

A Review: The Soluble Sugars Involved in The Process of Heartwood Formation

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Abstract

This study aims to examine the soluble sugars involved in the process of heartwood formation using 87 journal articles and non-articles. The data used was collected through an online search with 5 keywords, namely "heartwood formation", "reserve material of heartwood", "non-structural carbohydrate of heartwood", "starch of heartwood" and "sucrose of heartwood". By removing irrelevant papers, 44 suitable journal articles and non-articles were found. Studies showed that monosaccharide fraction was the largest group compared to the other fractions as well as dominated by the hexose group. In addition, several species such as *Swietenia mahagoni*, *Pinus sylvestris*, *Betula pendula*, and *Fagus sylvatica* were detected more complete than other species in the fraction of soluble sugars (monosaccharides, disaccharides, trisaccharides, tetrasaccharides, alditol, and cyclitol). Based on previous studies, the contents of glucose and sucrose compounds were the major compound and plays an important role in storing energy reserves and the process of heartwood formation. Meanwhile, the levels of arabinose and galactose were the minor components in several species. Within tree variation, soluble sugars drop from the sapwood to the heartwood and from the top to the bottom of the tree. Subsequently, the alditols and cyclitols fractions need special issues, especially for tropical species related to their role.

Keyword: Heartwood formation, reserve material, non-structural carbohydrate, starch, sucrose

Introduction

In most tree species, the xylem consists of two histologically similar but physiologically different wood zones (sapwood and heartwood). Sapwood (the outer wood zone) is composed of physiologically active, live cells and reserve substances, and the external rings transport water with minerals from roots to the cambium and assimilatory organs. Meanwhile, heartwood (the inner wood zone) is physiologically inactive and does not participate in the conduction of water (Nawrot *et al.* 2008).

Heartwood formation is an important process in perennial plants as trees. It is the ultimate process leading to the death of living sapwood tissues due to internal phenomenon depending on the cycle of tree life involving both water and mechanical gradients (Berthier *et al.* 2001). Physiological processes such as xylem dehydration (Kuroda *et al.* 2009), depletion of storage compounds (Magel *et al.* 1994; Piispanen and Saranpaa 2001), accumulation of heartwood substances (Magel *et al.* 1991; Nakada and Fukatsu 2012), and programmed cell death (Nakaba *et al.* 2012), often accompanies the process of the heartwood formation. In addition, there is also changes in the structure of the cell wall (Nakada and Fukatsu 2012; Song *et al.* 2014). The substance deposited in the heartwood is the most important investment because of its effect on the color value (aesthetics) and natural durability. Secondary metabolism in trees produces heartwood substances whose substrates come from nonstructural carbohydrate metabolism (NSC) (Cui *et al.* 2020).

Reserve materials are present in the wood as lipids and NSC. Storage of NSC is very important for woody species. These reserves were used in long-lived organisms for their

perennity by fighting against biotic and abiotic stress, including drought, disturbance, and pests (Dietze *et al.* 2014). NSC play an important role such as carbon providing for energy metabolism and osmoregulation, nutrient transport, and the biosynthesis of toxic extractives for defense mechanisms (Kampe and Magel 2013).

During the formation of the heartwood secondary components, NSC is the main photosynthetic storage compound which is transported inwards through the ray parenchyma cells (Hillis 1987). The appearance of cell death in the transition zone (sapwood-heartwood) begins with depletion of storage substances based on increased endoamylolytic activity. In all sapwood part of the trees shows a more or less even distribution of all NSC within the sapwood. However, the concentrations of starch and soluble sugars decreased steadily with increasing age of the sapwood to the heartwood boundary. In most species, the NSC is almost absent in the heartwood. This is found for both softwood and hardwood (Magel and Holl 1993; De Jardin *et al.* 1997). Hillis (1987) stated that the composition and distribution of NSC depend on the growing location, wood species, within tree variation, and genetic factors. Furthermore, NSC consists of starch and soluble sugars, such as sucrose, fructose, glucose, arabinose, galactose, and stachyose, etc., (Cui *et al.* 2020). Soluble sugars that are usually involved in the heartwood formation process are monosaccharides (e.g. glucose, fructose, mannose, xylose and galactose), disaccharides (sucrose), and a small number of trisaccharides (e.g. raffinose) and tetrasaccharides (e.g. stachyose). This review will be only focus on the soluble sugars involved in the process of heartwood formation.

This study aims to carry out a literature review of the soluble sugars involves in the heartwood formation. In this

study, articles and non-articles were investigated through online searches. The keywords used to search for journals and non-journal articles including “heartwood formation”, “reserve material of heartwood”, “non-structural carbohydrate

of heartwood”, “starch of heartwood” and “sucrose of heartwood”. Furthermore, a total of 87 journal articles and non-articles were found. However, only 44 suitable papers were used for review (Figure 1).

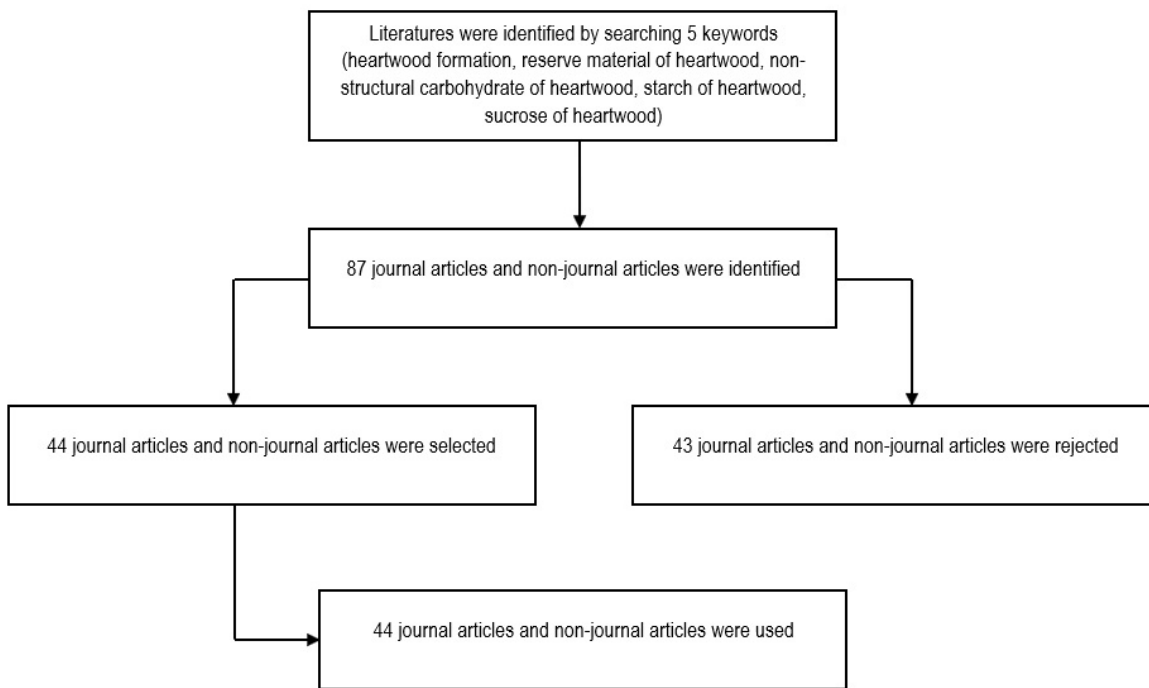


Figure 1. Review processes for this study

Soluble Sugars in Some Species

In mahogany species such as *Swietenia mahagoni*, fractions of monosaccharides, cyclitols, alditols and disaccharides were found, while in *Swietenia macrophylla* only monosaccharide was detected. The similar pattern was also found in same families (*Meliaceae*), such as in seedling of *Cedrela fissilis* (Aragao *et al.* 2015), stem bark of *Azadirachta indica* (Chitra *et al.* 2017) and in wood of *Acacia melanoxylon* (Lourenco *et al.* 2008). Furthermore, in other species like *Quercus faginea* and *Trema orientalis*, mostly monosaccharide groups were also found (Jahan and Mun, 2003; Miranda *et al.* 2017). On the other hand, monosaccharide and disaccharide groups were obtained in,, for instance, *Tectona grandis*, *Robinia pseudoacacia*, and *Schinopsis balansae* (Magel *et al.* 1994; Streit and Fengel 1994; Niamke *et al.* 2010, 2011). Furthermore, in the *Pinus* species, there were several slightly different patterns.

Saranpaa and Holl (1989) and Funda *et al.* (2020) reported that monosaccharides, disaccharides, trisaccharides, and tetrasaccharides fractions were detected in *Pinus sylvestris*. Meanwhile, Turfan *et al.* (2018) stated that monosaccharides (glucose) and disaccharides (sucrose) groups were detected in *Pinus nigra*. On the other hand, it was just monosaccharides observed in *Pinus radiata* (Uprichard and Lloyd 1980; Berrocal *et al.* 2004). Subsequently, in *Delbergia odorifera* species, monosaccharides, disaccharides (sucrose) and tetrasaccharides (stachyose) were detected. The similar trend was also shown in *Betula pendula* detecting monosaccharides, trisaccharides (raffinose) disaccharides (sucrose), cyclitols (myo-inositol) and in *Fagus sylvatica* namely, monosaccharides, disaccharides, trisaccharides (raffinose), tetrasaccharides (stachyose), alditols, and cyclitols (inositol). The complete soluble sugar groups and compounds in the several species mentioned previously are presented in Table 1.

Table 1. Soluble sugars in some species both in hardwood and softwood (stem wood part)

Wood categories	Species	Soluble sugars	References
Hardwoods	<i>Swietenia mahagoni</i>	monosaccharides (glucose, fructose, mannose, arabinose, galactose, xylose), cyclitols (myo-inositol and neo-inositol), alditols (meso-erythritol, arabitol, mannitol), disaccharides (sucrose)	Arisandi <i>et al.</i> 2022
	<i>Swietenia macrophylla</i>	monosaccharides (glucose, mannose, arabinose, galactose, xylose, rhamnose)	Rutiaga-Quiñones <i>et al.</i> 1998
	<i>Acacia melanoxylon</i>	monosaccharides (glucose, mannose, arabinose, galactose, xylose)	Lourenco <i>et al.</i> 2008
	<i>Dalbergia odorifera</i>	monosaccharides (glucose, fructose, arabinose, galactose) disaccharides (sucrose), tetrasaccharides (stachyose)	Ciu <i>et al.</i> 2020
	<i>Tectona grandis</i>	monosaccharides (glucose, fructose), disaccharides (sucrose)	Niamke <i>et al.</i> 2010, 2011
	<i>Robinia pseudoacacia</i>	monosaccharides (glucose, fructose), disaccharides (sucrose)	Magel <i>et al.</i> 1994
	<i>Schinopsis balansae</i>	monosaccharides (glucose, fructose, mannose, galactose, xylose, rhamnose), disaccharides (sucrose)	Streit and Fengel 1994
	<i>Betula pendula</i>	monosaccharides (glucose, fructose, raffinose, disaccharides (sucrose), cyclitols (myo-inositol)	Piispanen and Saranpaa 2001
	<i>Quercus faginea</i>	monosaccharides (glucose, arabinose, mannose, galactose, xylose, rhamnose)	Miranda <i>et al.</i> 2017
	<i>Fagus sylvatica</i>	monosaccharides (glucose, fructose, arabinose, mannose, galactose, xylose, rhamnose), disaccharides (trehalose, saccharose), trisaccharides (raffinose), tetrasaccharides (stachyose), alditols (erythritol, glycerol, arabitol and mannitol, sorbitol, xylitol), cyclitols (inositol)	Dietrichs 1964; Kubel <i>et al.</i> 1988; Irmouli <i>et al.</i> 2002; Zule and Moze 2003; Vek <i>et al.</i> 2014, 2016
	<i>Trema orientalis</i>	glucose, arabinose, mannose, galactose, xylose	Jahan and Mun 2003
Softwood	<i>Pinus radiata</i>	monosaccharides (glucose, mannose, arabinose, galactose, xylose)	Uprichard and Lloyd 1980; Berrocal <i>et al.</i> 2004
	<i>Pinus sylvestris</i>	monosaccharides (glucose, fructose, mannose, arabinose, galactose, xylose), disaccharides (sucrose), trisaccharides (raffinose), tetrasaccharides (stachyose)	Saranpaa and Holl 1989; Funda <i>et al.</i> 2020
	<i>Pinus nigra</i>	monosaccharides (glucose), disaccharides (sucrose)	Turfan <i>et al.</i> 2018

In the compound levels, glucose is the largest component in *Swietenia mahagoni*, *Swietenia macrophylla*, *Acacia melanoxylon*, *Pinus radiata*, *Pinus sylvestris*, *Dalbergia odorifera*, *Tectona grandis*, *Schinopsis balansae*, *Quercus faginea*, *Fagus sylvatica*, and *Trema orientalis*. However, the opposite pattern was found in sucrose levels found in *Robinia pseudoacacia*, *Pinus sylvestris* or *Fagus sylvatica*. The low sucrose content occurs due to reduced transport in the phloem (Niamke *et al.* 2010). The relatively low phloem activity can be associated to the harvest season (Nobuchi *et al.* 2005) which corresponds to the begin of the dry season and shows high enzymatic hydrolysis of sucrose to fructose and glucose (Magel *et al.* 1994). Meanwhile, species such as *Pinus nigra* (Turfan *et al.* 2018) and *Robinia pseudoacacia* (Magel *et al.* 1994) are detected the highest sucrose compared to glucose. The low glucose and high sucrose content indicate that glucose are metabolized to sucrose and used to increase osmotic potential (Turfan *et al.* 2018). In addition, levels of arabinose and galactose are generally low in several species, especially in the species *Dalbergia odorifera*, *Swietenia mahagoni*, *Acacia*

melanoxylon, *Pinus radiata* and *Pinus sylvestris* (Uprichard and Lloyd 1980; Saranpaa and Holl 1989; Berrocal *et al.* 2004; Lourenco *et al.* 2008; Funda *et al.* 2020; Ciu *et al.* 2020; Arisandi *et al.* 2022). This might be related to their function and characteristics (Hansen *et al.* 1997). Saranpaa and Holl (1989) reported that these sugar compounds were the smallest storage materials. Therefore, it was the most easily utilized carbohydrates in trees. With regard to hexose and pentose compositions, hexoses were greater than pentoses. Important metabolic intermediates i.e., hexoses (particularly glucose and fructose) can be used to form storage groups of carbohydrates (particularly starch, which is a glucose polymer), and other disaccharide compounds for transport throughout the body from organisms (Sage 2008).

At some species were also detected not only monosaccharide and disaccharide fractions, but also sugar alcohol group including alditols and cyclitols such as in *Swietenia mahagoni*, *Betula pendula*, and *Fagus sylvatica*. In mahogany, alditols and cyclitols have not known regarding their role in the heartwood, because they usually play a specific role in temperate species. For example, in *Betula*

platyphylla var. *japonika* (Kasuga *et al.* 2007), where alditols and cyclitols play an important role for abiotic stress tolerance. They are primarily involved in tolerance to drought, salt stress, and low temperatures. Cyclitols and alditols in mahogany are involved in certain activities and functions which are tropical species. Magel *et al.* (2000) stated that alditol is involved in cell elongation, carbon transport and cryoprotection and is synthesized in appreciable quantities under specific metabolic conditions. Additionally, the biological functions of cyclitol differ from one another. Piispanen and Saranpaa (2001) mentioned that myo-inositol in silver birch serves as a reserve for oligosaccharide metabolism intermediates of the raffinose family, which is required during cold acclimatization in autumn. In mahogany, cyclitol can function as a metabolic reserve pool for the more active parts of the stem (wood cells near the cambium) (Piispanen and Saranpaa 2001). Several other species such as the heartwood of *Planchonella vitiensis* (Cambie *et al.* 1997) and *Sequoia sempervirens* (Anderson *et al.* 1968) and also in the stems of *Betula pubescens* and *Betula pendula* stems (Linberg *et al.* 1958), myo-inositol was detected.

In general, hardwood contains more pentosans (C-5 sugars) such as xylose and arabinose, while softwood contains more hexosans (C-6 sugars) such as mannose, glucose and galactose. Lachowicz *et al.* (2019) stated that softwood hemicellulose consists of pentosans and hexosans, but hardwood hemicellulose consists mainly of pentosans. In addition, the main differences between tropical and temperate species that NSC, starch and soluble sugars in tropical species during the dry season are generally higher than in temperate species such as in the species *Acer saccharum* and *Betula alleghaniensis* in North America (Gaucher *et al.* 2005). However, in the rainy season, the NSC content is relatively the same between tropical and temperate species (Würth *et al.* 2005; Myers and Kitajima 2007), for example, in the Panama area and temperate in East China (Chen *et al.* 2012; Zhang *et al.* 2013).

Within and Among Tree Variation

Lachowicz *et al.* (2019) stated that the relationship between wood properties and tree age has long been a topic of interest for many researchers. Berrocal *et al.* (2004) reported that the glucose and mannose contents increased, while the xylose, galactose, and arabinose concentrations decreased with tree age from 1 to 15 years in *Pinus radiata*. Rencoret *et al.* (2011) stated the content of arabinan, galactan, and mannan decreased, while the amount of glucan and xylan increased, with increasing age of *Eucalyptus globulus* trees from 1 month to 9 years. Other studies have also reported the effect of tree age on sugar components in several species such as *Eucalyptus globulus* and *Pinus radiata* (Uprichard and Lloyd 1980; Miranda and Pereira 2022).

NSC and lipids as reserve materials are transported from sapwood through ray parenchyma cells to supply the formation of secondary compounds in heartwood. These

compounds are usually stored in the part of sapwood (Magel *et al.* 1994). Some NSC such as glucose, fructose and sucrose were detected in sapwood and their amount decreased from cambium to heartwood (Dietrichs 1968). Meanwhile, other sugars, namely xylose and arabinose were detected in *Quercus sp* heartwood and mannose Norway spruce heartwood.

Arisandi *et al.* (2022) reported that the main soluble monosaccharide sugars (glucose, fructose, mannose, and xylose) in *Swietenia mahagoni* accumulated in the sapwood and decreased progressively from the sapwood to the heartwood. This is indicated that these compounds are metabolized at the heartwood-sapwood boundary (Niamke *et al.* 2011). The high contents of the major components in sapwood could be a high demand for NSC which were degraded for energy and the carbon skeleton needed for metabolic activities such as photosynthesis, the formation of secondary metabolites (phenolics), and cell respiration (Datta and Kumar 1987; Magel *et al.* 1994). In addition, the heartwood-sapwood boundary proved to be the site where the highest NSC catabolic activity occurred (Magel *et al.* 2001). Transition of metabolic activity from sapwood to extractive forms of heartwood (phenolic compounds) from reserves (NSC) has also been reported (Datta and Kumar, 1987; Nobuchi *et al.* 1996). Niamke *et al.* (2011) found that NSC (starch, glucose, fructose and sucrose) decreased drastically from sapwood to heartwood in teak wood.

In the transition zone, the amount of starch can be hydrolyzed into glucose through the hydrolysis of the amyloglycosidase enzyme (Magel *et al.* 1997; Magel *et al.* 2001). In other species such as teak, the key enzymes for NSC catabolism are succinate-dehydrogenase and glucose-6-phosphate involved in reducing NSC and accumulates in the inner sapwood and the transition zone (Datta and Kumar 1987). In addition, several minor monosaccharide components (arabinose and galactose) are absent in heartwood. Similar results were found in *Dalbergia odorifera*, where this may be related to its characteristics and function (Cui *et al.* 2020). Saranpaa and Holl (1989) reported that monosaccharides are small storage materials and are the most easily used carbohydrates in trees.

Sucrose is one of the major carbohydrate components, but this compound is only found in a small proportion of heartwood, or not detect (Streit and Fengel, 1994; Magel *et al.* 1994; Niamke *et al.* 2011). Arisandi *et al.* (2022) reported that sucrose is low detected in mahogany sapwood. However, based on the results of the principal component analysis (PCA), the sucrose component was always found during the formation of heartwood. Therefore, this shows that the presence of sucrose is very important in the process of heartwood formation. The content of sucrose decreased from heartwood to sapwood at 4 years, but it was not found at 5 years old in heartwood part (Arisandi *et al.* 2022). Furze *et al.* (2018) stated that in the ray parenchyma cell, NSC can be transported in two opposite directions. It means that the NSC transported inward can be used as a substrate for secondary

metabolism in the xylem, including for the synthesis of heartwood substances. While NSC transported outside retain the phloem “Leakage-retrieval Mechanism” (De Schepper *et al.* 2013). Magel *et al.* (1994) mentioned that the nature and radial distribution of carbohydrate reserves in wood indicated that the youngest zone of wood (outer sapwood) contains high concentrations of soluble sugars (sucrose, glucose and fructose predominately) and starch, whereas the heartwood part is almost absent of storage material. IAWA (1964) reported that in living trees, the sapwood contains cells, reserve materials, and is rich in nutrients that are attractive to biotrophic pathogens. Meanwhile, heartwood is rich in secondary metabolites (flavanols and other phenolic compounds) to protect tree from wood destroying microorganism.

Conclusions

Soluble sugar is one of the nonstructural carbohydrate metabolism that play an important role in the process of heartwood formation. They are metabolized in the transition zone to produce substance heartwood products (phenolic compounds) during the process of the formation of heartwood. Apart from monosaccharide and disaccharide groups, several fractions of trisaccharides, tetrasaccharides, alditols, and cyclitols were also detected in *Swietenia mahagoni*, *Pinus sylvestris*, *Betula pendula*, and *Fagus sylvatica*. Glucose and sucrose were the largest compounds in several species in this study. Therefore, their role is very important in the process of heartwood formation. On the other hand, hexose group in the monosaccharide fraction is the largest group. Subsequently, further studies need to be carried out to examine the role of alditol and cyclitol compounds found in tropical species.

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