



3rd International Conference on Natural Fibres: Advanced Materials for a Greener World, ICNF  
2017, 21-23 June 2017, Braga, Portugal

## Bast fibre formation: insights from Next-Generation Sequencing

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### Abstract

Bast fibres are extraxylary sclerenchymatous cells characterized by a noteworthy length and by a cell wall composed of crystalline cellulose. Bast fibres support mechanically the phloem and are used for different industrial applications by the textile and biocomposite sectors. Fibre crops like hemp (*Cannabis sativa*), flax (*Linum usitatissimum*), ramie (*Boehmeria nivea*), jute (*Corchorus olitorius*, *C. capsularis*), kenaf (*Hibiscus cannabinus*) are therefore important natural resources which can help develop a sustainable economy. Despite the importance of bast fibres, not all the features related to their initiation and growth are fully explored and understood. In this review we will focus on the current knowledge concerning bast fibre initiation and development by using a transcriptomic angle, in the light of the great advances that Next-Generation Sequencing (NGS) has fostered in the last years. We discuss the results obtained recently on different fibre crops and we conclude our survey with a perspective on future molecular studies aimed at valorising neglected fibre crops, e.g. nettle (*Urtica dioica*).

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Peer-review under responsibility of the scientific committee of the 3rd International Conference on Natural Fibres: Advanced Materials for a Greener World.

**Keywords:** Bast fibres; Fibre crops; Transcriptomics; Intrusive growth; Cell wall; Cellulose; Lignin.

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## 1. Main text

Bast fibres are unique cells characterized, at maturity, by a thick cellulosic cell wall and by a noteworthy length. Bast fibres show a diffuse (intercalary or global) anisotropic expansion, i.e. the expansion is uniform by apposition of new cell wall components over the whole surface [1]. The mechanism through which bast fibres reach their final length is intrusive (or invasive) growth, a type of growth where the tip of the fibres invades the middle lamellas of the adjacent cells [1-5]. Bast fibres first grow symplastically with the surrounding cells, then their flat ends change to tapered ones, thereby marking the onset of intrusive growth; in the case of hemp primary fibres, the distance from the shoot apical meristem (SAM) at which these structures have been observed is ca. 2 mm [6].

Fibre crops are not only important for bio-economy, but they also represent powerful models for cell wall-related studies: their stems have a woody core and a cortex harboring the cellulosic bast fibres and they show a basipetal lignification gradient where the expression of genes involved in the provision of the precursors for lignin biosynthesis is progressively upregulated [7]. Additionally, an empirically-determined region along the stem and known as snap point (SP), marks the shift from elongation to fibre cell wall thickening [8]. Therefore, sampling stem internodes above and below the SP allows the study of the dynamics in cell wall-related gene expression [7,9].

Next-Generation Sequencing (NGS) has been a real revolution in plant biology [10], because its depth of analysis allows the study of the expression dynamics of thousands of genes, as well as the detection of transcript variants. The application of NGS, i.e. transcriptomics, to fibre crops has provided crucial data that help us better understand the regulation of bast fibre formation and subsequent development.

In this review, we discuss the recent transcriptomic data obtained on different fibre crops, namely flax, ramie, hemp, jute and kenaf. We differentiate the group of plants producing gelatinous fibres (with a G-layer, i.e. flax, ramie and hemp) from those depositing fibres with a xylan-type cell wall (with an S-layer, i.e. jute and kenaf). We conclude our survey by highlighting the importance of future transcriptomics studies on neglected fibre crops, as for example common nettle *U. dioica*.

### 1.1. Flax

Flax is a member of the Linaceae family and has been the object of several transcriptomic studies. We will here review the most recent transcriptomic data available for this fibre crop.

The hypolignification of flax gelatinous bast fibres has been studied in detail by Chantreau and colleagues [11] in a work reporting ethyl methanesulfonate mutagenized flax lines. We believe it is important to describe the results of this work, although a microarray approach was used (and not a NGS strategy), as it allows a clear understanding of the mechanisms regulating flax bast fibre hypolignification. Mutant flax lines (called *lignified bast fibers*, *lbf*) showing lignified bast fibres were identified in this study (93 M2 families in total) and subdivided into 8 different groups, depending on the type of altered lignification profile (i.e. lignification in bast fibres only, or in the surrounding cells too). Chemical analyses of the lignin content allowed the identification of one mutant line, *lbf1*, showing a significant increase in lignin content in the outer stem tissues (350% increase). The microarray analysis of this mutant identified 959 transcripts which were more abundant and 806 less expressed in the outer tissues of the mutant with respect to the wild-type: transcripts involved in monolignol biosynthesis (*CCR*, *COMT*, *CAD*) and polymerization (orthologs of *Arabidopsis* *PRX52*, *PRX53*, *PRX71*) were more expressed in *lbf1*. These results demonstrate that the hypolignification observed in flax bast fibres is linked to the transcriptional regulation of genes involved in monolignol oxidation [11].

The intrusive growth of bast fibres is a fascinating process that awaits characterization. For example, key players involved in this process are still to be identified (e.g. transcription factors, TFs). The characterization of marker genes of intrusive growth would open the way to important functional studies, as for example done for the TFs regulating secondary growth.

The availability of the transcriptome of the SAM of flax, reported by Zhang and Deyholos in 2016 [12] is in this respect an important resource. In this study the authors analyze the transcriptome of the apical-most 0.5 mm of the stem (AR) and the whole stem region excluding the apical-most 1 cm (BR) and provide a rich list of candidates. These genes clearly deserve further investigation to be able to shed light on the molecular factors determining the

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