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MINIREVIEW

Adventitious root formation in tree species: involvement of transcription factors

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Adventitious rooting is an essential step in the vegetative propagation of economically important horticultural and woody species. *Populus* has emerged as an experimental model for studying processes that are important in tree growth and development. It is highly useful for molecular genetic analysis of adventitious roots in trees. In this short review, we will highlight the recent progress made in the identification of transcription factors involved in the control of adventitious rooting in woody species. Their regulation will be discussed.

Introduction

In contrast to lateral roots (LRs), which are formed on primary roots, adventitious roots (ARs) are formed from above-ground organs such as hypocotyls, stems and leaves. A further major distinction between LRs and ARs is that unlike LRs, which originate from pericycle cells, ARs originate from cambial or other meristematic cells. Thus the study of ARs provides an experimental system to investigate mechanisms of secondary root formation distinct from the well-characterized LR system.

The ability to rapidly form numerous ARs offers a selective advantage to plant species that propagate vegetatively, so playing a central role in clonal propagation. Clonal propagation is of particular relevance to forestry and horticulture, since genetic improvement in long-lived species with long generation cycles is often limiting. Despite this importance, our knowledge of adventitious rooting is limited in trees. To date, only a few genes have been identified that regulate the AR in woody species. This review charts the most recent progress in understanding AR control in woody plants.

***Populus* as a tree model for deciphering AR molecular mechanisms**

Understanding AR formation in trees is important when devising strategies for large-scale vegetative propagation in these economically important plants. However, in most tree species, the ability to form ARs declines with age. The molecular basis of this decline is not known. Physiological and anatomical studies on AR formation have long been published, but the factors underlying ARs in trees remain largely unknown, for lack of a good model. In recent years *Populus* has emerged as an experimental model for studying processes that are important in tree growth and development, and is highly useful for molecular genetic analysis of ARs in trees. The genus *Populus* is a typical woody species propagated by direct planting of stem cuttings in the field (Bonduelle 1989, Dickmann 2006). Represented by approximately 30 species widely distributed in the Northern Hemisphere (Eckenwalder 1996), poplars are fast-growing plants showing high adaptability to marginal soils, making them plants of choice for timber,

Abbreviations – ACC, aminocyclopropane-1-carboxylate; AR, adventitious root; ARF, auxin response factor; LR, lateral root; RNAi, RNA interference; TF, transcription factor.

pulp and bioenergy-related applications. For poplars, clonal propagation is the only way to deploy genetically improved varieties. Therefore identification of the molecular mechanisms underlying adventitious rooting should not only provide insight into the control of AR formation in trees, but also open up possibilities for improving this trait in economically important plants including *Populus*, for which clonal propagation is a requirement. There have recently been important developments in the molecular genetics and genomics of *Populus*, resulting in a consensus among the scientific community for employing poplar as a woody perennial plant (Brunner et al. 2004, review Busov et al. 2009, Yang et al. 2009). First, genetic and genomic resources have increased in the last 10 years. The sequencing and annotation of the black cottonwood genome (Tuskan et al. 2006) are up-dated regularly and are implanted in the Phytozome web site (<http://www.phytozome.net/poplar.php>). Whole-genome oligo-array data generated create an opportunity to identify differential regulation of gene expression relative to some developmental events including LR and AR formation (Quesada et al. 2008, Felten et al. 2009, Ramírez-Carvajal et al. 2009, Gou et al. 2010, Rigal et al. 2012). Second, efficient transformation systems for many *Populus* species including the hybrid *Populus tremula* × *Populus alba* clone INRA 717-1B4 and *P. tremula* × *P. tremuloïdes* have been reported by several laboratories (Leple et al. 1992, Han et al. 2000), and allow the construction and the regeneration of a large number of transgenic plants including RNA interference (RNAi) lines and activation-tagged mutants (Busov et al. 2005, 2009). For example, activation-tagged mutants have been successively used for identifying genes involved in LR and AR formation (Busov et al. 2010, Wang et al. 2011, Trupiano et al. 2013). In parallel, the technique of enhancer and gene trap mutagenesis has been applied to *Populus* to identify gene expression patterns correlating with different stages of AR formation (Ramírez-Carvajal et al. 2009, Rigal et al. 2012). Third, the easy vegetative propagation of many genotypes of *Populus* plays an important role in the successful production of elite clones.

Cellular events during AR formation

The processes involved in AR formation are complex, and occur in four stages (Fig. 1): (1) activation, where the cells become competent to respond to signal factors, (2) induction, when cell cycle re-activation leads progressively to the formation of primordium, and the cell division is visible, (3) activation of root primordium and progressive formation of new tissues and (4) out-growth, where root primordium elongates and vascular

connections are established. These rooting phases are distinguished from a broad variety of genera including apple microcuttings, from *Eucalyptus*, *Pinus* and from *Populus* cuttings (De Klerk et al. 1997, 1999, Fett-Neto et al. 2001). In woody plants including *P. trichocarpa*, the first mitotic divisions, leading to root primordia formation, take place more frequently from the cambium and vascular tissues from ray cells adjacent to the vascular cambium (De Klerk et al. 1997, Rigal et al. 2012). In some *Populus* species, the formation of a callus is observed prior to differentiation of root primordia at the base of the cuttings (Lovel and White 1986). Although in many respects the stages in AR formation resemble what occurs during LR formation, the target tissues are different for LRs and ARs, with LRs originating from pericycle cells, whereas ARs seem to derive from cambial meristem tissues for trees species. Also, unlike LRs, in which one of the first stages is asymmetric cell division in the pericycle, asymmetric division in AR formation has not been reported to date.

Transcription factor families: master regulators of adventitious rooting

Understanding the molecular basis of LR formation has been aided by transcriptomic approaches. These have identified (1) gene expression programs associated with distinct stages of LR formation and (2) key players, many of which are transcription factors (TFs) in the model plant *Arabidopsis*. The success of these approaches has prompted similar analysis of ARs in trees. The transcriptomic analysis performed in poplar at different stages of AR formation has revealed significant transcriptome remodeling during the AR formation including *Pinus taeda* (Brinker et al. 2004), *Populus* sp. (Ramírez-Carvajal et al. 2009, Rigal et al. 2012) and *Eucalyptus grandis* (Abu-Abied et al. 2012). Among transcripts, genes encoding putative TFs belonging to 35 TF families have significant expression changes at the successive stages of poplar AR formation (Rigal et al. 2012). The function of these genes is not yet known. Induction of increased mRNA levels of genes homologous to *SCR* (*SCR*-like or *SCL*) in rooting-competent cuttings of *Pinus radiata* and *Castanea sativa* species was observed within the first 24 h of the root induction process, a time when cell reorganization takes place, and preceding the establishment of AR primordium (Sanchez et al. 2007). SCARECROW (*SCR*) is a member of the GRAS family of TFs, acting in the control of cell division, differentiation and cell homeostasis (Heidstra et al. 2004, Wildwater et al. 2005) during the establishment of *Arabidopsis thaliana* root meristem. Interestingly, *SCR* is downstream-regulated by a

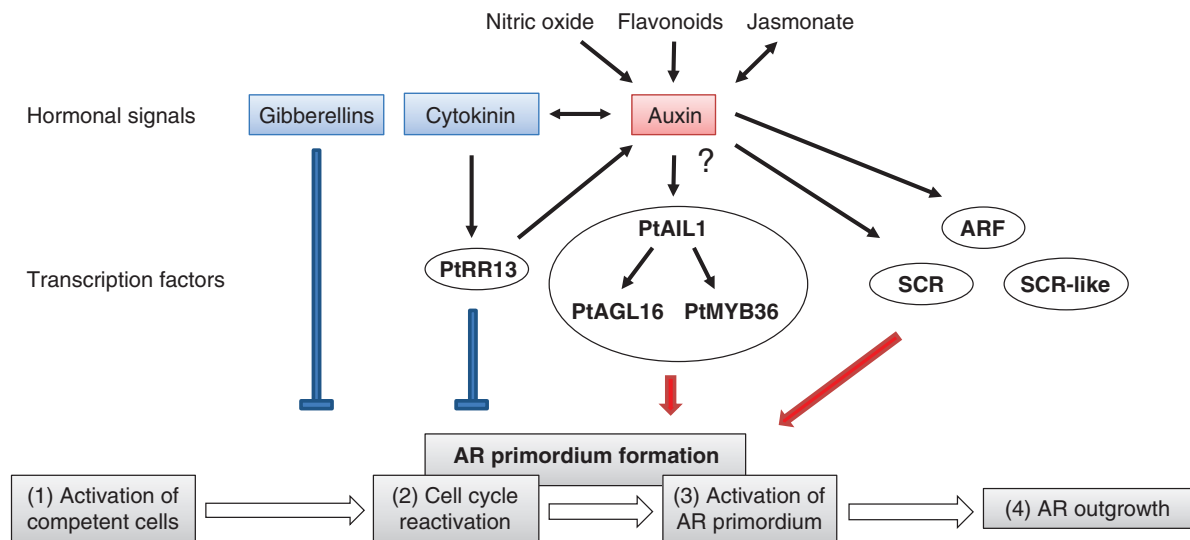


Fig. 1. Possible hormonal regulation of TF during the successive stages of the adventitious rooting in tree species. The AR formation can be seen as a four-stage process starting with the activation of cells in response to signal factors (1). This step is followed by the cell cycle re-activation (2), which leads progressively to the AR primordium formation. The activation of root primordium (3) allows the formation of new tissues and (4) AR outgrowth. Auxin promotes the activation of competent cells and then the formation of AR primordium. NO may participate in this process through the auxin signaling pathways. In parallel, the auxin transport may be influenced after the cutting and may be regulated by the accumulation of jasmonates or flavonoids. In contrast, cytokinin and GA have an inhibitory effect on adventitious rooting. Some transcription factors have been identified as regulators of AR formation in trees including PtRR13, which is regulated by a cytokinin/auxin balance, and SCR is regulated by auxin. PtAIL1, a member of AP2/ERF family plays a major role in the formation of AR primordium, and could take part in the PtAGL16- and PtMYB36-dependent regulatory network.

plant homolog of the tumor suppressor Retinoblastoma (pRb), the RETINOBLASTOMA-RELATED (*RBR*) gene is considered a key cell cycle regulator (Borghi et al. 2010). In root-forming shoots, *CsSCL1*, *SCL* in *C. sativa*, mRNA was specifically located in the cambial zone and derivative cells, which are rooting-competent cells, whereas in rooting-incompetent shoots the hybridization signal was diffuse and evenly distributed throughout the phloem and parenchyma (Vielba et al. 2011). These studies highlight an important role for SCR in meristem determination and maintenance during the formation of AR primordium.

An up-expression of LR primordium (*lrp1*), which is an *SRS*-type TF, has been detected. This gene is known to be involved in lateral and AR primordium formation in *Arabidopsis* (Smith and Fedoroff 1995). Transcriptomic data obtained in *P. trichocarpa* adventitious rooting (Rigal et al. 2012) reveal a modulation of some members of the auxin response factor (ARF) family. ARF proteins are TFs that regulate the expression of auxin response genes. Genetic analysis in *Arabidopsis* clearly shows the importance of this family in the adventitious process (Gutierrez et al. 2009).

One of the best characterized TFs with a role in AR formation in trees is the AP2/ERF protein family comprising TFs unique to plants (Reichman and Meyerowitz 1998), which all contain the conserved AP2 DNA-binding

domain (Jofuku et al. 1994). This super-family consists of 210 members in poplar and regulates two major processes in plants including response to stress and control of development. *AINTEGUMENTA*-like subgroup members, such as *PLETHORA* (*AtPLT*), *BABY BOOM* (*AtBBM*), *AINTEGUMENTA* (*AtANT*) and *AINTEGUMENTA*-like (*AtAIL*) play a major role in the establishment and maintenance of meristems (Krzek et al. 2000, Mizukami and Fischer 2000, Nole-Wilson et al. 2005, Imin et al. 2007, review, Horstman et al. 2014). *AINTEGUMENTA* (*AtANT*) plays a role in the regulation of shoot development during organ primordium initiation and growth (Elliott et al. 1996), and in maintaining meristematic competence of cells during shoot organogenesis (Mizukami and Fischer 2000). Interestingly, some members of this family show a regulation of their expression, suggesting a key role for this subgroup in the control of adventitious rooting in poplars (Rigal et al. 2012). The organization of the poplar root primordium is accompanied by the up-regulation of *PtAIL1*, *PtAIL9*, *PtPLT1.2* and *PtBBM2*, while the differentiation of the root primordium showed expression regulation of *PtAIL1*, *PtAIL5*, *PtAIL9*, *PtPLT1.1*, *PtPLT1.2* and *PtBBM2*. In contrast to the others, the expression of *PtAIL1* transcript levels shows a very specific expression regulation during AR primordium activation and formation. Moreover, transgenic poplar lines over-expressing *PtAIL1* exhibited an increased

number of ARs, while RNAi downregulation of *PtAIL1* transcript showed a reduced number of ARs. *AINTEGUMENTA LIKE 1* (*PtAIL1*), which has been noted to be a *Populus* homolog of the *Arabidopsis* gene *AINTEGUMENTA* (*ANT*) (Karlberg et al. 2011), is expressed in the cambial zone within cells that undergo intensive cell proliferation (Schrader et al. 2004). In addition, *PtAIL1* has been shown to bind to the D-type cyclin promoter in hybrid aspen trees and *Arabidopsis* (Karlberg et al. 2011). Taken together, these data suggest that *PtAIL1* could be involved in cell proliferation occurring during the AR primordium formation. The comparison of global gene expression profiles between the wild type, *PtAIL1* overexpressors and RNAi suppression lines indicates a co-regulation of *AGAMOUS-Like16* (*PtAGL16*), *PtMYB36* and *PtAIL1*. This suggests that *PtAIL1*, *PtAGL16* and *PtMYB36* could be part of a regulatory network that controls AR formation in poplars (Rigal et al. 2012). Additionally, a member of the AP2/ERF family, called *PtERF003*, has a positive effect on both adventitious and LR proliferation in poplar (Trupiano et al. 2013).

AR formation integrates multiple hormonal pathways

Most research on AR formation has been centered on the role of phytohormones, mainly auxins (reviews: Geiss et al. 2009, Da Costa et al. 2013). Classically, treatments of cuttings with synthetic auxins have been used for many years to induce and accelerate rooting in difficult-to-root species (Kevers et al. 1997). In poplar cuttings, anti-auxin application at AR phases caused significant inhibition of AR (Bellamine et al. 1998). In *P. taeda* stem cuttings, the inability to root in mature cuttings was due to the lack of cell capacity to organize root meristems in the presence of auxin (Greenwood et al. 2001). More recently, Negishi et al. (2011) compared *E. globulus* easy- and difficult-to-root lines, and showed that the indole-3-acetic acid (IAA) level of the easy-rooting line was twice that of the difficult-rooting line, confirming the importance of auxin in AR formation ability.

Examining the loss of rooting capability following the transition from the juvenile to the mature phase in *E. grandis* (Abu-Abied et al. 2012), the authors observed a higher transient burst of nitric oxide (NO) in juvenile cuttings than in mature ones upon excision. A gene encoding for nitrate reductase (NIA), which is involved in NO production, was among the genes upregulated in juvenile cuttings (Abu-Abied et al. 2012). Thus NO may influence auxin signaling, as already observed in *Arabidopsis* (Mittler et al. 2011).

Overall changes in phytohormone balance during AR formation have been reported in several studies. In a recent review, the authors (Da Costa et al. 2013) propose an elegant view of phytohormonal control of AR formation and possible hormonal interactions during distinct phases of the adventitious rooting process. The importance of jasmonate-transport auxin interaction has been highlighted during the *Arabidopsis* root development (Sun et al. 2011, Raya-González et al. 2012). Interestingly, it encompasses the first hours after cutting removal; the observed local increase in jasmonate was associated with the phenolic compounds and auxin at the *Eucalyptus* cutting base (Schwambach et al. 2008). Phenolics are also important in modulating peroxidase activity, and may thus prevent auxin degradation at cutting bases (De Klerk et al. 1999, 2011). Flavonoids, a major class of phenolic compounds, can influence auxin transport (Peer and Murphy 2007, Buer et al. 2010). Auxin and cytokinins appear to play antagonistic roles in AR formation. The quantification of these two hormones in the basal part of cuttings from diverse woody species including *Populus* and *Malus* revealed an opposite pattern in auxin and cytokinin concentrations during the first steps of AR formation. In addition, exogenous application of cytokinin to cutting during the induction phase strongly inhibited *Malus* root formation (De Klerk et al. 1999). Ramírez-Carvajal et al. revealed an induction of transcript abundance of members of aminocyclopropane-1-carboxylate (ACC) synthase, and ACC oxidase, key enzymes involved in cytokinin synthesis (Ramírez-Carvajal et al. 2009). A TF, the cytokinin type-B response regulator *PtRR13*, which acts as a positive regulator in the cytokinin signaling pathway, has been shown to repress AR formation in intact plants, and reduced cytokinin signaling after shoot excision. Cytokinin may interact with ethylene and auxin pathways (Ramírez-Carvajal et al. 2009). Like cytokinins, gibberellins have been considered as inhibitors of AR formation in poplar (Busov et al. 2006).

Hormonal pathways: possible regulators of TFs

The root meristem formation and maintenance are controlled by the hormonal balance, where cytokinins and auxins act antagonistically (Dello Iorio et al. 2007, Moubayidin et al. 2009). Some auxin-responsive TFs have been shown to play roles in the control of cell division leading to root primordia differentiation in cuttings of tree species (Sanchez et al. 2007, Solé et al. 2008, Vielba et al. 2011, Rigal et al. 2012). Induction of increased mRNA levels of genes homologous

to *SCR* (*SCR*-like or *SCL*) in rooting-competent cuttings of *P. radiata* and *C. sativa* species in response to exogenous auxin was observed within the early steps of AR formation (Sanchez et al. 2007). The expression of two *APETALA2/ETHYLENE RESPONSE FACTOR* (*AP2/ERF*) TF genes has been inhibited by the expression of a cytokinin type-B response regulator (*PtRR13*) (Ramírez-Carvajal et al. 2009). More recently, the positive regulator *PtaERF003* of AR formation in *Populus* was up-regulated by auxin (Trupiano et al. 2013). Thus some findings suggest how hormonal balance triggers AR formation through the regulation of TFs expression. On the basis of these results, we propose a model illustrating the possible hormonal regulation of TF in the control of adventitious rooting in tree species (Fig. 1).

The further identification of target genes of the TF will offer a fuller understanding of the control of AR formation. Recently, an integrative database of the TFs from economically important tree crops including poplar called TreeTFDB (<http://treetfdb.bmep.riken.jp/index.pl>) has become available for the community, and offers genetic resources for performing comparative and functional genomics of the crop TFs (Mochida et al. 2013). Use of similar databases together with resources such as POPGENIE will allow better integration of transcriptomics data with physiological and anatomical approaches used previously for analysis of AR formation in trees, and will provide a much better insight into this important process. Concomitantly, the developments of genomic and transcriptomic tools in woody species including *Eucalyptus* and *Pinus* species will offer exciting perspectives in this research area. Comparative transcriptome analysis of genotypes that differ in their competence to adventitious rooting should be explored, and will be very helpful for understanding molecular mechanisms in AR formation in trees.

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