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Wood Formation in Trees

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ABSTRACT

Among the ecosystem services provided by forests, wood provisioning takes a central position. *Wood and derived products* have played a critical role in the evolution of human kind and demand for raw material is increasing in a foreseeable future. Wood is used for energy production, construction and a wide variety of products for which different properties are required. Anatomical, chemical and physical properties of wood are determined through a complex process called xylogenesis controlled by internal and external signals and occurring during the life of the tree. In this chapter we describe i/how wood is formed and ii/the different factors controlling this developmental process with emphasis on the molecular machinery involved, iii/the functions of wood and iv/the biotechnology approaches developed to improve wood biomass production and properties genetically.

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Introduction

Wood represents the main source of terrestrial biomass production and is a major sink for excess atmospheric CO_2. Wood is expected to play a significant role in the future as a renewable and environmentally cost effective alternative to burn fossil fuel. As the world population is predicted to reach over 9 billion in 2050, the global demand for wood for renewable energy, building and pulp and paper will grow rapidly. This increasing demand for wood threatens the conservation of natural forests in temperate and tropical areas. Indeed, to cover the predicted needs over the next 40 years, 20 to 40% of natural forests would be exploited. An alternative to this deforestation is to increase the area of plantation representing only 7% of the world's forest cover today (Forest Resources Assessment 2010) and to consider trees as crops. In view of global change, the sustainable management of such planted forests is also becoming a main focusing issue.

To face these challenges, sylvicultural practices will need to be optimized. In addition, modern genomic sciences should be promoted to improve the genetic material used in industrial plantations (reviewed by Harfouche et al. 2011). The use of functional genomics to identify key molecular players involved in wood formation, as well as new translational genomic approach such as marker assisted selection or genomic selection, should permit to increase efficiency by providing selection criteria based on DNA markers. Complementary to the exploitation of standing natural variation, genetic engineering is a possible alternative to support rapid domestication of forest trees, provided that biosafety issues are fully addressed (Fladung et al. 2012).

In this context it is important to understand the molecular, genetic, hormonal, environmental and ontogenic factors involved in xylogenesis since all these factors control the formation of the different types of wood observed in a single tree genotype (Table 1).

In this chapter we first describe the complex developmental process of wood formation. The following two sections develop the regulatory mechanisms involved in wood formation: i/the intrinsic developmental programs involving hormones, transcription factors, miRNA as well as cambium ageing; and ii/the environmental cues such as gravity and light, seasonal variation and changes in air compound levels. The fourth section presents the main functions of wood consisting of mechanical support, storage and hydraulic properties. Finally, forward and reverse genetic strategies to improve wood biomass and properties are explored.

Wood, a highly specialized tissue, originates from a very structured developmental process.

Wood is mainly formed of vertical elements and a few horizontal elements (ray cells or sclerified parenchyma). In angiosperm, vertical

Table 1. Characteristics of the different types of wood observed in a single tree and their effects on end-use products.

Wood characteristics	Types of wood								End-use products				
	EW	LW	JW	MW	TW OW angiosperm		CW OW gymnosperm		Lumber	OSB	Pulp and paper	Biofuel	Charcoal
MFA	+	–	+	–	–	+	+	–	–	–	–	*na*	–
Lignin content	+	–	+	–	–	+	+	–	–	–	–	–	+
Cellulose content	–	+	–	+	++	–	–	+	+	+	+	+	–
Cell wall thickness	–	+	–	+	++	–	+	+	*na*	+	+	*na*	+
Density	–	+	–	+	+	–	+	–	+	+	+	+	+
Tracheid length	–	+	–	+	*na*	*na*	–	+	+	+	+	*na*	*na*

EW: early wood; LW: late wood; JW: juvenile wood; MW: mature wood; TW: tension wood; OW: opposite wood; CW: compression wood; OSB: oriented strand board; MFA: microfibril angles; *na*: non-available

elements consist of fibers, vessel elements and in some species tracheids (Fig. 1A,B). In gymnosperm wood is mainly formed of tracheids with a small amount of axial parenchyma associated with resin ducts (Barnett 1981, Larson 1994). Wood originates from a complex developmental process called xylogenesis, divided in four main steps (Fig. 1A): cell division, cell expansion, secondary cell wall formation and programmed cell death (Fukuda et al. 1996).

Cell division results from the activity of the vascular cambium, a lateral meristem located at the periphery of the trunk, which is responsible for secondary growth (reviewed by Déjardin et al. 2010). The vascular cambium is formed of two types of highly vacuolated cells (i.e., high mitotic activity) called fusiform initials and radials. Elongated fusiform initials divide periclinally (i.e., tangential plan) to produce xylem and phloem mother cells which give rise to secondary vascular tissues either wood elements inwards or phloem cells outwards. This division occurs in a non-symmetric way leading to an overproduction of differentiating xylem compared to phloem production (reviewed by Plomion et al. 2001). Radial initials also divide periclinally to produce parenchyma ray cells involved in the nutriment

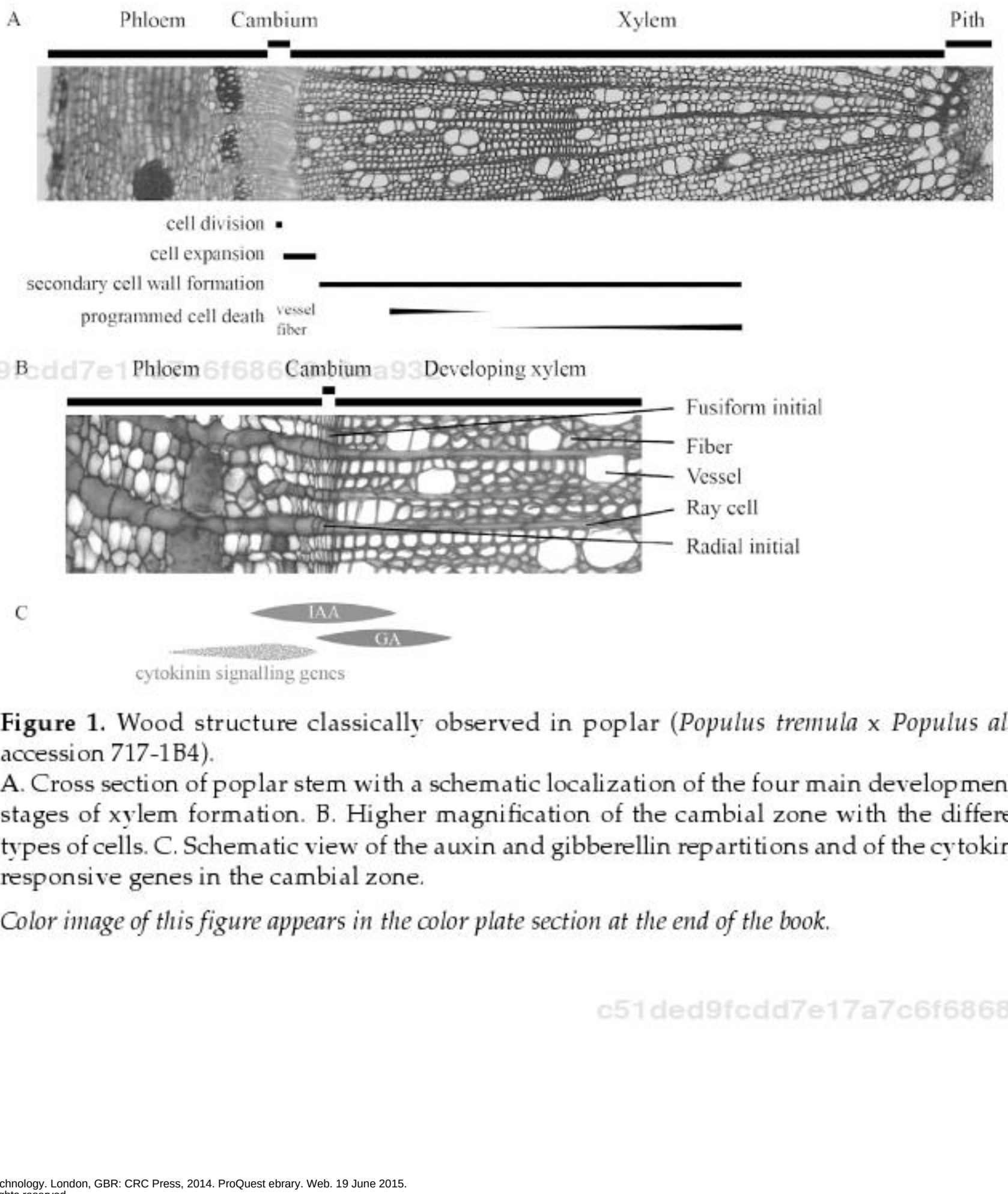

Figure 1. Wood structure classically observed in poplar (*Populus tremula* x *Populus alba*, accession 717-1B4).
A. Cross section of poplar stem with a schematic localization of the four main developmental stages of xylem formation. B. Higher magnification of the cambial zone with the different types of cells. C. Schematic view of the auxin and gibberellin repartitions and of the cytokinin responsive genes in the cambial zone.

Color image of this figure appears in the color plate section at the end of the book.

transport between xylem and phloem (Nilsson et al. 2008). Elongated fusiform initials can also divide anticlinally (i.e., radial plan) to increase the number of initials and ensure the integrity of the vascular cambium during radial growth (Karlberg 2011).

Once new cells are generated, they undergo a process of cell elongation and expansion to reach their final size. This expansion is asymmetric; first cells elongate and then increase their width. During this differentiation phase cells exhibit only a primary cell wall characterized by the absence of lignin and a high proportion of xyloglucan among the hemicelluloses compounds. The presence of xyloglucans keeps the strength of the primary cell wall, while allowing its extensibility (Takahashi-Schmidt 2008). The absence of lignin allows cell wall hydrolyzing enzymes (endoglucanases, xyloglucan endotrans glycosylases, expensins, pectin methyl esterases,…) to remodel primary cell wall components and thereby permit cells to elongate both in length and diameter with the requirement of microtubule network (Pauly et al. 1999). This expansion is also driven by the random orientation of the microfibrils conferring high elastic properties to the primary cell wall.

Once expansion is completed, cells start their secondary cell wall thickening. The secondary cell wall is composed mainly of cellulose, hemicelluloses, lignin, and pectin and cell wall proteins (approximately around 45%, 28%, 20% and 3% respectively) (Takahashi-Schmidt 2008). Secondary cell wall formation occurs in the fiber cells and vascular elements to provide them with a high rigidity due mainly to the elevated level of cellulose and hemicelluloses (glucuronoxylan). The organization of the cellulose microfibrils (microfibril angle) is different between the primary and secondary cell walls (Timell 1986) and differs also between the 3 layers of the secondary cell wall (S1–S3), responsible for wood properties (Timell 1967). The second major compound of the secondary cell wall is lignin which is a phenolic polymer (reviewed by Neutelings 2011) confering both rigidity to wood tissue and hydrophobic surface for water transport.

Finally, programmed cell death (PCD) occurs as a prerequisite for water transport. PCD is faster in vessel elements compared to angiosperm fibers and gymnosperm tracheids (Courtois-Moreau et al. 2009). This ontogenetic process is linked closely with secondary cell wall thickening and is therefore difficult to localize precisely during xylogenesis. PCD in tracheids and vessel elements involves modification of tonoplast permeability, vacuolar rupture, DNA degradation, final autolysis and partial hydrolysis of non-lignified primary cell wall. In fibers, the same steps occur in a slightly different way: vacuolar rupture is delayed and the primary cell wall is not partially hydrolyzed (reviewed by Bollhöner et al. 2012).

A last modification of xylem elements considered as a form of programmed cell death is the formation of heartwood (HW) mainly

involved in decay-resistance (Beauchamp 2011). HW is the inside darker colored section of the trunk adjacent to the transition zone (TZ) and characterized by a high level of secondary metabolites synthesized in the ray cells of the TZ. The external part of the trunk is called sapwood (SW). This part of the trunk is less colored and considered the living part of wood as it still contains living ray cell elements and is involved in sap transport.

The secondary metabolites present in high quantity in the HW are mainly flavonoids and derivatives. Their ability to induce wood decay-resistance is also of great interest for agrochemical and pharmaceutical applications. Indeed, these compounds once extracted from HW, either as essential oils or as purified compounds, present an antimicrobial activity and the ability to reduce reactive oxygen species (ROS) production by inhibiting cytochrome P450 activity (McNulty et al. 2009, Waikedre et al. 2012). HW extracted molecules have been tested for their inhibition selectivity on different types of cytochromes (human, fungal…) in order to evaluate their potential as antifungal and cancer chemo preventative agents (McNulty et al. 2009).

Intrinsic Developmental Programs Involved in Wood Formation

Wood is the result of a complex developmental process. The roles of intrinsic factors—hormones, transcription factors, small RNAs—and of an ontogenic process—cambium aging—involved in this regulating process are described below.

a. Hormones signaling pathways

Several hormones—auxin, gibberellin, cytokinin, ethylene and strigolactone—are known to be involved in the different phases of cell development: cell proliferation and cell differentiation (Elo et al. 2009, Nieminen et al. 2012). Here we synthesize their roles and show how the most studied hormone (IAA) interacts with the others during wood formation.

Auxin (IAA) is a major hormone involved in the regulation of xylem production by controlling cambial initial divisions and cell differentiation. Indeed, an IAA gradient has been measured in the cambial region of hybrid aspen and scots pine (Uggla et al. 1996, 1998, Tuominen et al. 1997): IAA concentration peaks in the cambial initials and decreases to both the outer and inner sides of the stem where cells are differentiating (Fig. 1C). Consequently, and because exogenous IAA treatments induced reduced radial growth, IAA has been described as responsible for cambial initials

divisions (Uggla et al. 1996). In a more recent work, using transgenic hybrid aspen with a reduced auxin signaling, Nilsson et al. (2008) showed that IAA indeed plays a crucial role in the regulation of cambial initial divisions (both anticlinal and periclinal divisions) and affects only xylem production. Besides, they showed that hybrid aspen with decreased auxin signaling were affected in fibers and vessels shapes: they were shorter and slimmer.

Gibberellin (GA) applied on intact or on decapitated stems stimulated radial growth (Digby and Wareing 1966, Björklund et al. 2007). Hybrid aspen overproducing GA also exhibited a higher wood production (Eriksson et al. 2000, Mauriat and Moritz 2009). However, addition of IAA to GA treatments showed a stronger increase in xylogenesis compared to what has been observed with only one hormone at a time (Digby and Wareing 1966, Björklund et al. 2007). In the same study, these authors showed that GA promoted IAA transport, IAA stimulated GA production and both hormones shared a common transcriptomic signature. These 2 hormones thus have a synergistic function in cell division of cambial initials. However, Ragni et al. (2011) showed in Arabidopsis that an IAA transport inhibitor (NPA) treatment did not affect the increased xylogenesis due to GA signal. Another interesting observation is the peak of bioactive GA in the cambial zone located in the differentiating xylem area (Israelsson et al. 2005) (Fig. 1C) where IAA is almost not present, which is in agreement with the fact that GA alone can stimulate xylem fiber elongation (Eriksson et al. 2000, Mauriat and Moritz 2009).

Cytokinin is also a major molecule affecting only cell division during xylem formation. Indeed, the application of exogenous cytokinin and the use of transgenic hybrid aspen with reduced cytokinin signaling in the cambial zone have permit to conclude that cytokinin plays a major role in cell division (Saks et al. 1984, Nieminen et al. 2008). Moreover, in the cambial zone the cytokinin receptors have a high peak of expression in the cambium (Fig. 1C). This is coherent with the fact that wood anatomy is only slightly affected in the transgenic hybrid aspen with reduced cytokinin in the cambial zone (Nieminen et al. 2008).

In the same way, ethylene has been shown to promote radial growth by an increased xylem production in poplar and pine treated with ethylene or ACC (1-Aminocyclopropane-1-carboxylic acid, its precursor). The same results were obtained in transgenic hybrid aspen overexpressing ethylene biosynthesis genes (Junghans et al. 2004, Love et al. 2009). In hybrid aspen as IAA treatment induced ethylene biosynthesis in cambial zone (Nilsson et al. 2008), ethylene could act through IAA signaling. Nevertheless, ethylene seems also to have a role by itself in tension wood (TW) formation (Andersson-Gunnerås et al. 2003, Love et al. 2009). Indeed, tension and compression woods (TW and CW) present increased expression of ethylene biosynthesis and signaling genes and transgenic hybrid aspen *ethylene*

insensitive displays a reduction of TW formation when tilted compared to wild-type plants (Love et al. 2009).

A last group of hormones, strigolactones (SL), has been recently characterized as involved in secondary growth in *Arabidopsis thaliana* and *Eucalyptus globulus* (Agusti et al. 2011). Exogenous application of artificial SL (GR24) induced cambium division and Arabidopsis SL deficient mutants exhibited less radial growth while presenting high IAA levels and signaling (Agusti et al. 2011). The use of double mutants SL and IAA deficient proved that SL is required in IAA signaling pathway controlling wood formation.

b. Transcription factors network

Tremendous progresses regarding the transcriptional regulation of the biosynthesis of secondary cell walls have been obtained during the last decade, highlighting a complex hierarchical network of transcription factors whose majority belongs to two large families, i.e., R2R3-MYB and NAC (NAM/ATAF/CUC) (Demura and Fukuda 2007, Zhong et al. 2007, 2010b, Umezawa 2009, Zhong and Ye 2009, Zhao and Dixon 2011, Grima-Pettenati et al. 2012, Wang and Dixon 2012).

If many breakthroughs can be attributed to the model plant *Arabidopsis*, it should be emphasized that the R2R3 MYBs acting as master regulators of the secondary cell wall (SCW) formation were first identified in trees. *EgMYB1* and *EgMYB2*, both preferentially expressed in *Eucalyptus* differentiating xylem were shown to regulate the synthesis of the three major secondary wall components (cellulose, hemicelluloses and lignins) acting as a repressor (Legay et al. 2007, 2010) and as an activator (Goicoechea et al. 2005), respectively. Both of them regulate the whole secondary wall developmental programme and as such can be considered as second levelled "master switches" since the top level of the hierarchical network is occupied by NAC transcription factors like SND1 (SECONDARY WALL-ASSOCIATED NAC DOMAIN PROTEIN1). Indeed, *AtMYB46*, the functional ortholog of *EgMYB2* is a direct target of SND1. Similarly, the expression of the *P. trichocarpa PtrMYB3* and *PtrMYB20* is also directly activated by *Ptr*WND2, a poplar ortholog of SND1 (McCarthy et al. 2010).

In contrast to the *Arabidopsis* NACs that exhibit either fiber- or vessel-specific expression, the poplar NACs *PtrWNDs* are expressed in both vessels and fibers and also in ray parenchyma cells of *P. trichocarpa* (Zhong et al. 2010a). Ohtani et al. (2011) identified 12 *PtVNS/PtrWND* genes that control the differentiation of both vessels and fiber cells redundantly during xylem tissue formation by modulating their activity depending on the situation. They act on genes involved in secondary wall formation and programmed cell death but also on other TFs (Zhong et al. 2010a, Ohtani et al. 2011).

Other NAC and MYB participating to the regulation of SCW have been identified both in *Arabidopsis* and trees. They comprise *PtrMYB28* (Zhong and Ye 2009) and *PtMYB1* (Bomal et al. 2008) potential orthologs of the lignin-specific MYB activators (*AtMYB58, 63* and *85*, Zhou et al. 2009), the *P. trichocarpa*: *PopNAC118, 122, 128, 129* (Grant et al. 2010) potential orthologs of *XYLEM NAC DOMAIN 1* (*XND1*) a transcriptional repressor regulating the expression of genes involved in both programmed cell death and secondary wall formation (Zhao et al. 2008), *PopNAC154* (a *SND2/SND3* ortholog) (Grant et al. 2010). Interestingly, *SND2* over expression was associated with different phenotypes when expressed in woody and herbaceous stems (Hussey et al. 2011).

In addition to the major NAC and MYB families, members of other TF families were shown to be involved in the regulation of secondary cell wall biosynthesis. For instance, *KNOTTED1-LIKE HOMEODOMAIN PROTEIN7* (*KNAT7*) was shown to be a direct target of *SND1* (Zhong et al. 2008). KNAT7 is a negative regulator of secondary wall biosynthesis both in *Arabidopsis* and poplar, and functions in a negative feedback loop repressing metabolically inappropriate commitment to SCW formation, thereby maintaining metabolic homeostasis (Li et al. 2012). *NtLIM1* was reported to regulate the lignin pathway both in transgenic tobacco and *Eucalyptus camaldulensis* plants carrying an antisense *NtLIM1* (Kawaoka et al. 2000, 2007, Kawaoka and Ebinuma 2001).

c. Small RNAs in cell differentiation and patterning during the secondary growth

Micro RNAs (miRNAs) and small interfering RNAs (siRNAs) are the two major classes of endogenous small RNAs in plants. miRNAs are functionally similar to siRNAs and both are ~20–24 nucleotides in length and can direct the cleavage or inhibit the translation of target gene transcripts and can thus mediate the phenomena of RNA interference (RNAi), post-transcriptional gene silencing (PTGS), and transcriptional gene silencing (TGS). MicroRNAs (miRNAs) derive from stem-loop region of endogenous nontranslated transcripts precursor whereas siRNA are processed from double-stranded RNA molecules (Bartel 2004, Mallory and Vaucheret 2004, Jones-Rhoades et al. 2006). The development of bioinformatics prediction tools (Rhoades et al. 2002) and more recently high throughput degradome sequencing (Addo-Quaye et al. 2008) have revealed that a large proportion of miRNAs/siRNAs gene targets encoded proteins with transcription regulatory activity particularly those with known or suspected roles in developmental patterning or cell differentiation (Rhoades et al. 2002, Bartel 2004). So, since their discovery 10 years ago miRNA/siRNA have been involved in various biological and physiological processes (Chen 2012) but our knowledge for

their involvement in regulating secondary growth is still scarce. As detailed in the previous part, transcriptional profiling as well as functional studies, performed not only in model plants such as *Arabidopsis* and Zinnia but also in tree species such as poplar and eucalyptus have demonstrated the fundamental importance of transcription to secondary growth regulation. Besides or/and in relationship with transcription factors, miRNAs/siRNAs represent potential important regulators in such transcriptional regulation networks. The first example came from *Arabidopsis* mutants with defects in the determination of xylem–phloem identity and plant adaxial-abaxial polarity (Emery et al. 2003). Two classes of transcription factors, Class III homeodomain leucine-zippers (HD-ZIPIII) and KANADI (KAN) genes, members of the GARP-type transcription factor family, are involved in such tissue patterning and polarity in *Arabidopsis*. In this genetic system, five *HD-ZIP* genes *PHABULOSA (PHB/ATHB14), PHAVOLUTA (PHV/ATHB9), REVOLUTA (REV/IFL1), ATHB8*, and *CORONA/ATHB15* (*CNA*), and three *KAN* genes (*KAN1–KAN3*) have been documented (Demura and Fukuda 2007, Zhang et al. 2011). *PHB*, *PHV*, and *REV* work antagonistically to *KAN* genes to regulate patterning and polarity. In the meantime, *CNA* and *ATHB8* have functions antagonistic to the *REV* in interfascicular fiber formation. Interestingly, all gain-of-function mutations of the HD-ZIPIII genes map to miR165/166 target sequence. Moreover, overexpression of miR166 results in overproduction of xylem cells in *Arabidopsis* (Kim et al. 2005). Thus, miR165/166 acts in meristem maintenance, vasculature patterning and leaf polarity specification.

Recently, functional studies of poplar orthologs of three of these HD-ZIPIII genes (*REV*, *CNA* and *ATHB8*) have also been carried out in poplar taken as a model tree species for studying vascular cambium differentiation during wood formation. Transgenic poplars expressing a microRNA-resistant form of the *REV* poplar ortholog (*popREVOLUTA/PRE*) cause patterning defects in both primary and secondary growth and more remarkably can induce cambium initiation in abnormal positions (Robischon et al. 2011). Using a similar approach, functional study of one poplar ortholog of *CORONA/ATHB15* (*POPCORONA/PCN*) was carried out using gain-of-function and knockdown approaches (Du et al. 2011). The authors showed that ectopic expression of microRNA-resistant form of PCN drastically impacts plant architecture, whereas knockdown of *PCN* showed subtle phenotypes at the tissue level. Overexpression of *PCN* results in delayed lignification of xylem and phloem fibers during secondary growth, whereas knockdown of *PCN* results in abnormal lignification of pith cell types that are normally not lignified. Although not reported by the authors, a precocious differentiation of xylem cells seems perceptible in the transition zone from primary to secondary growth but should be verified. Thus, *PCN* in poplar similarly to its *Arabidopsis* ortholog *CNA*,

may negatively regulate secondary vascular cell differentiation (Kim et al. 2005, Du et al. 2011). More recently, a poplar ortholog to *ATHB8* (*PtrHB7*) was shown to play an essential role in controlling a balanced differentiation between secondary xylem and phloem tissues (Zhu et al. 2013). These studies indicate that conserved regulatory mechanisms for xylem specification and vascular development exist between *Arabidopsis* and Poplar, despite their evolutionary distance (Zhang et al. 2011). In root development it has been suggested that miR165/166 moves and forms a gradient emanating from the endodermis and regulates its targets in a concentration-dependent manner. So, mobile microRNAs could be essential for xylem cell-type specification, regulating the activity of their targets in a dosage-dependent manner (Moreno-Risueno et al. 2012). Small RNA mobility in plants and their potential role as morphogen-like signals become a topic of growing importance (Skopelitis et al. 2012).

d. Cambium ageing

The age of the cambium has an important effect on the type of wood produced. Indeed, during the first 10–12 years of the tree life, Juvenile Wood (JW) is produced typically. The young cambium located in the crown of adult trees also produces JW. The length of juvenility (or the number of years that the tree produces JW) depends on the species. Once this period is finished another type of wood, called Mature Wood (MW), is produced by the old cambium. Researchers have found it difficult to define the age of demarcation between JW and MW because the change in wood properties is gradual and not abrupt, since wood properties do not mature at the same rate.

Differences between MW and JW have been described largely at anatomical, ultrastructural, chemical and technological levels, and constitute one of the sources of variation in wood traits (Zobel and van Buijtenen 1989, Zobel and Sprague 1998). MW differs from JW by having thicker cell walls, narrower cell lumens, larger cellulose microfibril angles, larger spiral-grain angles and a higher specific density. JW can occasionally present disproportionate amounts of compression wood (CW), distorted grain patterns and pith deposits (Larson et al. 2001). In terms of chemical composition, MW shows higher cellulose and lower lignin contents (Zobel and Sprague 1998). Overall, the anatomical, structural and chemical characteristics of JW affect solid wood product performances adversely (e.g., strength, stiffness and warning upon drying) as well as pulp and paper manufacture (e.g., yield, tearing strength, and bleach) (Fengel 1970, Zobel and van Buijtenen 1989, Zobel and Sprague 1998).

Key molecular players involved in JW vs. MW forming tissues were first described using different differential transcriptomic approaches. In

Pinus taeda, Lorenz and Dean (2002) used serial analysis of gene expression (SAGE) and showed that 60 genes presented at least 10-fold differences in their relative abundance between JW and MW. Using a modified differential display technique in *Pinus radiata*, Cato et al. (2006) correlated cellular morphology of JW and MW forming tissues with gene expression. Genes putatively involved in cell division and expansion were more expressed in JW, while genes putatively involved in secondary wall formation were up-regulated in MW. In *Pinus pinaster*, Paiva et al. (2008) used spotted cDNAs macro-arrays to identify genes, characterizing both types of wood. On the other hand, using a comparative genomic approach, Kumar et al. (2009) identified candidate genes from *P. taeda* which could have a role in the transition between JW and MW in *P. sylvestris*. Five out of the ten candidate genes evaluated showed significant differences between both types of wood. The genes *Porin MIP1*, lipid transfer protein and aquaporin like protein showed higher expression in MW. While, α-tubulin and calreticulin were highly expressed in JW.

Proteomic approaches have also been used to discover the main proteins involved in these two types of wood (Plomion et al. 2000, Gion et al. 2005, Fiorani Celedon et al. 2007, Herrera et al. 2010). In maritime pine, Gion et al. (2005) were the first to report on a reference map of Wood forming tissues associated with six different types of wood including JW and MW. In the same species, Paiva et al. (2008) reported 33 proteins overexpressed between JW and MW providing a first indication on the proteins differentially expressed between these two types of wood. It is clear that JW and MW display distinct proteomic signatures. Proteins of defense and amino acids metabolism were described as overexpressed in MW. More interestingly, enzymes involved in cell wall polysaccharides and lignin biosynthetic pathways were also overexpressed. In this sense, the over expression of two cellulose synthases are a clear indication of secondary xylem formation in MW. Contrarily, proteins involved in energy were found mainly in JW as well as glyoxalase and HSP which belong to the defense category. Moreover, the identification of actin and tubulin in JW, two cytoskeleton related proteins, is an indication of the active cell division, intracellular movement and cell expansion which occur mainly in this type of wood.

Effects of Environmental Cues on Wood Formation and Characteristics

Environmental cues trigger the formation of different types of wood, which can be found within a single tree genotype. In this section, the effects on wood formation of gravity and light, seasonal variation and modifications in Ozone and CO_2 levels in the atmosphere are described.

a. Gravity and light produce structurally modified wood: reaction wood and opposite wood

Several definitions have been raised to define reaction wood. Boyd (1977) enounced that reaction wood is a response of the tree to an external stress. Wilson and Archer (1977) proposed a theory based on equilibrium position of axes: any difference in the equilibrium position is corrected by the formation of reaction wood. The equilibrium position is to link with the gravitropic set-point angle defined by Digby and Firn (1995). Reaction wood is produced on one side of the organ. The wood on the opposite side is called opposite wood (OW) and can be different from normal wood.

Signals that trigger the formation of reaction wood are not yet fully identified and it is difficult to link the shape of a tree at a given time to the presence of reaction wood. Indeed a tilted axis does not compulsorily contain reaction wood indicating that inclination is not the sole triggering signal; conversely, a straight trunk can contain a lot of reaction wood (Chanson 1989).

Reaction wood is differentiated in case of gravitropic and phototropic reactions. Indeed in elongating organs tropic reactions are due to differential growth (one side of the organ elongated faster than the other). In organs where elongation is achieved but where the cambium is still active (trunk and branches except in the elongating zones) the motor process is the differentiation of reaction wood on one side of the organ. Studies on artificially tilted poplars, revealed different phases during the gravitropic reaction: it has been shown that tension is first produced on the upper side of the trunk during the gravitropic phase and then on the opposite side during the decurving phase called autotropism. An analysis of the kinematics of tropic movements showed that autotropism propagates from tip to base and is triggered before the trunk has reached the vertical axis, indicating that inclination of the apex is not the sole signal piloting TW formation (Coutand et al. 2007).

Some recent studies demonstrated that reaction wood can also be differentiated in the case of phototropism to achieve trunk movements towards unilateral light (Matsuzaki et al. 2007).

Gravitropic reactions are triggered when the tree is tilted or when, after the death of the apical bud, a branch rights-up to become the new leader. Phototropic reactions are triggered when the tree has to escape shade to access more light or as a response to differential of light. Reaction wood can also be differentiated because of the increment of self-weight during growth (see part 5a for more details) to counteract the effect of gravity (Fournier et al. 1994).

In most of angiosperms woody species, reaction wood is called tension wood (TW) because it is under tension within the living tree;

in most gymnosperms reaction wood is called compression wood (CW) because it is under compression within the living tree. Relatively often, the production of reaction wood is accompanied by eccentric growth. Some TW are characterized by the presence of an additional layer of cellulose within the secondary cell wall; this layer which is composed of cristalline cellulose is called G layer (gelatinous layer). CW is composed of round tracheids with thicker cell walls that miss the S3 layer. But the anatomical differences between TW and CW are not absolute, indeed G layered cells characteristic of TW of angiosperms have been found in gymnosperms like *Cryptomeria* or *Juniperus* (Chanson 1989); conversely, *Buxus* produces CW. The presence of G layer enables to detect TW by its shiny appearance when it is observed with oblique light (Barbacci 2008). TW can also be revealed by double stained thin cross sections (astra blue and safranin). CW is generally visible to the naked eye due to its brownish color. Kinematics studies have shown that the first G layered cells are differentiated in poplar within 48 hours after artificial tilting (Jourez and Avella-Shaw 2003).

In some species tension wood does not contain a G layer, in this case the only way to detect its presence is the measurement of autostresses of maturation at the trunk periphery. Autostresses are created during the wood maturation phase. Reaction woods exhibit different levels of autostresses than normal and opposite woods. The microfibril angle of the S2 layer is smaller in TW and higher in CW than the microfibril angle in normal wood which confers specific mechanical properties (see part 5a). The autostresses due to reaction wood lead to technical problems during wood machining (plank twisting, breakage, etc.) (Table 1) (Thibaut 1997).

Transduction pathways involved in phototropism and gravitropism perception have been mainly discovered with agravitropic *Arabidopsis thaliana* mutants. The majority of these mutants were affected in auxin transporters, photoreceptor genes or both (Hopkins and Kiss 2012, Baldwin et al. 2013). However, these pathways are poorly understood in perennial species because most of the studies published so far have focused on reaction wood formation but not on gravity sensing (Le Provost et al. 2003, Lafarguette et al. 2004, Yamashita et al. 2009). These studies were performed at the transcriptome level and identified mainly cell wall associated proteins during reaction wood formation both in angiosperms and gymnosperms. At the proteomic level a recent study in maritime pine (Herrera et al. 2010) identified proteins associated with the early gravitropic response in CW, most of these proteins were related to energy and primary metabolism.

b. Seasonal variation affects wood formation

The earth climate naturally varies on diverse time-scales, from diurnal to geologic time. In temperate climates, seasonal variation seems to be

essential for wood formation: to a large extent, intra ring variation is the most important source of variation in wood density (Larson 1994, Zamudio et al. 2002). Seasonal variation is driven by changes in the amount of solar radiation to earth's atmosphere and surface. It directly affects temperature and photoperiod and less directly rainfall and wind patterns. During winter cambium is dormant. This dormancy is composed of autumn rest followed by cold-imposed quiescence (Little and Bonga 1974, Begum et al. 2013). At the beginning of the growing season the cambium reactivates to produce a new layer of secondary xylem. Repeated cambium pinning (Seo et al. 2007) and xylem microcoring experiments (Bäucker et al. 1998) as well as point dendrometers studies (Deslauriers et al. 2007) have shown that date of cambium reactivation is highly controlled by end-of-winter/early-spring temperature (Begum et al. 2013). In tropical climate the dormant period coincides with the dry season while the active period coincides with the wet season (Marcati et al. 2006). Rossi et al. (2008) found that onset of temperature of xylogenesis is not very variable among the species. Conversely, for a different set of species Begum et al. (2013) concluded that threshold temperature for spring xylogenesis varies among species.

The conspicuous earlywood (EW)-latewood (LW) pattern in temperate tree-rings is well-known to reflect climate variation during the growing season. Wide-lumen and narrow-wall EW cells are formed during the comparatively fresh and humid opening of the growing season. Narrow-lumen and thick-wall LW cells are formed during the second part of the growing season, when temperature increases and water availability and day-length decrease.

A deviation from this model is called false ring (a band of LW-like cells located in EW) or more generally IADF, Intra Annual Density Fluctuation (Wimmer and Strumia 1998). Such feature is mostly attributed to drought (below-average rainfall–called drought ring in *Picea glauca* and *Pinus resinosa* (Glerum 1970)), or better said, to the variation of the balance between water availability and water demand during the growing season. False rings and IADFs are indicators of water stress in many species, like in *Pinus strobus* (Marchand and Filion 2012). At least in one case, *Pinus sylvestris* trees under drought stress built larger tracheids with thinner cell-wall (Eilmann et al. 2011). Other factors have been associated with false rings, like cool and snowy springs in *Pinus banksiana* and *Picea mariana* (Hoffer and Tardif 2009). False ring characteristics have been shown to be genetically determined in *Picea abies* (Rozenberg et al. 2002).

Recent studies of the dynamic of wood formation have revealed close relationships between intra-annual variation of wood anatomy and of wood density and radial growth (Cuny et al. 2012). Different factors control the dynamics of wood formation: xylem microcoring experiments have shown that maximum day-length coincides with maximum growth rate in

Fagus orientalis (Oladi et al. 2011), in *Araucaria angustifolia* (Oliveira et al. 2009) and in *Picea*, *Pinus*, *Abies* and *Larix* in temperate and boreal zones (Rossi et al. 2006). Controlled-condition experiments in *Pinus radiata* have shown that EW tracheids are formed during long-days while LW tracheids are formed during short-days (Jenkins et al. 1977).

According to authors and species, transition from EW to LW is often triggered by a parallel decrease of water availability and increase of water demand. In subtropical *Pinus elliotii* a major factor of wood formation seems to be seasonal variation of solar insolation (Harley et al. 2012). According to Begum et al. (2012), a rapid decrease in temperature induces LW formation in *Abies firma* after artificial cambium reactivation. LW width increases with length of growing season. Cessation of cambial activity is generally triggered by variable combination of environmental cues such as critical photoperiod or cold temperature (Heide 1974). Severe heat and drought may trigger early stop of cambial activity, like in 2003 in France for *Pseudotsuga menziesii* (Martinez-Meier et al. 2009). Dormancy-breaking is conditioned by species chilling requirement.

Many dendrochronological studies have shown that not only current season conditions, but also previous-season weather conditions affect wood formation (Lebourgeois et al. 2010).

Seasonal variation of cambial activity is a way for woody plants to acclimatize to new environmental conditions: it is a manifestation of phenotypic plasticity (Fonti and Jansen 2012). The main climatic variables involved in seasonal variation of wood formation, solar insolation, photoperiod and temperature, follow parallel trends. Sanchez-Vargas et al. (2007) related intra-ring microdensity variation with a simple seasonal drought index combining temperature and rainfall to calculate norms of reaction and estimate phenotypic plasticity in *Pinuspinaster*. Using a similar method on *Pseudotsuga menziesii* Martinez-Meier et al. (2009) showed how intra-ring phenotypic plasticity could be linked with adaptation to drought. Both authors found moderate to quite strong genetic determinism of cambium plastic response to seasonal variation. Such approaches provide a comprehensive picture of cambium response to seasonal climatic variation as an adaptation mechanism.

At the molecular level, several investigations have been carried out to identify the main genes involved in EW vs. LW formation. A first study on loblolly pine by Egertsdotter et al. (2004) reported that genes involved in lignification were up regulated in differentiating xylem associated with LW formation. Li et al. (2010) reported in *Pinus radiata* a similar trend with transcripts involved in primary and secondary cell wall formation differentially expressed respectively in EW and LW. A similar result was obtained in *Pinus pinaster* for a glycine rich protein specifically expressed during LW formation (Le Provost et al. 2003). Finally Paiva et al. (2008) using

cDNA macroarrays characterized the expression profile of thousands of genes along a growing season in a single genotype of maritime pine. These authors reported that genes involved in cell division, energy, sugar transport and cell wall biogenesis were upregulated in EW whereas genes involved in the cytosqueleton network and transcription were more represented in the LW forming tissue.

c. Modification in Ozone and CO_2 levels in the atmosphere induces changes in cell wall structure

Wood formation in trees is a dynamic process that is strongly affected by environmental factors (Mellerowicz and Sundberg 2008). Although it is commonly admitted, few reports deal with the impact of abiotic stress on wood component abundance and synthesis and most studies addressed wood anatomy. Trees have to cope with new stresses such as greenhouse gas, which appeared since the pre-industrial era. Tropospheric ozone and CO_2 are two of the most important greenhouse gases of our atmosphere that are predicted to continue increasing during the next century (IPCC 2007).

Tropospheric ozone is now considered to be the most important air pollutant affecting vegetation (Karnosky et al. 2007). It is generally accepted that ozone strongly reduces the growth of trees, including diameter growth and biomass of the trunk (Isebrands et al. 2001, Wittig et al. 2009) as a result of decreased photosynthesis (Wittig et al. 2007). Angiosperms are generally more sensitive to ozone than gymnosperms with a drop twice important for stem biomass dose equivalent (Wittig et al. 2009). Nevertheless, knowledge on the effects of ozone on wood is very limited. Most studies were performed in free air experiments and showed a decrease in vessel diameter, fibers and an increase in wall thickness in poplar and birch (Kaakinen et al. 2004, Kostiainen et al. 2006, 2008). Conversely experiment in controlled chambers resulted in an increase of vessel lumen diameter and a decrease of vessel frequency, whereas fiber frequency was enhanced in tension wood in poplar (Richet et al. 2011). Chemical composition of wood was also affected by ozone, a reduction of cellulose amount was observed in poplar and an increased of hemicellulose in birch (Kaakinen et al. 2004, Richet et al. 2011). Lignin content was increased after three years (Kaakinen et al. 2004) in trembling aspen and silver birch, but this observation did not remain after five years (Kostiainen et al. 2008). Increased lignin content was found in young poplars subjected to tropospheric ozone (Richet et al. 2011, 2012a). These results indicate an effect of tree age on the response and the relative importance of reaction wood. Otherwise, few studies dealt with the effect of ozone on wood compound metabolism. Lignin and cellulose metabolisms were reduced under ozone in poplar stems (Richet et al. 2011, 2012a, 2012b).

Such a reduction was mainly attributed to a decrease of cambium activity and a reduced radial stem growth (Richet et al. 2011).

CO_2 is the first greenhouse gas of anthropogenic origin involved in climate change. The effects of high CO_2 on tree growth are fairly well known. It is generally accepted that, unlike ozone, high CO_2 stimulates photosynthesis and growth in height and diameter of trees (Ainsworth and Long 2005). Elevated CO_2 decreased cell wall thickness (Luo et al. 2005) in poplar, increased number of vessels (Atkinson and Taylor 1996), as well as increased vessel lumen area (Gartner et al. 2003) in oak and in poplar (Luo et al. 2005). Stem wood composition undergoes several changes under elevated CO_2. A decrease of lignin content was reported in various studies (Cotrufo and Ineson 2000, Blaschke et al. 2002, Kostiainen et al. 2006) as well as in cellulose content (Kostiainen et al. 2006). However, an increase of lignin content was observed in hybrid poplar (Richet et al. 2012a). Increased concentrations of starch (Kaakinen et al. 2004), soluble sugars (Kaakinen et al. 2004) and extractives (Kaakinen et al. 2004, Kostiainen et al. 2006) were also found in response to elevated CO_2.

Ozone and elevated CO_2 have often been regarded for their opposite effects as single factors on plant growth and biomass, but their combinatory effect are less documented. Previous studies showed a compensation of the negative effects of ozone by elevated CO_2 (Isebrands et al. 2001, Saxe 2002, Karnosky et al. 2003, Riikonen et al. 2004, King et al. 2005, Wittig et al. 2007). The protection provided by the CO_2 enrichment could result from the stimulation of photosynthesis, which would support the detoxification process (Sehmer et al. 1998). Effects of elevated CO_2 and ozone on wood composition and structure are not well-known. The increase in lignin concentration in response to elevated ozone in aspen and birch was accentuated by elevated CO_2, whereas the combined treatment counteracted the CO_2-induced decrease in cellulose in aspen (Kaakinen et al. 2004), but none of these interactions were maintained two years later (Kostiainen et al. 2008). Kostiainen et al. (2006) showed that elevated CO_2 improved the decrease in vessel percentage induced by ozone in silver birch. Authors supposed that elevated CO_2 and ozone can counteract each other concerning some effects on wood properties (Kostiainen et al. 2008).

To our knowledge, only few global analyses about the effects of elevated levels of ozone and CO_2 on trees have been carried out with transcriptomic or proteomic approaches and they mainly studied the effects on leaves and not on wood formation (e.g., Olbrich et al. 2005). However, one recent study by Wei et al. (2013) in aspen described the effects after long term of elevated CO_2 on leaves and vascular cambium zone. They found that genes involved in cell division, cell growth, hormone metabolism and secondary cell wall formation were up-regulated in cambium zone in response to CO_2 and

that genes involved in lignin biosynthesis pathway were down-regulated which was in accordance with what was shown in hybrid poplar (Richet et al. 2012a).

Wood Functions

In this section we discuss the main functions of wood consisting of mechanical support, storage and hydraulic properties.

a. The mechanics of wood in living trees

General consideration on tree biomechanics

Tree biomechanical control (Fournier et al. 2006) is based on three main processes corresponding to: (i) the regulation of the secondary growth that affect the size and shape of the cross-sections of stem and branches, and consequently modifies their bending stiffness; (ii) the control of the chemical and physical characteristics of wood cells, as well as their spatial organization, that affect wood material properties; (iii) the induction of unsymmetrical stresses within cross-sections of axes, which is due to the formation of reaction wood involved in negative gravitropism. The following sections will focus on the second and third processes that concern the mechanics of wood in living trees.

The mechanical properties of wood material and their variability within the tree

Wood mechanical properties are highly orthotropic, e.g., wood properties are very different in the direction of fibers compared to other perpendicular directions, i.e., redial and tangential (Bergman et al. 2010). It comes from its cellular honeycomb-like structure that makes wood more than 10 times stiffer along the fiber than perpendicularly. This ratio between along and across the grain can change from species to species depending on the fiber wall thickness and the organization of cell types (vessel, rays,…) in the species. It is due to the fiber geometry and the structure of the fibers themselves which are much stiffer along their axis than transversally.

Wood elastic properties depend firstly on wood density. The denser the wood, the stiffer it is. Whatever the growing condition, oak will be always stiffer than poplar. Secondly, especially within the same species or within a tree, wood properties come from the properties of the cell wall material which depend on the organization of its components. The stiffness of the cell wall is ensured by the stiff crystalline cellulose microfibrils which are

helicoidally organized around the fiber cells. Trees can adapt this helix angle to regulate their modulus of elasticity (MOE), e.g., to produce a more compliant wood along the stem axis with a large microfibril angle (MFA) or a stiffer wood with a low MFA. The chemical composition of the wall (ratio of cellulose, hemicellulose and lignin or lignin types) will influence elastic properties only in the third instance.

During the tree life, new formed wood can adapt to the need of the tree. On a seasonal time scale, EW formed during spring needs to answer the high demand in sap conduction whereas the wood formed at the end of summer will need to ensure the mechanical support of the tree during winter. It results in a lighter structure in early-wood with more vessels in angiosperms or tracheids with larger lumen and thinner cell wall in gymnosperms. LW is denser with fewer vessels with smaller diameter and more fibers in hardwood and thicker tracheids with small lumen in softwood. At the tree life time scale, young tree or upper part of adult trees form a more flexible wood by changing its MFA. This wood, called JW, allows the stem to bend easily under wind flow. Later, in the trunk far from the crown, a stiffer wood will be produced thanks to a smaller MFA called MW. Finally, trees can adapt their wood properties to react to specific events (Clair et al. 2003). For example when a tree needs to produce reaction wood, its properties are strongly modified. CW of conifer is characterized by a very large MFA and a high lignin content reducing largely its MOE whereas tension wood in angiosperms is more cellulosic with more crystalline microfibrils aligned along the fiber axis generating a stiffer wood (Timell 1986).

The mechanical state of wood in trees

Describing the kinetics of wood formation is fundamental in order to understand the evolution of the mechanical state of wood in trees. New wood cells are formed centripetally. The accretion of new cells at the periphery of the lignified axes does not disturb the cell organization of the existing wood core and thus its mechanical properties. However at a given development stage, the initial mechanical strains and stresses, which result from the tree growth history, are affected by two main processes associated with the gravity and maturation of newly formed cells respectively (Fournier et al. 2006).

Trees being submitted to forces of gravity, the formation of new wood results in an increase in weight. This weight increment is balanced by an increase in mechanical stresses, and consequently an increase in strains depending locally on wood material properties. Considering that new peripheral cells do not participate in the mechanical equilibrium of the whole structure before their date of creation, the total stresses and strains due to gravity in a given wood ring are proportional to its age. In addition,

because compressive stresses (resp. bending stresses) are proportional to the surface $A \sim r^2$ (resp. to the second moment of inertia $I \sim r^4$) of the considered cross-sections, local stress increments decrease with radial growth for a given external load. Integrating these mechanical processes during the lifespan of the whole tree gives rise to non-classical stress and strain profiles with high negative stresses (compression) in the older wood located near the pith and zero stresses in the newly formed cells at the periphery of the stem.

The maturation process of wood cells, which starts after elongation, holds for about two weeks. This physico-chemical transformation process causes a change in size of the cells that is regarded as a wood intrinsic variable called "maturation strain" (Fournier et al. 2006). During the maturation process, most of wood fibers (normal wood) tend to become shorter in the longitudinal direction, when their diameter expends. As the newly formed cells are stuck on the xylem core, they exert a compressive stress to the inner wood and by reaction stay in a tensile state. When integrating this process during the lifespan of the tree, the resulting auto-equilibrated stress field exhibits high negative longitudinal stress (compression) in the older wood near the pith and positive stress values (tension) at the periphery of the cross-section. This mechanical system can be compared to a tree log on which rubbers in tension were pinned at the surface in the axial direction. The rubbers are kept in tension and compress the log.

The biomechanical processes associated with the maturation of wood cells are also involved in tree tropisms when the stem or branches have to move in a preferential direction, e.g., upward (negative gravitropism) or in the direction of light (phototropism). The principle is to develop a differential of maturation strain in the plane of bending, which induces a curvature of the axis as if a moment of force was applied. Two opposite strategies are distinguished depending on tree species. In angiosperms strain differential results from the formation of TW on the concave face of the bending stem. TW fibers "shrink" more than the OW during the maturation phase (Clair et al. 2011), which generates a curvature of the axis in their direction (pulling strategy). On the other hand, gymnosperms produce CW on the concave face of the stem, which "elongate" during the maturation phase and create a bending movement in the opposite direction (pushing strategy).

All these biomechanical processes related to wood formation are involved in acclimative or adaptative growth responses (Moulia and Fournier 2009). These capabilities are essential for the survey of trees growing in different ecological and climatic contexts.

b. Storage in tree wood

Storage is a key process for mature trees exhibiting a large biomass and high maintenance cost. Heartwood (HW) is the inner layers of the wood of a living tree, which has ceased to contain living cells and in which the reserve materials have been removed or converted into HW substance (IAWA 1964). Sapwood (SW) is the portion of the wood that contains living cells and reserve materials (IAWA 1964). Two types of storage are distinguished depending on whether they are located in living or dead tissues, with short or long term residence time. Between living and dead wood compartments, a transition zone is characterized by an active process of translocation for the HW formation (Saranpää and Höll 1989, Magel et al. 1997) and the resumption of nutrients.

Storage in the heartwood

The HW exhibits a low water content, storage is less dynamic and could be assimilated to immobilization of chemicals with specific role in wood durability. HW is a long-term storage compartment for special secondary metabolites like flavonoids, lignans, terpenes, phenols, alkaloids, sterols, waxes, tannins, oils, waxes, gums and rubber. Such biochemical products, so called extractives (Taylor et al. 2002), contribute to the durability of HW by protecting against water penetration thanks to waxes or oils or against fungi decay and insect penetration, because readily assimilable carbohydrates are lacking. The special metabolites are used in biotechnology, even if they represent as little as 1 per cent, sometimes as much as one-third of their dry weights, this maximum being reported in tropical tree species (Obst 1998).

Storage in the sapwood

SW serves as a storage site for water (Waring and Running 1978) but also for reserve energy components such as starch, soluble sugars, lipids or non-structural nitrogen (Höll 1997). Parenchymatous cells of both the wood and the phloem are storage tissues where starch, sugars, vegetative storage proteins and fats are accumulated. Water is stored in most of the tissues of the tree, the larger storage capacity being in SW Daily and seasonal stem circumference shrinkage illustrates the mobilization of water contained in elastic tissues (Milne 1989, Zweifel et al. 2000) in case of non-steady state water flux, i.e., during the morning when canopy transpiration is higher than water uptake or under soil water deficit and high potential

evapotranspiration. The temporarily stored water in stem tissue partially fulfills the transpiration demand (Lassoie 1973). A large volume of internal stored water is reported for species with wide SW, like most of the coniferous tree species. In broadleaved tree species, like oak (Hinckley and Bruckerhoff 1975) or European beech (Betsch et al. 2011), the volume of water withdrawn daily for tree transpiration remained low when soil water was not limiting, but increased during water stress.

Storage in SW is a highly dynamic function thorough the season in both content and composition (Fischer and Höll 1992). All living tissues are filled during accumulation period and unfilled at times of demand, driven by phenology, climate, biotic hazard and needs for defence, adverse climatic conditions during the growing season (i.e., water shortage, lack of radiation) or during the period of dormancy (i.e., frost hardiness, maintenance). Periods of replenishment occur during active carbon assimilation and nitrogen uptake. Budburst time and spring growth reactivation are processes with high water, carbon and nitrogen demand inducing a sharp decrease in stored reserves (Barbaroux and Bréda 2002, El Zein et al. 2011). Over mobilization of stored carbohydrates may be observed in case of tree decline, leading to carbohydrate depletion (Gérard and Bréda 2012) and hence starvation with increasing probability of mortality (Marçais and Bréda 2006).

Mineral nutrient in sapwood and heartwood

Mineral elements (N, P, Ca, Mg, K, Mn, Al) are stored in wood biomass in varying concentrations depending on the species, the site fertility and its changes throughout stand aging (Ranger et al. 1995) and acidification due to atmospheric deposition (Penninckx et al. 2001). The SW of oak exhibits high concentration, suggesting that nutrients are actively resorbed from transition zone, resulting in very low elemental concentrations in HW. This is a general pattern, with lower concentration of N, P and K in the HW (Meerts 2002). Gymnosperms have lower mineral nutrient concentration in wood compared to Angiosperms (Meerts 2002), but mineral nutrient concentrations are detected in both the SW and the HW. As a result of high storage capacity of mineral nutrient in trees, biomass exports by harvesting and wood export induce nutrient losses which could lead to long term decrease in site fertility.

c. Xylem hydraulic

Wood variability within trees: a hydraulic cause?

The changes previously described from pith to bark and from base to top influence wood physiological traits and the ability of tree to transport

water. Another explanation for many of the JW and MW patterns is that the radial changes are driven by a need for higher water transport (Domec and Gartner 2002b, Domec et al. 2005, Gartner 2006). There is a universal pattern of increase in length and diameter of tracheids with radial position throughout the JW zone (Megraw 1985, Zobel and van Buijtenen 1989). The longer the tracheid, the higher the specific conductivity (K_s), because in longer tracheids, the water will traverse more pits per tracheid but fewer pits per unit path length (Petty and Puritch 1970, Pothier et al. 1989, Wimmer et al. 2002) and because in longer wider tracheids, water can move faster (flow is related to radius to the fourth power; (Zimmermann 1983)). These facts are consistent with the hypothesis that the wood formation and the radial changes in the wood structure from pith to bark have evolved to increase K_s as trees increase in age and diameter.

In conifers it has been reported that the ability of JW to move water, defined as its specific conductivity (K_s), is 40–60% lower than that of MW (Phillips et al. 1996, Spicer and Gartner 2001, Domec et al. 2005, 2009). Results from Douglas-fir and ponderosa pine trees revealed that common trends in trunk K_s exist with rings from pith or cambial maturation (Fig. 2A). This trend is generally inversely proportional to the trend in wood density. Therefore, because of the increase in tracheids dimensions with cambial age within the JW zone, K_s increases until the maturation of the xylem. It also suggests that small increases in the proportion of JW would have a large negative effect on K_s.

Axial trends in hydraulic properties from root to branches

The bulk of recent work in plant hydraulics has compared functionally significant traits across species. This has been crucial in distinguishing strategies of different plant functional groups for coping with water stress and in advancing our understanding of community level differences. Fewer studies have focused on axial variation in hydraulic traits within adult individuals. Furthermore most of the work comparing different organs has examined differences between small-diameter roots and branches (Cochard 1992, Martínez-Vilalta et al. 2002, Burgess and Pittermann 2006) and rarely on segments from the main stem (Domec and Gartner 2002b, Dunham and Lachenbruch 2006, Rosner et al. 2007, 2008). This is certainly understandable given the difficulty of making measurements on large trees. However, only by studying hydraulic traits and relationships between plant organs can we understand fully their integration at the organismal scale and ultimately at the community and larger scales. Several hypotheses predict how xylem structure should change along the root-to-terminal branch water transport pathway to optimize whole tree hydraulic efficiency and protection from embolism (Comstock and Sperry 2000, McCulloh and Sperry 2005) but

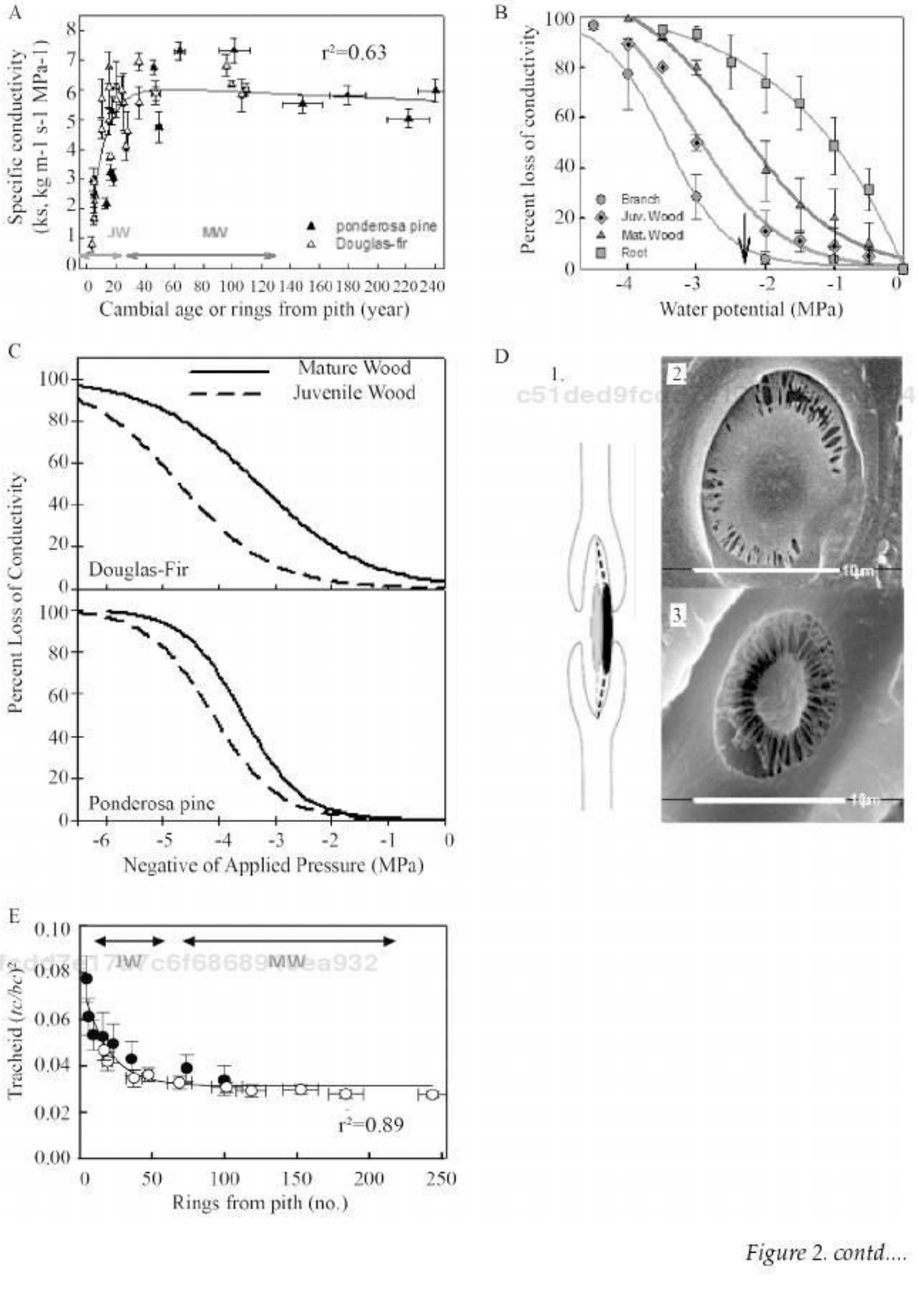

Figure 2. contd....

there are only a few studies that have sampled more than two points along the entire pathway (Domec and Gartner 2002b, McElrone et al. 2004, Choat et al. 2005, Domec et al. 2005, Burgess and Pittermann 2006, Dunham and Lachenbruch 2006, Rosner et al. 2006).

As tension in the water column increases, vessels and tracheids become embolized (air-filled), and K_s declines. The 'vulnerability curve' is a plot of percentage loss of K_s as a function of tension in the water column (Fig. 2A). Different parts of plants, ages of plants, and plants from different environments have different characteristic vulnerability curves influencing drought tolerance (Tyree and Sperry 1988, Sperry 1995, Delzon et al. 2010) and plant architecture (Tyree and Ewers 1991). Within trees, the xylem pressure resulting in a 50% loss of hydraulic conductance (P_{50}) has widely been observed to be more negative in small diameter stems than roots (McElrone et al. 2004, Maherali et al. 2006, Willson et al. 2008, Domec et al. 2009). This trend is consistent with the need for more embolism-resistant xylem as the pressure drops along the flow path from the roots to the leaves. In each of these studies the decrease in P_{50} in the stems came at the cost of higher flow resistance than in the roots (Fig. 2A). This tradeoff is also observed among organs within trunk wood, going from JW to MW (Figs. 2B, 2C). The intra-specific data in Figs. 2A and B include measurements made on samples from the trunk, which are rarely made. Although there should not be a large pressure difference between the trunk points, they show the greatest scatter in the tradeoff, which highlights the need to include the

Figure 2. contd.

Figure 2. Hydraulic efficiency and safety of conifer wood.

A. Hydraulic conductivity as a function of cambial age in two conifer species (redrawn from Domec et al. 2012).
B. Vulnerability curves showing the increase in percent loss of wood conductivity (Ks) as a function of xylem water potential in root, trunk (MW and JW) and branch of loblolly pine (*Pinust aeda*) trees. The arrow represents the minimum water potential (maximum stress level) measured in the field.
C. Vulnerability to embolism curves showing the percentage loss of specific conductivity (ks) versus the negative of applied pressure (surrogate for tension in living trees).
D. (1) Schematic representation of a bordered pit membrane of conifer, showing the torus valve effect (i.e., pit aspiration and torus overlap between torus and pit aperture). Torus is represented both in its unaspirated (grey) and aspirated positions (black). On the right, comparison of bordered pit membrane anatomy between (2) a species vulnerable to cavitation (*Pinusalbicaulis*) and (3) a species resistant to cavitation (*Caryaglabra*). White bars represent 10mm.
E. Conduit thickness-to-span ratio (tc/bc)2 versus rings from pith in trunk samples from Douglas-fir (close symbols) and ponderosa pine (open symbols) trees. X axis: rings representing Juvenile and Mature Wood.

Color image of this figure appears in the color plate section at the end of the book.

trunk to fully understand the woody plant hydraulics. The intra-specific trends depicted in Figs. 2A and B also show that JW can handle much greater water tensions than MW can before losing its conductivity and that JW is more drought-tolerant than MW. In other words, JW confers higher drought resistance to stems. For example, in loblolly pine (Fig. 2B) and Douglas-fir (Fig. 2C) MW begins losing K_s between –0.5 and –1.0 MPa, whereas JW does not lose K_s before –2 MPa.

Differences in anatomical properties explain wood hydraulic differences

The safety vs. efficiency tradeoff (P_{50} vs. K_s) is not only observed when whole-wood properties are compared between organs within individuals but also at the anatomical and finer scale of individual pits, the valves that allow water but prevent air from traveling between conduits (Domec 2006, Pittermann et al. 2006, Domec et al. 2008, Delzon et al. 2010). In conifers, the inter-specific variability of cavitation resistance variability appears to be explained by the functional properties of the bordered pit, specifically the capacity of the torus to seal the pit aperture, the so-called "valve effect" (Domec 2006, Pittermann et al. 2006, Delzon et al. 2010) (Fig. 2D). Moreover, a recent study suggests that the torus in conifer pit membranes is not always as airtight as thought previously. A lot of vulnerable species to cavitation in the *Pinaceae* family present punctured tori, which have a plasmodesmatal origin, through which air-seeding can occur (Jansen et al. 2012).

Hacke et al. (2001) calculated that embolized conduits experience large bending stresses that could lead to cell collapse under drought conditions. The basis for this relationship is that the double-cell wall shared by adjacent cells behaves in a manner similar to a long plate of width b (cell diameter) and thickness t (double-cell wall thickness), and this plate will buckle under a force proportional to $(t/b)^2$. Furthermore, Hacke et al. (2001) showed that $(t/b)^2$ calculated from cell anatomical dimensions are correlated with the overall sample wood density. However, wood density is mainly dependent on the LW proportion (Zobel and Sprague 1998, Rosner et al. 2007), whereas K_s and resistance to embolism are largely determined by the properties of EW (Domec and Gartner 2002a). Therefore an adjustment of lumen diameter/wall-thickness ratios in the EW could enhance K_s and reduce resistance to embolism without compromising overall wood density and mechanical strength if the LW percentage remains constant. Within trunk wood, the resistance to embolism (as characterized by P_{50}, the tension to induce 50% loss of K_s) in trunk wood of two conifer species was related to the value of $(t/b)^2$ (Domec et al. 2009) and trunk tracheid $(t/b)^2$ decreased logarithmically with cambial age, with large decreases in the JW stabilizing in MW (Fig. 2E). These results are consistent with Figs. 2B and C showing that JW can handle more water stress than MW before losing conductivity.

New Strategies to Improve Wood Biomass Formation and Properties

With the objective to improve wood formation and properties, different strategies are worth-considering. They are summarized below. However, as a prerequisite for implementing these strategies, genomic resources have to be developed.

a. Development of genomic resources

Wood formation is the result of the coordinated expression of a thousand genes involved in several biological processes (i.e., cell division and expansion, secondary cell wall thickening and program cell death). The high throughput characterization of the molecular mechanisms involved in wood formation started fifteen years ago both in angiosperm (Sterky et al. 1998) and gymnosperm (Allona et al. 1998) with the first production of Expressed Sequence Tags (ESTs) from differentiating xylem. Since then, the increasing number of systematic sequencing program led to the generation of 57,979 ESTs for this highly specialized tissue. Currently, 48,394 and 9,585 ESTs are available in the NCBI database using both Magnoliophyta or Coniferophyta and xylem as keywords. Most of these approaches have identified many genes involved in xylogenesis, especially in secondary cell wall thickening but also a high proportion of unknown function genes suggesting that the molecular mechanisms involved in wood formation remains partially understood (Whetten et al. 2001, Pavy et al. 2005, Sterky et al. 2004, Andersson-Gunneråsa et al. 2006). Although these approaches led to the identification of genes involved in wood formation; to our knowledge only a few studies used the highly organized structure of differentiating xylem to reveal transcriptional dynamics during wood formation. Hertzberg et al. (2001), identified relevant candidate genes involved in several biological processes (i.e., cell fate, cell expansion, secondary cell wall formation and PCD) using cryo-sectioning methods and cDNA microarray. Moreau et al. (2005) identified genes specially involved in PCD using similar approaches. More recently, Goué et al. (2008), applied cell micro-dissection technique to decipher the molecular mechanisms involved in the functioning of both fusiform cambial cells which give rise to the axial elements and ray cambial cells which produce ray elements. These authors showed that cell wall related genes displayed specific expression pattern with pectin and xyloglucan metabolism genes up-regulated in the two cell types of the vascular cambium.

With the development of second generation high throughput sequencing technologies large transcriptomics analysis will be developed in forest trees and will set the stage to identify gene networks related to xylogenesis.

However, these approaches still remain in their infancy. Only one study performed in eucalyptus has used the Illumina sequencing technology to identify GO term (Gene ontology term) over-expressed in differentiating xylem (Mizrachi et al. 2010). Different laboratories have also developed tools to facilitate the integration of functional genomic data and allow researchers to explore the function and the tissue specificity of the identified genes (http://popgenie.org/; http://bar.utoronto.ca). These tools constitute useful complements of the genomic resources available.

Over the last few years several genome sequencing programs have also emerged and delivered powerful resources (e.g., gene models) and bioinformatic tools (e.g., genome browsers) for researchers to scrutinize more comprehensively their functional role in xylogenesis. The poplar genome was the first fully characterized using shotgun sequencing (Tuskan et al. 2006) (resource available at http://www.phytozome.net/). As for large transcriptomic analysis, the rise of second generation sequencing technologies will led to the establishment of full genome sequences for many other tree species of interest, that of eucalyptus (Myburg et al. 2011), Loblolly pine (http://pinegenome.org/pinerefseq/) and Norway spruce (http://www.congenie.org/) being the next to come. Several other sequencing programs have also started more recently both for Angiosperm (e.g., *Quercus robur,* Plomion C. personal communication) and gymnosperm (e.g., *Pinus sylvestris* and *Pinus pinaster,* Cervera M.T. personal communication). These resources will also constitute important prerequisites for new breeding strategies based on DNA markers.

b. Genetic parameters and architecture of trait variation

Most phenotypic characteristics of a tree, including wood biomass production and wood properties (WPs), exhibit a continuous distribution. In genetics, this means that such a quantitative trait is controlled by an infinite number of loci and that each locus has an infinitely small effect (either increasing or decreasing the value of the trait): the so called infinitesimal or polygenic model (Fisher 1918, Mather 1941). These loci are generally studied collectively under the general framework of classical quantitative genetics (Falconer and Mackay 1996). The genetic determinism of tree growth and WPs has been fairly well studied in most forest tree species of commercial interest for which a breeding program has been developed for the deployment of improved varieties for pulp and paper, energy wood or timber production (e.g., reviewed for the conifers by Mullin et al. (2011)). Taken collectively, these studies show a higher heritability (fraction of phenotype variability that can be attributed to genetic variation) for WPs (especially chemical characteristics) than growth performance as well as an inconsistency regarding the extent of genetic correlations between WPs and

growth (Cornelius 1994, Raymond 2002). As discussed by Grattapaglia et al. (2009) tree growth is a highly complex process involving the interaction of many genetic and epigenetic factors that respond dynamically to internal and environmental signals. Conversely, chemical properties are much less complex, often involving a single biosynthesis pathway. Therefore, they present fewer opportunities of interaction with environmental factors than traits affected by many different physiological processes.

The advance of DNA marker-based technologies in the 1980s and the parallel development of dedicated statistical methods to analyze the relationships between DNA polymorphism and phenotypic variation, have made it possible to study the genetic architecture (number, map location and effect of quantitative trait loci 'QTLs' (Gelderman 1975)), of quantitative traits, opening a first door toward DNA marker-assisted selection in plants (Bernardo 2008). Thus, over the past 15 years, many studies have been undertaken to detect QTLs controlling part of the phenotypic variation of wood biomass and WPs in forest trees (reviewed in Kole 2007, Grattapaglia et al. 2009). With respect to WPs, Gion et al. (2011) conducted the most comprehensive study aiming at detecting QTLs for a series of wood and end-use properties. They found 117 QTLs for chemical, technological, physical, mechanical and anatomical properties that clustered into five linkage groups of their *Eucalyptus grandis* and *E. urophyla* genetic maps. As expected by the oligogenic model (Morton and McLean 1974), which states that a quantitative trait is controlled by a few genes with large effects and many genes with small effects, only 13 QTLs had major effects (phenotypic variance explained > 15%). Their study also suggested some form of pleiotropic relationships between different WP-QTLs or close linkage between the genes controlling these traits. They also found that functional candidate genes co-localized with trait-QTLs, suggesting causal relationships. In particular, the major wood property QTL, that of lignin content, harbored a gene encoding a Cinnamoyl CoA reductase (CCR) a structural enzyme of the monolignol-specific biosynthesis pathway.

While advances in genotyping and phenotyping technologies have resulted in an exponential increase in the number of published QTLs, very little progress has been made in the positional cloning or identification of the relevant gene(s) affecting complex traits. If a handful of successful cases have been reported in model and crop plants (Price 2006), the identification of genes within QTL intervals remains a major challenge in trees to be addressed. However, with the unprecedented progress in the sequencing of whole genomes, and the development of ultra-high density linkage maps (e.g., Neves et al. 2011, Pavy et al. 2012), the discovery of genes that matter for trait variation is now becoming feasible in long-lived species as well.

Considering the poor resolution of QTL mapping (resulting in large QTL intervals spanning several cM, i.e., 100s of genes) and bearing in mind

that QTL effects depend on the genetic background in which they have been detected and the fact that QTL experiments in trees have been mainly carried out using biparental crosses, it has been clear that QTL information would be of limiting utility in genetic tree improvement, especially when breeding material from different genetic backgrounds is used. Association mapping (AM), also known as linkage disequilibrium mapping, has thus been proposed as an alternative approach to overcome the limitations of pedigree-based QTL mapping to study more comprehensively the genetic architecture of quantitative traits and detect the causative genetic variants underlying phenotypic variation (Neale and Savolainen 2004). Indeed, by taking advantage of the large number of historical recombinations present in the gene pool of an organism, AM mapping shows a much higher resolution than QTL mapping since only DNA markers in strong LD with a causative allele will show significant associations with targeted traits (Cardon and Bell 2001). This allows for a fine mapping scale (<1 cM) and, in some cases, for the detection of causative polymorphisms as illustrated by Ingvarsson et al. (2008) for bud set within the phytochrome B2 locus in poplar. In this context, AM has gained increasing interest in forest tree genetics, because it could be readily applied *in situ* to random mating tree populations (reviewed by Khan and Korban 2012) without recourse to dedicated trial establishment. Besides, most forest tree species can be considered as good models for AM due to their generally high levels of genetic diversity and pollen flow and large population sizes that lead to rapid LD decay between genes or single nucleotide polymorphisms (SNPs). However, the direct consequence of such rapid drop in LD has led to the conclusion that millions of polymorphisms would be required for successful whole genome scan association mapping, unless obvious candidate genes could be proposed for the analysis. Thus, given the cost associated with genome wise association studies, candidate-gene-based approaches have been largely favored. The very first AM study in a forest tree species was in *Eucalyptus* (Thumma et al. 2005). Two SNPs in the CCR gene associated with microfibril angle were found in a *E. nitens* population involving 290 unrelated genotypes. Existing breeding populations have also been used for AM as they generally include several hundreds of unrelated families. For instance, based on breeding values obtained for elite trees of the first and second generation of the maritime pine breeding program, Lepoittevin et al. (2012) identified two mutations that were significantly associated, one with variation in radial growth (in a gene encoding for a HD-Zip III transcription factor) and the other with variation in wood cellulose content (in a gene encoding for a fasciclin-like arabinogalactan protein). Markers identified in such association studies could, in principle, be immediately applied in breeding. However, even if these studies have demonstrated the potential of AM to reveal functional variants affecting phenotypic traits and therefore

yield useful markers for forest tree breeding programs, the rather small proportions of phenotypic variability (often <5%, even for high heritability traits) explained by individual SNPs (reviewed in Thavamanikumar et al. 2013) and the ascertainment biased due to the *a priori* selection of a small number of candidate genes, has prompted forest tree geneticists to more comprehensive predictive selection models aiming at capturing a larger proportion of genetic variance. Such new genomic selection strategy has became possible only in forest trees thanks to the recent development of next-generation sequencing and high-throughput genotyping technologies (Elshire et al. 2011, Nielsen et al. 2011).

c. Genomic selection

As illustrated in the previous sections, advances in genomic resources and statistical methodologies to identify marker-trait relationships, even though extremely beneficial, have resulted in a situation where far more QTLs have been detected than the underlying genes/polymorphisms. This has raised doubts about the utility of QTL and AM mapping for marker-assisted selection and proposals of alternate predictive approaches to improve breeding strategies. In this context, genomic selection (GS), an approach pioneered by Meuwissen et al. (2001), for domestic animals, was proposed as a strategy for molecular breeding in crop plants (Bernardo and Yu 2007, Heffner et al. 2009, Jannink et al. 2010) and more recently forest trees (Grattapaglia and Resende 2011). This method first assays markers throughout the genome with no *a priori* knowledge of QTL locations, then estimate breeding values for each marker in a reference population where robust phenotypic evaluation of genotypes is performed, and finally make selections in subsequent generations using genomic estimated breeding values. Given decreasing genotyping costs and stagnant or increasing phenotyping costs, and the ability to select individual trees much earlier in the breeding cycle, GS is expecting to revolutionize tree breeding by increasing genetic gain per time unit and possibly improving accuracy when selecting low heritability traits. Proof-of-concept experiments of GS have been reported in *Pinus taeda* (Resende et al. 2012b, 2012c, Zapata-Valenzuela et al. 2012) and Eucalyptus (Resende et al. 2012a) and confirmed the initial expectation from (Grattapaglia and Resende 2011) who proposed that GS could radically improve the efficiency of forest tree breeding if applied to small size elite populations of advanced tree breeding programs (i.e., Ne<60) with a relatively modest number of markers (i.e., 3 markers/cM). The application of GS in operational tree breeding programs is still to come but promises to have a major impact on genetic improvement of forest trees for biomass production, wood and end-use properties as well as adaptive capacity to abiotic and biotic stresses.

d. Emerging opportunities for wood engineering through genetic transformation of trees

Enhanced wood biomass productivity is expected from faster growing trees together with increased tolerance to environmental stress. Transgenic approaches have been designed for a variety of biotic (insects, diseases, weeds) and abiotic (drought, nitrogen, cold, pollutants, oxidative stress) growth-limiting factors (Ye et al. 2011, Harfouche et al. 2011, Osakabe et al. 2011). However, strategies to improve growth *per se* remain in their infancy in most forest trees (Trontin et al. 2007, Hinchee et al. 2009, Girijashankar 2011). Progress in the model tree poplar came from deregulating genes involved in gibberellins biosynthesis, oxidative stress and auxin-response pathways, developmental regulation, secondary cell wall formation, cellulose biosynthesis or nitrogen use efficiency (Table 2). Enhanced processability of lignocellulosic feedstoks for pulp, biofuel or bioenergy production may arise from altering secondary cell wall composition (Table 2) in developing xylem (Fig. 1). Lignin has been relatively amenable to useful quantitative (decreased content) and qualitative changes (increased syringyl/guaiacyl ratio or free phenolic units) by targeting genes from the well-assembled phenylpropanoid pathway (Vanholme et al. 2008, Lu et al. 2010, Ye et al. 2011). There was strong evidence for both increased pulping efficiency (Pilate et al. 2002, Huntley et al. 2003, Wadenbäck et al. 2008, Wei et al. 2008) and saccharification potential (Wang and Dixon 2012) of low-lignin wood, including from field-grown trees (Pilate et al. 2002, 2012, Huntley et al. 2003, Wadenbäck et al. 2008, Wei et al. 2008). Severe lignin depletion could however adversely affect tree productivity (Leplé et al. 2007, Wagner et al. 2009, Voelker et al. 2010). Engineering major carbohydrates (cellulose, hemicellulose) remains challenging owing to high complexity of related biosynthetic pathways (Lu et al. 2010). Cellulose content was usually increased as a compensatory effect of reduced lignin. More direct strategies relied on overexpressing genes involved in cellulose biosynthesis (or carbon partitioning to cellulose biosynthesis), regulation of secondary cell wall and wood development. Deregulation of glycosyltransferase and xylanase in poplar was also effective at reducing hemicellulose content for enhanced cellulose processing (Table 2).

New mechanical properties are rather speculative until new insights into xylem development are gained (Hinchee et al. 2009). Xylem formation (including changes in fiber/vessels size and density) could be stimulated by altering developmental regulation pathways, gibberellin, auxin or sucrose metabolisms. Wood density could also be increased by overexpressing genes involved in secondary cell wall formation, sucrose partitioning to cellulose biosynthesis and nitrogen metabolism (Table 2).

Table 2. Improving wood biomass formation and properties through genetic transformation of trees: selected achievements.

Modified wood properties[a]	Growth & morphology[a]	Target gene[b]	Deregulation strategy (promoter type)[c]	Species	Reference(s)
Gibberellin biosynthesis and signalling					
↑ Xylem fiber length	Normal	*RGA-like*	O (native)	*Poplar*	(Han et al. 2011)
Normal	↑ early growth	*GA20ox*	O (native)	*Poplar*	(Han et al. 2011)
↑ Xylem fiber length & density	↑ biomass, ↓ rooting	*GA20ox*	O (constitutive)	*Poplar*	(Eriksson et al. 2000)
Nd	Dwarfed plants	*GA2ox*	O (activation tagging)	*Poplar*	(Busov et al. 2003)
↑ Xylem development & fiber length	↑ stem biomass	*GA2ox*	S/RNAi (constitutive)	*Poplar*	(Gou et al. 2011)
Auxin biosynthesis and signalling					
Nd	↑ growth & biomass	*NDPK2*	O (oxidative stress-inducible)	*Poplar*	(An et al. 2011)
↓ Vessel size, ↑ vessel density, altered ray development	↓ growth & biomass	*iaaM/H*	O (constitutive)	*Poplar*	(Tuominen et al. 1995)
Developmental regulation					
↑ Xylem development & fiber length	↑ growth & biomass	*SHI-like*	S/RNAi (constitutive)	*Poplar*	(Zawaski et al. 2011)
↑ Cellulose & hemicellulose, ↓ lignin, ↓ wood density	Normal	*FPF1*	O (constitutive)	*Poplar*	(Hoenicka et al. 2012)
↑ Xylem development	↑ stem growth	*GTPase*	O (constitutive)	*Poplar*	(Kwon et al. 2011)
Sucrose metabolism & partitioning					
↑ Xylem fiber length	Altered phenology	*SPS*	O (constitutive/xylem-specific)	*Poplar*	(Park et al. 2009)
↑ Cellulose (6%), ↑ cristallinity, ↑ wood density	Normal	*SuSy*	O (constitutive/xylem-specific)	*Poplar*	(Coleman et al. 2009)

Table 2. contd....

Table 2. contd.

Modified wood properties[a]	Growth & morphology[a]	Target gene[b]	Deregulation strategy (promoter type)[c]	Species	Reference(s)
Nitrogen metabolism					
↓ Lignin, ↑ S, ↑ wood sugars, ↑ pulping efficiency ↑ Wood density & fiber length, ↑ microfiber angle	↑ growth, ↑ drought & herbicid tolerance	*GS*	O (constitutive)	*Poplar*	(Kirby et al. 2006) (Coleman et al. 2012)
Secondary cell wall development					
↓ Cellulose & ↑ crystallinity, ↑ hemicellulose & xylose	↓ growth	*KOR*	S/RNAi (constitutive)	*Poplar*	(Maloney and Mansfield 2010)
↓ Glucose	↓ growth	*KOR*	S/RNAi (constitutive)	*Spruce*	(Maloney et al. 2012)
↓ Cellulose crystallinity, ↓ xylose	Normal	*KOR*	O (constitutive)	*Poplar*	(Maloney and Mansfield 2010)
↑ Cellulose, ↑ hemicellulose	↑ biomass	*KOR*	O (constitutive)	*Poplar*	(Shani et al. 2004)
↑ Cellulose, ↓ hemicellulose, ↑ wood density	↑ biomass	*DOF*	O (xylem-specific)	*Poplar*	(Gerhardt et al. 2011)
Hemicellulose biosynthesis					
↓ Glucuronoxylan, ↑ cellulose digestibility	Altered root xylem	*GT47*	S/RNAi (constitutive)	*Poplar*	(Lee et al. 2009)
↓ Xylan, ↑ lignin, ↓ wood strength/stiffness	Normal	*GT8*	S/RNAi (native)	*Poplar*	(Li et al. 2011)
↓ Hemicellulose (15%), ↓ lignin	↑ stem growth	*Xylanase*	O (constitutive)	*Poplar*	(Park et al. 2010)
Cellulose biosynthesis					
↑ Cellulose (10%) & cellulose specific gravity ↑ Microfibril widths, ↓ hemicellulose (10%)	↑ stem growth ↑ internodes elasticity	*XGase*	O (constitutive)	*Poplar*	(Park et al. 2004) (Yamamoto et al. 2010)
↑ Cellulose (6.5%), ↓ lignin (12-21%), ↑ S, ↑ S/G	↓ growth & biomass	*UGPase*	O (constitutive)	*Poplar*	(Coleman et al. 2007)

Lignin biosynthesis					
↓ Lignin (45%), ↑ cellulose (15%)	↑ growth	*4CL*	S/antisense (constitutive)	*Poplar*	(Hu et al. 1999)
↓ Lignin (10%), ↓ S/G, ↑ H, ↑ cellulose ↑ Tension wood, ↓ wood stiffness & strength	↓ biomass Branchy/shrubby	*4CL*	S/antisense (xylem-specific)	*Poplar*	(Voelker et al. 2010, 2011)
↓ Lignin (36-50%), ↓ G, altered interunits linkage ↑ Compression wood, ↑ galactose	Dwarfed plants	*4CL*	S/antisense (xylem-specific)	*Poplar*	(Wagner et al. 2009)
↓ Lignin (40%), ↑ cellulose (14%)	Normal	*4CL*	S/antisense (xylem-specific)	*Poplar*	(Li et al. 2003)
↓ Lignin (52%), ↑ S/G, ↑ cellulose (30%)	Normal	*4CL/F5H*	S/antisense + O (xylem specific)	*Poplar*	(Li et al. 2003)
↑ S/G, ↑ pulping efficiency (↓ kappa, ↑ brightness)	Normal	*F5H*	O (xylem-specific)	*Poplar*	(Li et al. 2003, Huntley et al. 2003)
↓ Lignin (30%), ↑ cellulose, ↓ wood density/ stiffness	↓ growth	*C4H*	S/RNAi (constitutive)	*Poplar*	(Bjurhager et al. 2010)
↓ Lignin (20%), ↓ G, ↑ H/G, ↑ caffeylalcohol	Nd	*CCoAOMT*	S/RNAi (constitutive)	*Pine*	(Wagner et al. 2011)
↓ Lignin content (13%), ↑ S/G, ↑ fiber quality ↑ Pulp yield & quality, ↑ saccharification potential	Normal	*CCoAOMT*	S/antisense (constitutive)	*Poplar*	(Wei et al. 2008) (Wang et al. 2012)
↓ Lignin (47%), ↓ S/G, ↑ ferulic acid, ↑ cellulose (18%) ↓ Hemicellulose (24%), ↑ pulping efficiency	↓ growth	*CCR*	S/sense/antisense (constitutive)	*Poplar*	(Leplé et al. 2007)
↓ Lignin (50%), ↓ H, ↓ G, modified cell wall	Nd	*CCR*	S/RNAi (constitutive)	*Pine*	(Wagner et al. 2013 p. 201)
↓ Lignin (8%), ↓ H, ↑ pulping efficiency	↓ stem width	*CCR*	S/antisense (constitutive)	*Spruce*	(Wadenbäck et al. 2008)

Table 2. contd....

Table 2. contd.

Modified wood properties[a]	Growth & morphology[a]	Target gene[b]	Deregulation strategy (promoter type)[c]	Species	Reference(s)
↓ Lignin (55%), ↓ G, ↑ H, ↑ cellulose & hemicellulose	Nd	*C3′H*	S/RNAi (constitutive)	*Poplar*	(Coleman et al. 2008)
↓ Lignin (17%), ↓ S, ↑ G, ↑ condensed lignin ↑ Cellulose, ↑ pulping but ↓ bleaching efficiency	Normal	*COMT*	S/sense (constitutive)	*Poplar*	(Jouanin et al. 2000)
↓ Lignin, ↑ free phenolic groups, ↑ pulping efficiency	Normal	*CAD*	S/antisense (constitutive)	*Poplar*	(Pilate et al. 2002)

[a]In transgenic vs. non transgenic material. Increased (↑) or decreased (↓) trait. Lignin units: p-hydroxyphenyl (H), guaiacyl (G) and syringyl (S). Nd: no data available.

[b]CAD: cinnamyl alcohol dehydrogenase; C3′H: *p*-coumaroyl-CoA 3′-hydroxylase; CCoAOMT: caffeoyl-CoA *O*-methyltransferase; CCR: cinnamoyl-CoA reductase; 4CL: 4-hydroxycinnamoyl-CoA ligase; COMT: caffeate/5-hydroxyferulate *O*-methyltransferase; DOF: DNA-binding with one finger (transcription factor), F5H: ferulate 5-hydroxylase; FPF1: flowering promoting factor 1; GA: gibberellin; GA2ox: GA2-oxidase; GA20ox: GA20-oxidase; GS: glutamine synthetase; GT47/GT8: glycosyltransferase; GTPase: guanosine triphosphate hydrolase; iaa: indolacetic acid; KOR: Endo-β-1,4-glucanase; NDPK2: nucleoside diphosphate kinase 2; RGA-like: repressor of GA-like (transcription factor); SHI-like: short internode-like; SPS: sucrose phosphate synthase; SuSy: sucrose synthase; UGPase: UDP-glucose pyrophosphorylase; XGase: xyloglucanase.

[c]O: overexpression; S: silencing; RNAi: RNA-interference

Current achievements are mainly involving constitutive deregulation of structural genes. Such a rough strategy can induce pleiotropic effects through alternative regulation of gene family members or co-regulation of genes involved in the same or different pathway(s) (Vanholme et al. 2008, Ye et al. 2011). Fine-tuning is expected from specific down regulation of gene family members (Shi et al. 2010), a more extensive use of xylem/vascular-specific (Wagner et al. 2009, Voelker et al. 2010, Ko et al. 2012) or inducible transgene expression (Tang et al. 2005, Filichkin et al. 2006). Synergistic effects were obtained by multigene co-transformation of lignin-related genes (Li et al. 2003, see Table 2) thus opening the way towards effective metabolic engineering (Halpin 2005, Naqvi et al. 2010), preferably at specific loci using recombinase-mediated (Fladung and Becker 2010) or homology-dependent systems (Ow 2011).

Gene stacking appeared as a promising way to reduce interference of modified pathways with other processes. Targeting regulator genes (e.g., transcription factors) may also enable the coordinated modulation of whole cohorts of genes (Bomal et al. 2008, Hinchee et al. 2009). New transgenic strategies may now emerge rapidly from high-throughput molecular genetics aiming at elucidating intricacies in wood development (Mellerowicz and Sundberg 2008, Mizrachi et al. 2012, Nieminen et al. 2012). As cell development during wood formation appears to be largely governed by environmental stress, it is highly recommended to assess the effect of genetic modification not only in staked trees in greenhouse but also in long-term field tests (Wei et al. 2008, Voelker et al. 2010, 2011, Pilate et al. 2012).

Conclusion

In this chapter we described that wood formation leads to different types of wood—sapwood and heartwood, juvenile wood and mature wood, reaction wood and opposite wood, early wood and late wood—that can coexist partly in a single tree genotype. They present different physical and chemical characteristics resulting from their composition (cell type and cell wall structure) that give them different properties (Table 1).

Wood formation is strictly regulated by intrinsic and ontogenic programs consisting of a complex network of transcription factors and miRNA, themselves controlled by different hormones. Moreover, this complex developmental process is very much affected by environmental conditions: light, gravity, day length, temperature, water accessibility, atmosphere composition. The development of genomic tools in these long-lived species enables the expansion of knowledge about wood formation and associated regulating mechanisms.

As the demand in wood will continue to increase rapidly during the coming decades, the quality of the wood will also be of importance in order to improve the efficiency of paper, fuel and biomaterial transformations. Therefore, the necessity of developing new strategies to improve the sustainable production of wood biomass, as well as wood properties is of utmost importance. In the near future, the use of genomic selection and genetic engineering (probably in a complementary way) will have a major role in forest tree domestication and also in reducing our dependence on many inputs such as water, nutrients, pesticides, energy needed for wood treatment. More importantly, it should be kept in mind that these biotechnologies will need to be cost effective and meet with regulatory approval and public acceptance before they can be applied at the industrial scale.

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