The Evolutionary History and Dynamics of the Cellulose Synthase Superfamily

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Abstract

The plant cell wall is central to the success of the embryophyte radiation. The high tensile strength of the cell wall supports complex branching architectures adapted to a varying and highly competitive environment. The cell wall has also played an integral role during the evolution of multicellularity by bonding cells together, controlling cell differentiation, acting as an energy store and mediating chemical signals. Polysaccharides are the dominant component of the plant cell wall and the genes involved in their biosynthesis are a major focus of cell wall research. The work presented in this thesis aims to reconstruct the evolutionary history and selection dynamics of the embryophyte cellulose synthase (*CesA*) and cellulose synthase-like (*Csl*) superfamily.

The commercially significant Poaceae (grasses) have received considerable attention. The commercially significant Poaceae (grasses) have received considerable attention from the plant cell wall research community, not least because they are unique in containing a high abundance of (1,3;1,4)-β-glucan. Chapter 2 reconstructs the molecular phylogeny and evolutionary dynamics of the *CesA* superfamily in the Poaceae. Bayesian and likelihood-based models yielded a well-resolved gene tree for the superfamily and revealed heterogeneous selection pressures among amino acid sites. To provide a functional context to these findings, an energetically refined homology model of HvCslF6 was constructed — this is an important enzyme implicated in the biosynthesis of (1,3;1,4)-β-glucan — that was used to map amino-acid residues under selection onto a three-dimensional structure.

Analyses performed for Chapter 2 showed that the *CslJ* clade was conspicuous in having a level of historical divergence too high for the evolutionary models used. As high divergence could indicate functional shift, the focus in Chapter 3 was on the phylogenetic analysis and functional characterisation of *CslJ*. Phylogenetic analyses of *CslE, CslJ* and *CslG* families across an improved taxonomic sampling of fully sequenced eudicot and monocot species were performed and experimental evidence that *CslJ* is implicated in the biosynthesis of (1,3;1,4)-β-glucan is presented. Selection tests show that the *CslJ* lineage has undergone a significant long term shift in selection pressure and while the causative factors behind this are unknown, the presence of three highly diverged gene families mediating the synthesis of (1,3;1,4)-β-glucan presents an interesting case study in coevolution.

The broad distribution of gene families capable of (1,3;1,4)-β-glucan synthesis across the *CesA* superfamily tree highlights the difficulty in mapping polysaccharide product to phylogenetic structure. This difficulty is compounded by significant systematic confusion; superfamily members in species are named in order of discovery or by homology to different organisms. In Chapter 4, this confusion is addressed using model-based analyses to reconstruct phylogenetic relationships and infer duplication events among the *CesA* and *Csl* genes of 22 fully sequenced angiosperms. The recovered phylogenetic history and identified discriminatory protein motifs were used to construct a revised system for naming new and existing *CesA* and *Csl* genes.

Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree. I give consent to this copy of my thesis when deposited in the University Library, being made available for loan and photocopying, subject to the provisions of the Copyright Act 1968. I acknowledge that copyright of published works contained within this thesis resides with the copyright holder(s) of those works. I also give permission for the digital version of my thesis to be made available on the web, via the University's digital research repository, the Library Search and also through web search engines, unless permission has been granted by the University to restrict access for a period of time.

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