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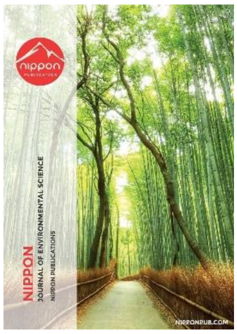

Review Paper

Effects of some important genes, phytohormones, and abiotic factors on wood formation in trees; an overview

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Abstract: Wood is vital for development and growth of trees since it offers long-distance conductance of water and nutrients from roots to leaves mechanical support. Therefore, we sought to define the important factors affecting the wood formation in trees. Wood (secondary xylem) is produced by five main phases, counting cell division, cell expansion, cell wall thickening, cell death, and heartwood (HW) formation. In woody plants, a coherent lateral sheet of meristematic tissue is called vascular cambium, which occurs between the secondary phloem and the secondary xylem. Some important hormones which influence vascular cambium activity include the 1-aminocyclopropane-1-carboxylate (ACC), brassinosteroids (BR), auxin (IAA), cytokinin, ethylene, jasmonic acid (JA), gibberellin (GA), S-adenosyl-L-methionine (SAM) and strigolactone (SL). Apart from that, four main transcription families, KNOX (Knotted-like homeobox), MYB (v-myb avian myeloblastosis viral oncogene homolog), WARKY, and NAC (NAM/ATAF/CUC), which regulate lignin biosynthetic pathway and wood formation in plants are discussed in this study. Moreover, several abiotic factors, such as temperature and seasonal conditions, as well as stresses could affect the wood formation.

Keywords: Genes; Hormones, KNOX; NAC; Vascular cambium; Wood formation

1. INTRODUCTION

Trees plays a vital role in sustaining earth's living environment and in providing several vital natural resources for life. Secondary growth, which gives rise to wood formation, is one of the main features that make trees biologically distinct (Li et al., 2006). Wood is vital for development and growth of trees because of offering mechanical support and long-distance conductance of water and nutrients from roots to leaves (Pilate et al., 2004). Wood, also known as the secondary xylem, is the product of vascular cambium (Begum et al., 2013) which is produced of two meristematic initials: fusiform initials and ray initials (Ye and Zhong, 2015). Besides, wood formation is remarked as the unique developmental procedure, which is considered for about 100 billion tons of CO_2 fixed per annum by plants (Li et al., 2006). In trees, wood tissue mostly consists of the secondary cell walls, comprising 42–50% cellulose. The most frequent biopolymer on Earth is cellulose, which is located in the cell walls of plant (Xi et al., 2017).

Plant cells form two types of cell walls, namely primary cell wall and secondary cell wall (Karahara et al., 2009). Primary cell wall is a fairly thin and extensible wall that the cells synthesize in cell division. Secondary walls are deposited after cessation of cell expansion in specialized cell types, comprising tracheids, vessels, sclereids and fibers, which are called the sclerenchyma. Secondary xylem is defined as the most abundant source of secondary wall-containing cells (Zhong et al., 2018). In woody tissues, plant cell walls mostly comprise the lignin, hemicellulose, carbohydrates, cellulose, microfibrils, proteins, etc. (Li et al., 2019). Secondary walls formation is a complex procedure that needs the coordinated expression of secondary wall-specific biosynthetic genes to direct biosynthesis and aimed secretion of secondary wall components. Some genes, such as: Knotted-like homeobox (KNOX), myeloblastosis (MYB), and NAC genes, have involved in biosynthesis of secondary wall components, comprising cellulose, xylan, glucomannan and lignin (Yuan et al., 2019). Besides, Li et al. (2017) stated that different classes of genes controlling wood formation. Some researchers (Gong et al., 2019; Wang et al., 2019) expressed that the KNOX, MYB, NAC families are key factors in controlling development, metabolism, regulating secondary wall biosynthesis, and responding to abiotic stresses. Wood is characterized chemically and anatomically, and our understanding of the wood formation is still in infancy. Apart from that, it is critical to understand the molecular and biochemical mechanisms affecting wood formation (Yuan et al., 2019). Therefore, formation of wood in terms of the secondary cell wall and involved genes were discussed in this review paper.

2. WOOD FORMATION

Wood (secondary xylem) is produced by the series of five key steps, comprising cell division, cell expansion (radial and elongation extension), cell wall thickening (involving hemicellulose, cell wall proteins, cellulose, and lignin biosynthesis and deposition), programmed cell death, and heartwood formation (Plomion et al., 2001). Six types of wood (Figure 1) might be identified on a single tree, containing early wood, late wood, juvenile wood, mature wood, reaction wood, and opposite wood. At the beginning of the growing season (spring wood), the early wood is produced; however, late wood is the part of an annual growth increment produced in the latter part of the growing season (summer wood). Early wood, which is made of large diameter cells, has a low density, while the late wood, which composed of smaller diameter, has high density because of the thicker cell walls (Carvalho et al., 2013).

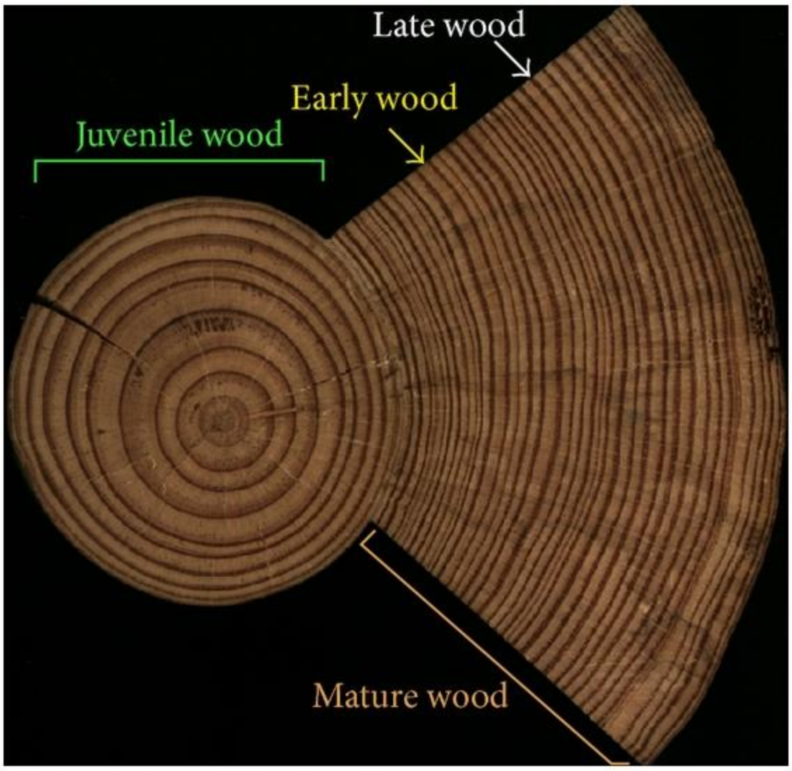


Figure 1: A stem from an adult tree showing juvenile to mature wood
(Source: Carvalho et al., 2013; the Open Access material under the Creative Commons Attribution License)

Wood formation contains growth and production of new cells by the cambium and their subsequent differentiation (Hartmann et al., 2017). Wood formation is considered as a continuous and dynamic process that comprises cambial cell proliferation, xylem cell specification and expansion, secondary cell wall (SCW) biosynthesis and programmed cell death (PCD). Internal and external features regulate each step (Zhang et al., 2014). In trees, the wood formation relies on the cambial activity (Begum et al., 2013).

2.1. Vascular Cambium

The vascular cambium in wordy plants is a coherent lateral sheet of meristematic tissue with a few cells thick, which occur between the secondary phloem and the secondary xylem. It occurs from the roots, over the stem, and up to the tips of branches (Montagnoli et al., 2019). The phloem or xylem mother cell is produced by dividing cambial initial, the other daughter cells keep the function and characteristics of a cambial initial. Before differentiating, xylem and phloem mother cells may divide several times (Figure 2; Lachaud et al., 1999).

Cambial initials comprise ray initials and fusiform initials. The ray initials are small cells and nearly isodiametric, which occur frequently in groups. They generate the radially-oriented ray cells reported in many woody plants, which have an important role in radial transport and storage functions (Du and Groover, 2010). Relative to the stem, the fusiform cambial initials are oriented longitudinally, and undergo periclinal divisions that generate two kinds of daughter cells, comprising the phloem mother cells to the outside of the stem and the xylem mother cells to the inside of the stem (Zhu et al., 2013).

Additionally, the sensitivity of cambium to plant hormones is vital for the activity of cambium and the dynamic mechanism of wood formation (Figure 3). Besides, cambial age supposedly has a moderate to strong impact on wood properties (Lenz et al., 2011). Recent advances in understanding of these procedures have discovered that wood formation is extremely controlled at the transcriptional level, and the strong correlation detected for transcriptional and metabolic component traits contributing to complex cytological and morphologic changes (Xu et al., 2016).

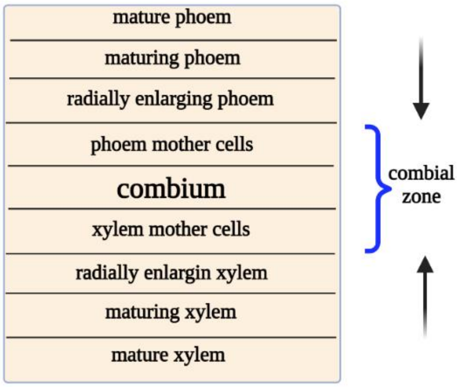


Figure 2: Cambium and production of secondary conducting tissues
(Sources: Lachaud et al., 1999)

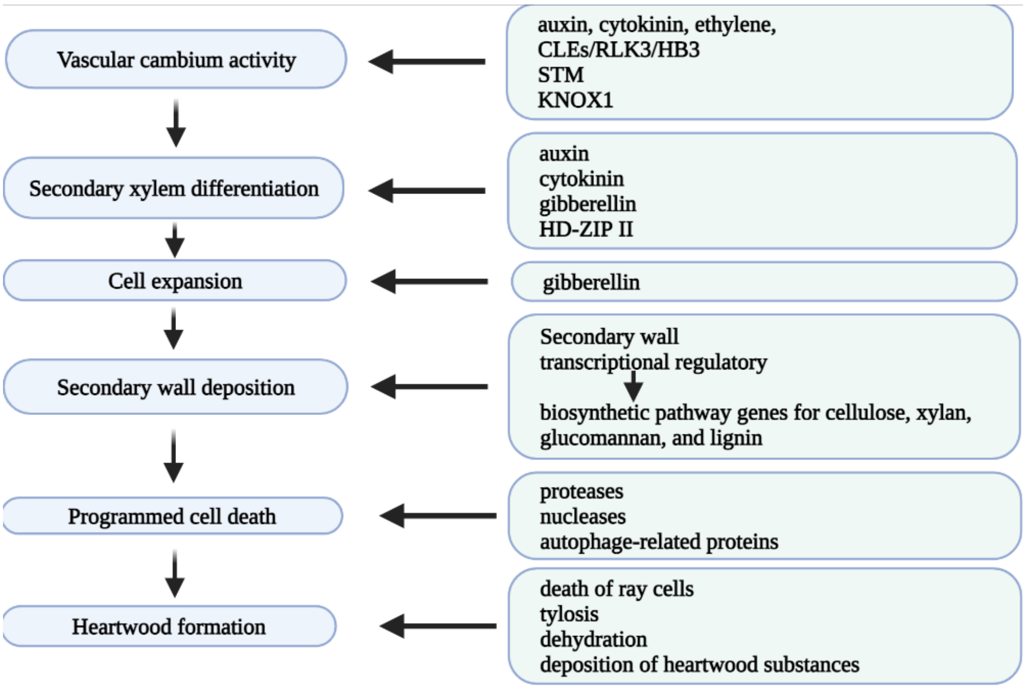


Figure 3: The developmental steps of wood formation, and factors involved in each phase
(Sources: Ye and Zhong, 2015; the Open Access material)

2.2. Control of vascular cambium activity

Secondary growth in root and stem tissues must be coordinated with primary growth at the shoot-root axis. Among different organs, phytohormones play important roles in communication, and may act as signal molecules between primary and secondary meristems (Wang, 2019). 1-aminocyclopropane-1-carboxylate (ACC), auxin (IAA), brassinosteroids (BR), cytokinin, jasmonic acid (JA), ethylene, gibberellin (GA), S-adenosyl-L-methionine (SAM) and strigolactone (SL) are some important hormones (Table 1) which affect vascular cambium activity (Etchells et al., 2012; Poel and Straeten, 2014; Wang et al., 2019). Zheng et al. (2019) expressed that brassinosteroid (BR), gibberellin (GA) and auxin (IAA) are the main promoting hormone for plant growth. Various plant hormones regulate the vascular cambium activity and the secondary xylem differentiation. While cambial cell division activity is controlled by cytokinins, auxin affects both cambial cell proliferation and xylem differentiation (Zhang et al., 2014). Likewise, specific aspects of xylem differentiation are controlled by gibberellins and brassinosteroids. The cambial growth is stimulated by the gaseous plant hormone ethylene (Seyfferth et al., 2018).

SAM produces ACC, which the reaction is catalyzed by the enzyme ACC-synthase (ACS). ACS, which applies vitamin B6 as a co-factor for its enzymatic function, is a member of the PLP-dependent enzymes. ACS is localized in the cytosol (Poel and Straeten, 2014). The most important three-membered ring non-protein amino acid is ACC, which is remarked as the direct precursor of the plant hormone ethylene (Vanderstraeten and Der Straeten, 2017).

Auxin is an indole acetic acid (IAA), a weak organic acid with the structure like the amino acid tryptophan (Paque and Weijers, 2016). It has and a carboxylic acid function and indole ring. A wide definition of auxin(s) can be a class of compounds that affects plant development in the way IAA (Paque and Weijers, 2016). In plants, auxin biosynthesis is very complex. In addition, IAA can be released from IAA conjugates by hydrolytic cleavage of IAA-amino acids, IAA-methyl ester and IAA-sugar.

In plants, brassinosteroids (BRs) are a type of polyhydroxylated steroidal phytohormones with similar structures to animals' steroid hormones (Tang et al., 2016). BRs are remarked as a kind of essential plant hormones that have diverse roles in controlling broad spectrum of plant growth and developmental procedures (Saini et al., 2015). At least 69 BRs, comprising 65 free BRs and 5 conjugated BRs, have been reported and characterized (Ohnishi, 2018). Fujioka and Yokota (2003) expressed that BRs are C27, C28, and C29 steroids depending on their C-24 alkyl substituents.

Cytokinins are a type of plant-specific hormones that have an essential role in the cell cycle and numerous developmental programs. Natural cytokinins are mainly and chemically the N6-substituted purine derivatives. Isopentenyladenine (iP), dihydrozeatin (DZ) and zeatin (Z) are the dominant cytokinins identified in higher plants (Werner et al., 2001). The phytohormone cytokinin has a diverse role in plant development, affecting several agriculturally vital processes, comprising growth, nutrient responses and the response to abiotic and biotic stresses. In plants, biosynthesis and inactivation pathways regulate cytokinin levels (Kieber and Schaller, 2018).

Ethylene has been reported as the first gaseous hormone discovered in plants. It is remarked as a vital regulator of several developmental and physiological procedures such as germination, seed dormancy, and vegetative growth. Moreover, ethylene plays a significant role in the plant's defense against biotic and abiotic stress factors (Houben and Poel, 2019). Additional studies also consider a potential role for ethylene in cell division (Love et al., 2009). In plants, the transformation of SAM to ACC by the ACC synthase (ACS) and the conversion of ACC to ethylene by the ACC oxidase (ACO) are two main stages in ethylene biosynthesis (Zhu et al., 2015). Commonly, the rate-limiting stage in ethylene biosynthesis contains the transformation of SAM to ACC, and an increase in ethylene production associated with a rapid increase in cellular ACS activity (Liu and Zhang, 2004). During tension wood formation, ethylene biosynthesis increases due to an asymmetric induction of ACO (Love et al., 2009).

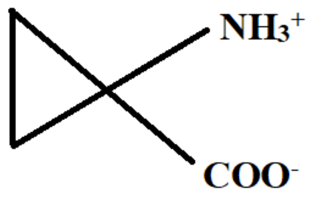
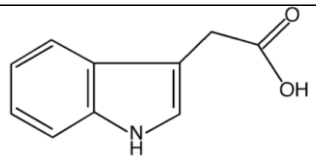
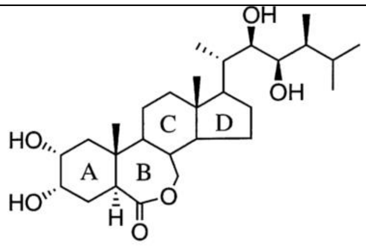
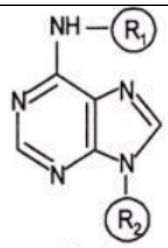
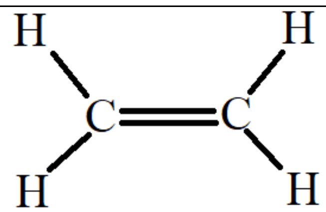
In plants, gibberellins (GAs) are vital hormones for various developmental procedures. The GA biosynthetic pathway has been explained by a combination of biochemical and genetic approaches (Weiss and Ori, 2007). In the life cycle of a plant, GAs act in both a continuous and a discrete way. GA promotes cell elongation during the entire life cycle. Also, GA acts as a regulator of vital transition points in the plant life cycle (Ogas, 1998). Several non-bioactive GAs exist in plants, and they act as precursors for the bioactive forms or are de-activated metabolites. GA1, GA3 as well as GA4 and GA7 are some important bioactive Gas, which frequently have a C3-hydroxyl group (Davière and Achard, 2013). Immanen et al. (2016) reported that bioactive gibberellin has its maximum in the developing xylem cells.

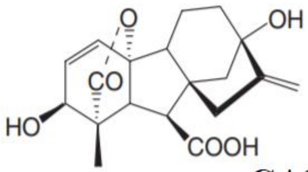
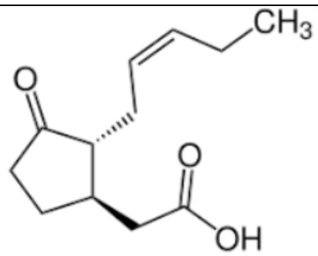
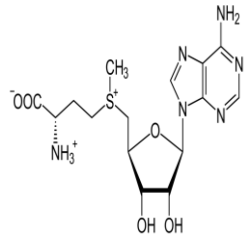
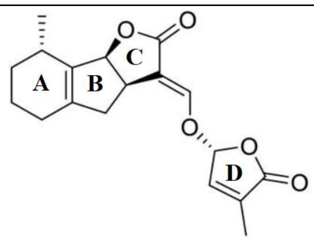
JAs are a class of lipidic plant hormones that derive from α-linolenic acids (α-LAs). They are involved in development (such as root development and trichome formation), abiotic stress responses and plant-microbes interactions in defense and symbiosis (Larrieu and Vernoux, 2016) but are also involved in plant development such as root development and trichome formation. JA can be further enzymatically transformed into many derivatives or conjugates, some of which have well-described biological activity such as free MeJA, JA, JA–Ile and cis-jasmone (Yan et al., 2013).

In plants, SAM is a common substrate for several biochemical reactions. Three key SAM dependent pathways are the biosynthesis of polyamines, ethylene and the transmethylation reactions. In all living organisms, SAM is the main methyl donor (Poel et al., 2012).

Strigolactones (SLs) are a new type of plant hormones which are important in plant science. They are the group of biologically active molecules, named semiochemicals, that are applied to disseminate information between individual species. They might be divided into two kinds, containing orobanchol and strigol (Zwanenburg et al., 2016). The structural of SLs is a tricyclic lactone with various carbon A-ring sizes and substitution patterns on AB-rings (Lopez-Obando et al., 2015).

Table 1: Hormonal control of vascular cambium (VC)

Hormones	Biosynthesis	Function in VC	Structure	References
ACC	1-aminocyclopropane-1-carboxylate synthase (ACS) [EC 4.4.1.14] catalyses the cyclization of SAM to 1-aminocyclopropane-1-carboxylic acid (ACC).	ACC promotes cambial division and wood formation. In transgenic trees, overexpression of ACC oxidase also increases cambial activity and secondary growth.		Ruduś et al. (2013); Wang (2019)
IAA	Auxin biosynthesis can be divided into two general categories: de novo auxin biosynthesis and the release from auxin conjugates.	IAA is produced in the young leaves, and it moves downward through the cambium to the root tips and constitutes the major hormonal signal which regulates wood formation, by controlling the cambial activity and inducing the xylem and phloem differentiation.		Zhao (2012); Carvalho et al. (2013); Seyfferth et al. (2018);
BR	The various chemical structures of BRs can be derived from a 5α-steroid skeleton and are arranged by the functional groups on the A ring, B ring, and side chain.	Gibberellins are important in the modulation of the cambial activity and the control of xylem differentiation.		Ohnishi (2018); Muñiz et al. (2008);
Cytokinin	The breakdown of tRNA was originally suggested as a possible mechanism for cytokinin synthesis. The released cis-zeatin could subsequently be converted to active trans-zeatin by the enzyme cis-trans-isomerase. Enzymatic activity that converts AMP and dimethylallyl-diphosphate (DMAPP) to the active cytokinin.	Cytokinins play roles in controlling the activity of the vascular cambium and the initiation of xylem development.		Haberer and Kieber (2002); Kieber and Schaller (2014); Muñiz et al. (2008);
Ethylene	The biosynthesis of ethylene begins with the conversion of the amino acid methionine to S-adenosyl-methionine (AdoMet) by the enzyme AdoMet synthetase	Ethylene is an endogenous stimulator of cell division in the cambial.		Love et al. (2009); Yoon and Kieber (2013);

GA	GAs are tetracyclic diterpenoids synthesized from geranylgeranyl diphosphate. The biosynthesis pathway that converts geranylgeranyl diphosphate to biologically active Gas.	GA regulates cambium activity and induces long fibers.	 GA3	Ogawa et al. (2003); Aloni (2013)
JA	The synthesis of 12-oxo-phytodienoic acid (12-OPDA) or deoxymethylated vegetable dienic acid (dn-OPDA) from unsaturated fatty acid takes place in the chloroplast, which is then converted to JA in the peroxisome.	JA positively regulates cambial activity. JAs are implicated in vascular formation.		Nandan and Melnyk (2018); Hellmann et al. (2018); Ruan et al. (2019);
SAM	S-adenosyl methionine (SAM) is synthesized from methionine and ATP by SAM synthetase (SAMS; EC2.5.1.6).	SAM causes dwarfism and enlargement of the Vasculature. And it is important in plant vascular development.		Vera-Sirera et al. (2010); Ezaki et al. (2016);
SL	SLs are synthesized from the key precursor CL, which is derived from all-trans β-carotene via the action of an isomerase (D27) and two carotenoid cleavage dioxygenases (CCD7 and CCD8).	SLs affect cambium cell division and SL increases cambium activity.		Lopez-Obando et al. (2015); Zwanenburg et al. (2016)

2.3. Effects of cambial age on wood properties

Several properties of wood and their genetic controls differ with the cambial age and follow distinct trends through the juvenile and transition wood, which points that the correlations among different wood traits also vary with development (Lenz et al., 2011). Zubizarreta-Gerendiain et al. (2012) expressed that radial growth of stem and wood properties are affected by cambial age (i.e. number of annual ring from pith towards bark) and genetic origin. Ikonen et al. (2008) reported that wood density and fiber length increase and early wood percentage decrease as a function of cambial age and distance from pith to bark in *Pinus sylvestris* L. and *Picea abies* (L.) Karst.

2.4. Involved genes in wood formation

Xu et al. (2016) stated the genes play a vital role in the vascular cambium and wood formation of plants. KNOX, MYB, NAC, and WRKY gene families regulate lignin biosynthetic pathway and wood formation in plants (Tian et al., 2013).

The Knotted-like homeobox (KNOX) genes are remarked as a large family of transcription factors named homeobox genes, which have a conserved DNA-binding domain (homedomain) and control pattern formation and growth during development in plants. KNOX genes have a role to regulate xylem and secondary wall formation (Woerlen et al., 2017). KNOX genes are divided in two classes based on the similarity of certain residues within the homeodomain, expression patterns and intron position (Hake et al., 2004). Class I KNOX genes are stated in shoot apical meristems. Class II KNOX genes contain more diverse expression patterns (Reiser et al., 2000). *STM* (SHOOTMERISTEMLESS), *BP* or *KNAT1* (BREVIPEDICELLUS), *KNAT2* and *KNAT6* are considered as the class I KNOX, while *KNAT3*, *KNAT4*, *KNAT5* and *KNAT7* are remarked as the class II KNOX (Hake et al., 2004). Class

I KNOX genes, such as *STM*, play a vital role in meristem maintenance, while class II KNOX genes, such as *KNAT7*, have a role in secondary wall regulation (Zhao et al., 2020).

MYBs (v-myb avian myeloblastosis viral oncogene homolog) are to one of important superfamilies of transcription factors. They mostly play a role in responses to abiotic and biotic stresses, histomorphogenesis, cell proliferation and differentiation, organ formation and the contents of primary and secondary metabolites of plant metabolic pathways (Xiao et al., 2021). the MYB genes are responsible in the formation of the tiny tube and xylem by regulating the expressions of the cinnamoyl-CoA reductase gene and cinnamyl alcohol dehydrogenase gene (Lu et al., 2014). Yang et al. (2017) stated that in some tress (such as poplar), at least four MYB transcription factors (PtrMYB2, PtrMYB3, PtrMYB20 and PtrMYB21), and in *Arabidopsis* MYB46 and MYB83 act controlling secondary wall biosynthesis. Wang et al. (2020) expressed that PtoMYB156, PtrMYB189, and PdMYB221 act as regulatory repressors in *Populus* species which negatively affect wood formation and cell wall properties.

NAC SECONDARY WALL THICKENING PROMOTING FACTOR (*NST*) 1–2 and NST3/SECONDARY CELL WALL ASSOCIATED NAC DOMAIN PROTEIN1 (*SND1*) belong to the NAC domain, which are regulators of secondary cell wall formation (Sakamoto et al., 2016). (VASCULAR-RELATED NAC-DOMAIN6) and VND7 are specifically expressed in vascular cells and function as transcriptional switches for metaxylem and protoxylem vessel differentiation, respectively (Zhao et al., 2020). Hurtado et al. (2020) expressed that the VND1–VND7, NST1 and NST2, and SECONDARY WALL NAC DOMAIN TFs (SND1/NST3 and SND2) are master regulators of NAC.

The WRKY gene family involves a class of vital transcription factors responsible in physiological change and response to abiotic and biotic stress (Wang et al., 2010). By binding to the promoter of NST2, *WRKY13* has been reported to positively regulate lignin biosynthesis. Moreover, WRKY12 has been reported to negatively regulate secondary cell wall formation by directly inhibiting NST2 (Yang et al., 2016).

2.5. Effects of abiotic factors on cambial activity and wood formation

In trees, cambial activity is controlled by both internal factors (such as plant hormones) and environmental factors (such as temperature, and rainfall) (Begum et al., 2013). In response to seasonal conditions, cambial activity plays as the dormant and active cycles in plants (Wang, 2019). Temperature has a vital role in vascular development of plants, as earlier warming of temperature induces an earlier onset of the growth season over stimulation of cambial activity (Swidrak et al., 2014). The xylogenesis is stimulated by the increased temperature of at least 6–8 ◦C at the onset of the growing season (Cufar et al., 2011), while initiation of advanced formation of phloem, compared to xylem cells, needs lower temperature, following which it is endogenously regulated. In woody plants, higher temperature may affect tracheid diameter based on the plant species (Qaderi et al., 2019). Budzinski et al. (2016) stated that the annual course of cambial activity is commonly related to the change of cold and warm, and/or dry and rainy seasons. Perennial woody plants from temperate zones have established mechanisms that undergo seasonal cycles of activity and dormancy, which are mutually stated as the annual periodicity (Begum et al., 2013). This periodicity has a significant role in the wood formation, and demonstrates the environmental adaptation of woody plants. Consequently, the quality and quantity of wood rely on the differentiation of cambial derivatives and the division of cambial cells (Budzinski et al., 2016).

Basically, plants need water, energy (light), mineral nutrients and carbon for growth. Abiotic stress is described as environmental conditions that decrease yield and growth lower than the optimum levels. Reactions of plants against abiotic stresses are dynamic and complex (Carmer et al., 2011).

Apart from the vital roles in a variety of cellular procedures, potassium (K) is remarked as a main osmolyte for wood formation (Ployet et al., 2019). Polyet et al. (2019) stated that K has a role in plant resistance to abiotic stresses, comprising drought, by enhancing processes (such as osmotic adjustment, photosynthesis activation, stomatal aperture control, and reactive oxygen species (ROS).

3. CONCLUSION

Trees play a vital role in sustaining earth’s living environment and in providing several vital natural resources for life. One of the main aspects of trees is wood formation, which are affected and controlled by several hormones, genes and abiotic factors. Hormones (such as ACC, IAA, BR, cytokinin, ethylene, GA, JA, SAM, and SL), abiotic factors (such as temperature) as well as several transcription factors (such as KNOX, MYB, NAC and WRKY) can affect wood formation.

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