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Mais do que um apoio: a conexão da uma liana a suportes leva a profundas mudanças na anatomia do xilema, de condutividade hidráulica, e do perfil transcricional do câmbio

More Than Supportive: Liana Attachment to Supports Lead to Profound Changes in Xylem Anatomy, Hydraulic Conductivity and Cambium Transcriptional Profile

Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Doutor em Ciências. Programa: Ciências Biológicas (Botânica).

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São Paulo
2020

Resumo

- O xilema secundário desempenha duas funções cruciais: o suporte mecânico e condução de água e minerais. Muitas lianas mostram duas fases anatômicas contrastantes em seu xilema, uma inicial, onde o xilema é homogêneo, fibroso e apresenta vasos de pequeno diâmetro, denominada xilema autoportante, e posteriormente o xilema lianescente, anatomicamente complexo, com vasos grandes e dimórficos e menos tecido de suporte. Não se sabe, no entanto, o que leva à mudança abrupta da formação do xilema.

- Neste estudo, abordamos as questões de o que inicia e quais são os determinantes genéticos das profundas mudanças durante a transição do xilema autossuporte para o xilema lianescente na liana *Bignonia magnifica*, Bignoniacae. Para esse fim, analisamos primeiramente as taxas de crescimento de plantas cultivadas com e sem suportes, como os parâmetros hidráulicos variavam ao longo do caule e descrevemos em detalhes a anatomia do xilema autossuportante e lianescente. Em seguida, construímos o transcriptoma do câmbio e do xilema em diferenciação dessas duas fases e realizamos uma análise de expressão diferencial dos dados gerados por RNA-Seq.

- Nosso trabalho mostra que a presença de suportes leva a alterações no padrão de crescimento e nos parâmetros anatômicos ao longo do caule, aumentando a condutividade potencial e promovendo a formação de xilemas lianescentes. Essas alterações estão associadas à expressão diferencial de genes relacionados à divisão celular e à biossíntese da parede celular, sobre-expressos na fase autoportante, e de fatores de transcrição, defesa / morte celular e genes responsivos a hormônios, sobre-expressos na fase lianescente.

- Concluímos que a anatomia mais complexa na fase lianescente é o resultado de uma regulação transcricional mais complexa no câmbio e xilema em diferenciação.

Palavras-chave: xilema; xilogênese; transcriptoma; anatomia funcional; condutividade hídrica

Summary

- Secondary xylem performs two crucial functions, namely mechanical support and water and mineral conduction. Many lianas show two contrasting xylem anatomy phases, the initial homogeneous, fibrous and small vesselled self-supporting xylem, and the later lianescent xylem, which is anatomically complex, with large and dimorphic vessels and less supportive tissue. It is not known, however, what leads to the abrupt change of xylem formation.
- In this study, we address the question of what triggers and which are the genetic determinants of the profound changes during the transition from self-supporting to the lianescent xylem in the liana *Bignonia magnifica*, Bignoniacae. For this purpose, we first analyzed growth rates of plants grown with and without supports, how hydraulic parameters varied along the stem and described in detail self-supporting and lianescent xylem anatomy. We then constructed cambium and differentiating xylem transcriptome of these two phases and conducted a differential expression analysis of RNA-Seq generated data.
- Our work shows that the presence of supports leads to changes in growth pattern and anatomical parameters along the stem, increasing potential conductivity, and promotes lianescent xylem formation. These changes are associated to differential expression of genes related to cell division and cell wall biosynthesis, overregulated in self-supporting phase, and of transcription factors, defense/cell death, and hormone-responsive genes, overregulated in lianescent phase.
- We conclude that the more complex anatomy in lianescent phase is the result from a more complex transcriptional regulation in cambium and wood forming tissues.

Keywords: xylem; xylogenesis; transcriptome; functional anatomy; hydraulic conductivity.

Introduction

Secondary xylem, or simply wood, performs two crucial functions for woody plants survival and reproductive success: mechanical support, optimizing light uptake for photosynthesis and exposure of reproductive organs; and the conduction of water and nutrients from the soil and between source and sink organs, serving yet as storage tissue during unfavorable periods (Baas *et al.*, 2004). In contrast to the homogeneous, almost entirely tracheid composed gymnosperm wood, cellular specialization evolution in angiosperm xylem led to a division of labor among the different cell types composing it, with support being carried out by fibers, conduction of water and minerals carried out mainly by vessels, and storage by axial and radial parenchyma (Bailey & Tupper, 1918; Tyree & Zimmermann, 2002; Evert, 2006). Despite the established relationship of cell types and their functions, there is a great diversity of arrangements, compositions and dimensions of these cell types in the xylem of plants. In turn, this anatomical structural diversity are under genetic control , which regulation has been unveiled with the studies in model species such as *Arabidopsis thaliana* and *Populus* (J. Zhang *et al.*, 2014; Ye & Zhong, 2015; Sundell *et al.*, 2017; J. Zhang *et al.*, 2019), and define how plants cope with the different functions (Zieminska *et al.*, 2013; 2015; Beekman, 2016). Overall, relations between genetic control, anatomy structure and functional implications are still poorly understood for wood plants.

Mechanical properties of fibers are controlled by the cell wall thickness, cell wall/lumen ratio (Zieminska *et al.*, 2013), as well as by cell wall hemicellulose and lignin composition, and cellulose amount and microfibril angle (Bergander & Salmén, 2002; Li *et al.*, 2009; MacMillan *et al.*, 2010; Bourmaud *et al.*, 2013). Water conductivity (*K*), in turn, is directly related to vessels diameter (*D*) raised to the fourth power and inversely related to the length (*L*) that the water must travel between roots and leaves. The relation of K with D^4 shows that even small increments of diameter profound considerable impacts on conductivity, while growth in L could lead to smaller water supply for distally located leaves and limitation in length growth due to an increase in conductivity resistance (Petit & Anfodillo, 2009; Anfodillo *et al.*, 2013). However, the increase of vessels diameter found along the stem allows for a compensatory effect on the path length resistance (West *et al.*, 1999), an hypothesis that was further reinforced by later works (Becker *et al.*, 2000; Sperry *et al.*, 2012). Olson *et al.* (2014), analyzing the stem xylem anatomy at the base and at the top of 257 angiosperm species, found a vessel widening ratio of $D = L^{0.22}$, independent of habit and habitats. This proportion between L and D describes a fast growth in diameter near the apex and a progressive lesser increase toward the base, and its value is consistent with previous models (Becker *et al.*, 2000). The controversy, as well as the insight, of the model lies in the assumption that length in the main factor, if not the only one, determining vessel diameter.

Nevertheless, different proportions of the different cell types that compose secondary xylem may lead to changes in stem properties and how they cope with support and conductivity (Zieminska *et al.*, 2013; 2015; Bittencourt *et al.*, 2016; Gerolamo *et al.* unpublished). Lianas, or woody vines, are an extreme example of reduced amount of supporting cells, namely xylem fibers, that accompanied the evolution of this life form, which uses other plants as supports. Although this iconic component of tropical forests has evolved several times in different groups (Gentry, 1991; Angyalossy *et al.*, 2015), the life form shows a series of striking converging anatomical features, as the presence of huge vessels, up to 500 micrometers in diameter (Angyalossy *et al.*, 2015), that are associated with small vessels (vessel dimorphism, Carlquist, 1981). Moreover, the reduction of fibers and increase of parenchyma in comparison to phylogenetically related species, and the presence of cambial variations, that are different arrangements of secondary vascular tissues (Carlquist, 1985; 2001; Angyalossy *et al.*, 2012) are characteristic of lianescent habit. All these features are collectively called lianescent vascular syndrome (Angyalossy *et al.*, 2015) and are observed in both existing and extinct liana species (Burnham, 2009).

Nevertheless, many lianas show a denser xylem at the beginning of their development, which is more fibrous and shows smaller vessels, resembling the xylem of self-supporting species (Schenck, 1893; Obaton, 1960; Caballé, 1998; Gallenmuller *et al.*, 2001). The transition from this denser xylem phase (termed as self-supporting xylem hereafter) to that showing the lianescent vascular syndrome (named as lianescent xylem hereafter) occurs abruptly, as seen in the adult stem cross-section (Fig. 1), and was observed in 85 % of the more than 13,000 specimens, belonging to 400 liana species of 50 different families analyzed by Caballé (1998). The beginning of lianescent xylem production occurs, in different stems, after the formation of different amounts of the self-supporting xylem (Caballé, 1998), which suggests that it is not as a result of a pre-defined developmental program. It is not known, however, what leads to the abrupt change of xylem formation (Rowe & Speck, 1996; Caballé, 1998). While several reports have investigated the exuberant anatomical architectures formed due to cambial variants (Rajput *et al.*, 2008; Pace *et al.*, 2009; Tamaio *et al.*, 2010; Cabanillas *et al.*, 2017), the sudden change in lianas xylem anatomy has been poorly addressed (Obaton, 1960; Caballé, 1993; 1998; Gallenmüller et al., 2001). The detailed characterization of the two anatomy phases, not only contributes to the better understanding of the control of their formation, the demands suffered and met by lianas xylem and the evolution of this important life form, but also shed light on factors that modulate the development of secondary xylem, with underlying genetic traits and the implications for hydraulic conductivity and mechanical performance, in plants as a whole.

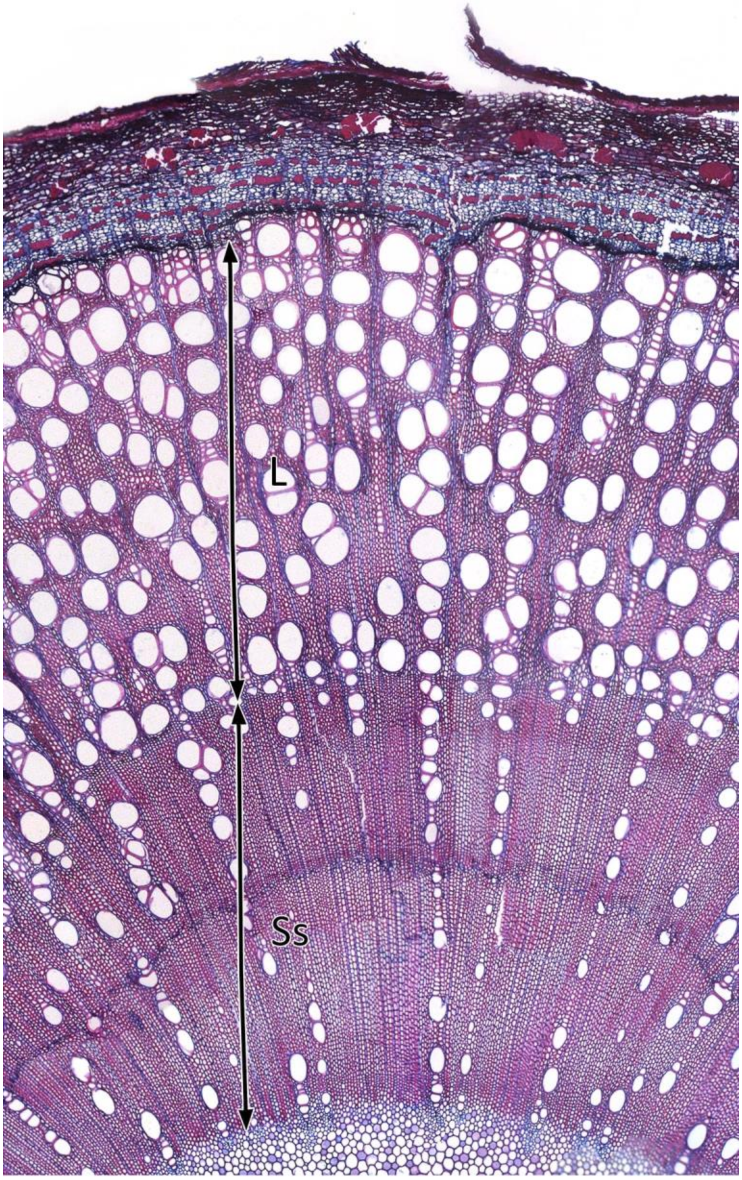

Fig. 1. *B. magnifica* stem cross section. As *B. magnifica*, many lianas show the formation of a denser xylem at the beginning of the secondary growth, composed by a high proportion of fibers and with small vessels, denominated here self-supporting xylem (**Ss**), and a sudden change to a xylem showing the lianescent vascular syndrome, *i.e.* with less fibers and large vessels, which are associated with small vessels, denominated lianescent xylem (**L**).

The use of model species, as *Arabidopsis thaliana* and *Populus*, has provided invaluable advances in the understanding of cambium installation and activity, as well as xylem formation and differentiation (Groover, 2005; Hirakawa *et al.*, 2010; Agusti *et al.*, 2011; Robischon *et al.*, 2011; J. Zhang *et al.*, 2014; 2019; Ye & Zhong, 2015; Sundell *et al.*, 2017). The signaling pathway regulating cambial maintenance and proliferation is conserved from herbaceous to woody species, as described in both *A. thaliana* and *Populus*, and is controlled by the module TDIF/CLE41/CLE44-TDR/PXY-WOX4 (Zhang *et al.*, 2014). TRACHEARY DIFFERENTIATION INHIBITORY FACTOR (TDIF) peptides, which are products of the posttranslational process of CLAVATA/EMBRYO SURROUNDING REGION (CLE41 /CLE44) protein are produced in the phloem and perceived in the (pro)cambium by the receptor-like kinase TDIF RECEPTOR/PHLOEM INTERCALATED WITH XYLEM (TDR/PXY). This interaction induces the expression of the *WUSCHEL-RELATED HOMEOBOX* gene (*WOX4*), which in turn regulates cell proliferation (Hirakawa et al., 2010; Etchells & Turner, 2010). Secondary cell wall (SCW) biosynthesis regulation by the primary and secondary master switches NAM/ ATAF1/CUC2 (NAC) and MYB (V-MYB protein from avian myeloblastosis virus) transcription factors, respectively, was also described in *A. thaliana* (Kubo et al., 2005; Zhong et al., 2006; McCarthy et al., 2009; Ko et al. 2009). The elaborated transcriptional network controlling fiber and vessels differentiation was further characterized in numerous other species, such as *Populus trichocarpa*, *Oryza sativa*, *Brachypodium distachyon*, *Eucalyptus grandis* and *Zea maize* (Hu et al., 2010; Nuruzzaman et al., 2010; Valdivia et al., 2013; Soler et al., 2015; Zhong et al., 2011).

Molecular studies in non-model species, on the other hand, have become possible in an unprecedented way thanks to the use of new technologies, such as next-generation sequencing (Wang *et al.*, 2009), and allowed to unravel many unique features and processes absent in model species (Carpentier *et al.*, 2008). In this study, we made an integrative approach to address the question of what triggers and which are the genetic determinants of the profound changes during the transition from self-supporting to the lianescent xylem in the liana *Bignonia magnifica* W.Bull (Bignoniaceae). For this purpose, we first analyzed growth rates of plants grown with and without supports, how xylem parameters varied along the stem, described in detail self-supporting and lianescent xylem anatomy and what are the implications for hydraulic conductivity. We then constructed cambium and differentiating xylem transcriptome of these two phases and conducted a differential expression analysis of RNA-Seq generated data.

Our work shows that the presence of supports leads to changes in growth pattern and anatomical parameters along the stem, increasing specific conductivity, and promotes lianescent xylem formation. These changes are associated to differential expression of genes related to cell division, cell wall, transcription factors, defense/cell death, and hormone-responsive genes.

Conclusions

In the present study, we verified profound impacts of support on the liana *B. magnifica* shoot development, increasing growth in length, decreasing growth in thickness and promoting the formation of the lianescent xylem. The detailed xylem anatomical characterization showed that the onset of lianescent phase is characterized by much larger vessels, whose production is not anymore restricted to the front of protoxylem poles, that drastically increase specific conductivity. The comprehensive integration of anatomical and differential expression analysis data allows us to propose a model to characterize the molecular control of the lianescent vascular syndrome establishment (Fig 11). Our model shows that the more complex lianescent xylem reflects an also more intricate transcriptional regulation network, involving a more diverse repertory of transcription factors and hormone responsive genes.

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