger diameter trees. In addition, tree diameter is also known to be positively correlated with the color of heartwood in *A. melanoxylon* and *Calycophyllum spruceanum* (Benth.) K.Schum. (Bradbury et al. 2005, Sotelo Montes et al. 2008).

Apart from the effect of tree age and diameter, family differences also affect the proportion of heartwood as reported by Miranda et al. (2014). They stated that family affects this relation of heartwood dimension with tree growth, as shown by the differences between genetic and phenotypic correlations. Heartwood proportion of cross-sectional area on average amounted to 41% with significant between-family variation ($P=0.016$), ranging from 27 to 53%. In addition, there were also important within-family differences with coefficients of variation of the mean between 4 and 48%.

Growing Condition (Site and Environmental)

The variation in heartwood percentage is a major parameter studied in relation to the site and environmental conditions. Thulasidas and Bhat (2009), who examined teak trees from wet and dry areas in India, revealed that there was no significant difference in the proportion recorded at the sites. This finding is consistent with Bhat (2000) and Bhat et al. (2004), where similar results were also obtained. However, large differences were found in relation to the tree

and heartwood diameter, where larger values were recorded in the wet sites. Crespo et al. (2008) and Perez and Kanninen (2003) reported that a larger proportion was obtained in the dry areas of Ecuador and Costa Rica compared to the wet areas.

In the wet regions, tree growth occurred almost continuously for 8-12 periods, while growth was more intense in dry areas containing inert material, and heartwood was produced in a shorter growing season. An increase in diameter often occurs in wet locations, but the development of the xylem tissue was slower compared to the dry region where tree growth stopped for months and led to annual heartwood formation. Kjær et al. (1999) revealed that the proportion obtained in 5 countries, namely in Puerto Rico, India, Mexico, Indonesia, and Ghana was significantly different. Furthermore, the values recorded in Indonesia and Ghana were lower than those of India and Mexico. The amount of rainfall can also affect the proportion of heartwood. Kokutse et al. (2004) revealed that higher amounts of annual rainfall, such as 1,200-1,500 mm per year, were more favorable for tree growth and the wood content of teak growing in Togo.

Silvicultural Treatment

Several studies reported that silvicultural activities, such as widening tree spacing, thinning, and pruning have effect on the proportion of heartwood. This is in line with Gominho and Pereira (2005), who found that the content obtained in *Eucalyptus globulus* was affected by an increase in spacing. Furthermore, heartwood percentages of 45%, 52%, and 69% were obtained for 2x1 m, 3x2 m, and 3x3 m of distancing, respectively. Similar results were also obtained in previous studies for the *E. globulus* tree (Miranda et al. 2003). They reported that the use of 4x4 m, and 4x5 m spacing can reduce pulp quality and paper due to the high extractive content and low degree of delignification. This condition is associated with an increase in heartwood proportion along with diameter. Pimentel et al. (2008) used different patterns for teak wood in Brazil, namely 3x1.5 m, 3x2 m, and 3x2.5 m. The results showed that the 3x2 m, and 3x2.5 m spacing resulted in the largest proportion. Moya and Perez (2008) also revealed that the heartwood percentage in 14-year-old teak trees was related to the stand density as well as diameter. However, Santos et al. (2020) stated that plant spacing affects growth rate, but has no effect on the xylem tissue content of eucalyptus clonal plantation (*E. grandis* × *E. urophylla* hybrid).

Several studies also reported that thinning has a significant effect on the percentage of heartwood. Vallejos et al. (2015) investigated the effect of thinning intensities of 60%, 70%, and 80% on the percentage and diameter of the tissue in a 8-year-old *Gmelina arborea* Roxb. tree. The results showed that the highest proportion was obtained with the 80% treatment, while there was no significant difference between the 60% and 70% intensities. However, thinning does not always increase the proportion, because it only has a temporary effect. Ramanan et al. (2018) stated it does not have a direct association with the increase in heartwood content, but the mechanism functions through an increase in tree diameter caused by the treatment. The result is

based on thinning experiments carried out on 7-year-old *Acacia mangium* Willd. stands from Kerala, India. These findings are consistent with those of Pérez and Kanninen (2005), who used different treatments for teak plantations in Costa Rica. The results showed the impact of thinning on wood properties, such as heartwood percentage and density, tended to be temporary in nature, and the effects were nullified after a long period. Furthermore, the content obtained in young teaks of 4 and 6 years with light thinning was slightly higher compared to the moderate and heavy categories. The moderate treatment involves the removal of 25% of the original trees in the 4th year and another 25% in the 5th year or only 40% in the 4th year, while 60% was removed in the 4th year for the heavy treatment.

Previous studies revealed that pruning can also increase the proportion of heartwood. Langstrom and Hellqvist (1991) conducted 4 different pruning treatments on a 25-year-old pine stand in Jdraas, Central Sweden, namely: (1) unpruned control (UC); (2) unilateral pruning (UP), where all live branches were cut on one side of the crown; (3) pruning from below (PB), where all live circles were removed below the 1981, leaving the top four, and the expanding current circle was kept intact; and (4) pruning from above (PA), including all branches from 1984-1982 as well as the tops of others (segments 1985-1982 and its side branches) in the live circles below 1982, as shown in Figure 2. The result showed that UP reduced growth along the stem, while PB caused greater reductions in the lower stem. Furthermore, PA increased radial growth above and decreased development below the pruned crown fraction. The branch bottom area (needle biomass) of the developing new whorls was increased in the trees were pruned from above, and height growth was only slightly affected by the treatments. The treated groups had a total growth volume loss of 24-33% during the study period, compared to the

controls. The pruning caused a decline in the conducting sapwood area as well as an increase in the non-conducting heartwood at breast level. The results also showed that the homeostatic adjustment was still incomplete after four growing seasons, except for the upper whorls, which developed after the process.

Viquez and Perez (2005) carried out different treatments on four experimental plants with a density of 3.5x3 m and an age of 2.2 years, namely the control group, as well as pruning at a height of 3 m, 4 m, and 5 m. The second treatment was carried out at the age of 5.2 years to a height of 7 m in all groups, except the control. The results showed that larger volumes of heartwood were found at 3 m, but they were not statistically different from the control group. The treatment also produced 142% more volume than 4 and 5 m, as well as 35% more than the control group.

Other studies stated that pruning has no effect on the heartwood proportion of trees. Bergstrom et al. (2004) reported that there were no changes in the proportion or the number of growth rings for five growing seasons. The study was carried out on 50 years old *P. sylvestris* trees from a natural stand, north-west of Umeå, belonging to the Swedish University of Agricultural Sciences. However, increases can still occur over a longer period. This indicates that pruning is not a practicable silvicultural method for regulating heartwood formation in *P. sylvestris*. These findings are consistent with O'Hara (2012), stating that it had no effect on the proportion. The results revealed that the effect of the treatment on heartwood was minimized six years after pruning. It was observed that the pruned trees have reestablished their crown foliage, and required the same amount of sapwood for water transport as the unpruned variants.

Apart from tree spacing, thinning and pruning, fertilization, and irrigation, several factors were also

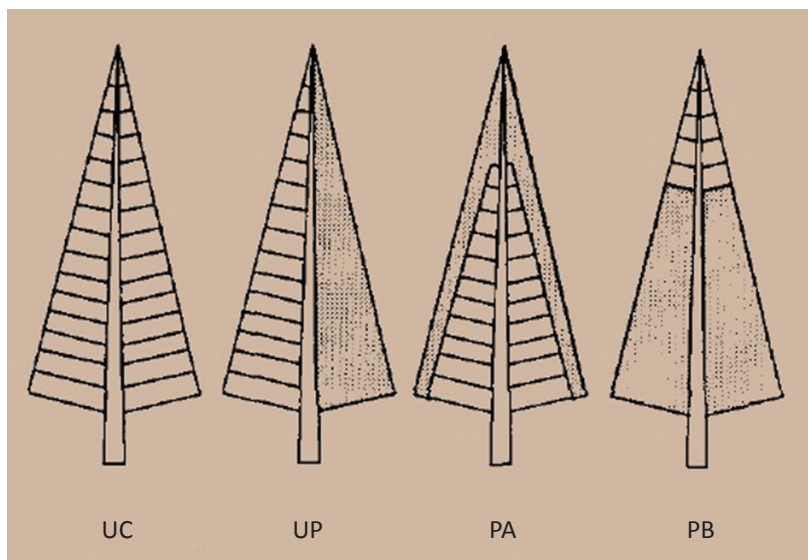


Figure 2. Schematic drawing of the treatment showing the appearance of the tree after pruning in June 1985 (Langstrom and Hellqvist 1991).

reported to affect the proportion of heartwood. Miranda et al. (2006) revealed that an 18-year-old *E. globulus* wood treated with fertilization and irrigation (FI) in the first 6 years of growth showed a larger volume than the control (C), namely 65.6% and 55.6%, respectively. Furthermore, in the FI and C trees, the tissue's distribution decreased by 77.7% and 67.6% at the bottom, as well as by 7% and 4.8% at a height of 29.3 m, respectively. Morling and Vallinger (1999) reported different results in *P. sylvestris*, where the increase in heartwood area after fertilization and thinning was not statistically significant, while sapwood thickness increased significantly. The number of growth rings in the heartwood at breast height was not influenced by treatment.

Relationship Between Genetic and Environmental Factors on Heartwood Proportion

Tree growth is influenced by genetic factors as well as environmental conditions, and this interaction affects the nature of the wood formed (Freitas et al. 2019). The heartwood, bark, and pith tissue in tree formation are often influenced by the environment, but are also under strong genetic control (Zobel and Jett 1995). Several studies have explored their effect on wood properties (Bradbury et al. 2011, Li et al. 2018, Rodríguez-Pérez et al. 2022). However, the factor that controls the proportion of heartwood in trees is still discussed the most. Freitas et al. (2019) stated that the environment did not affect the xylem content of *Eucalyptus grandis* × *Eucalyptus urophylla* clones, but it was influenced by clonal effects. Similar results were also obtained in *Eucalyptus cladocalyx* F. Muell (Bush 2011) and *P. sylvestris* (Ericsson and Fries 1999), where the proportion of heartwood was affected by genetics. Miyamoto et al. (2016) reported that its color was mainly controlled by genetics rather than the environment based on the spatial autocorrelation analysis. Previous studies also revealed that the color was influenced genetically, and there were clear differences between the clones (Kurinobu et al. 1992, Nakada 2007). However, other studies showed that *C. japonica* was affected by environmental factors, such as water and soil type (Kansai Regional Office of Breeding, Forest Tree Breeding Center 1977), and a similar effect was observed in *A. melanoxylon* (Harrison 1975a, Harrison 1975b, Nicholas et al. 2007).

Based on the results, genetic factors have more influence on the proportion of heartwood than the environment. Bradbury et al. (2011) reported that the absolute amount of heartwood in blackwood was mainly affected by the growth rate, but the relative amount was related to variations in the width of the sapwood, which has a strong genetic basis. This finding indicates that increasing the growth rate as well as the heartwood content through genetic selection can be carried out independently. Several studies also reported that its percentage was influenced by genetic control in other *Acacia* species (Searle and Owen 2005). Tree diameter is more significant in the initiation of heartwood production

in *A. melanoxylon* compared to age (Bradbury et al. 2011). Increasing the growth rate helps to increase the proportion, although it has a minimal effect, and can also have a negative impact on other properties, such as color, basic density, and stiffness. Breeding efforts also need to concentrate on increasing provenance collections and native families, which increase their best genetic base.

CONCLUSIONS

A high proportion of heartwood will increase the quality of timber for construction, as it is more durable and more aesthetic. In this study, heartwood proportion varied greatly in each species and this affected the end use of the wood. Furthermore, the influential factors include within tree variation and among tree variation, such as age, growth rate, and species/genera as well as growth conditions, including location and environment. The percentage of heartwood was also affected by various silvicultural treatments, namely spacing, thinning, pruning, fertilization, and irrigation. The amount of heartwood in a tree can be controlled by the growth diameter, because it has more influence than age. The faster the growth rate of a plant, the greater the effect on the proportion. Previous studies reported that its increase also led to the formation of larger sapwood rings. This indicates that the growth rate caused a decrease in the percentage of heartwood. Efforts through genetic and environmental control are expected to produce a tree with faster heartwood growth than sapwood thickness, especially genetic factors, which have more influence than the environment. Therefore, further studies need to investigate the genetic factors that influence or play a role in controlling these properties. Apart from the proportion of heartwood, which is often considered in global markets, other wood properties, such as basic density, color, and stiffness are also important. Therefore, it is necessary for tree breeders to also concentrate on other traits that are of interest for further studies.

Author Contributions

RA conceptualized and designed the study, derived models, analyzed data and wrote the original draft of the manuscript, RA and GL collected and processed the data, SNM, JPGS and GL checked and edited the manuscript, GL performed methodological discussions and gave final approval of the manuscript.

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Conflicts of Interest

The authors declare no conflict of interest.

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