13th *New Phytologist* Symposium

The role of the extracellular matrix in the control of plant development

The Linnean Society
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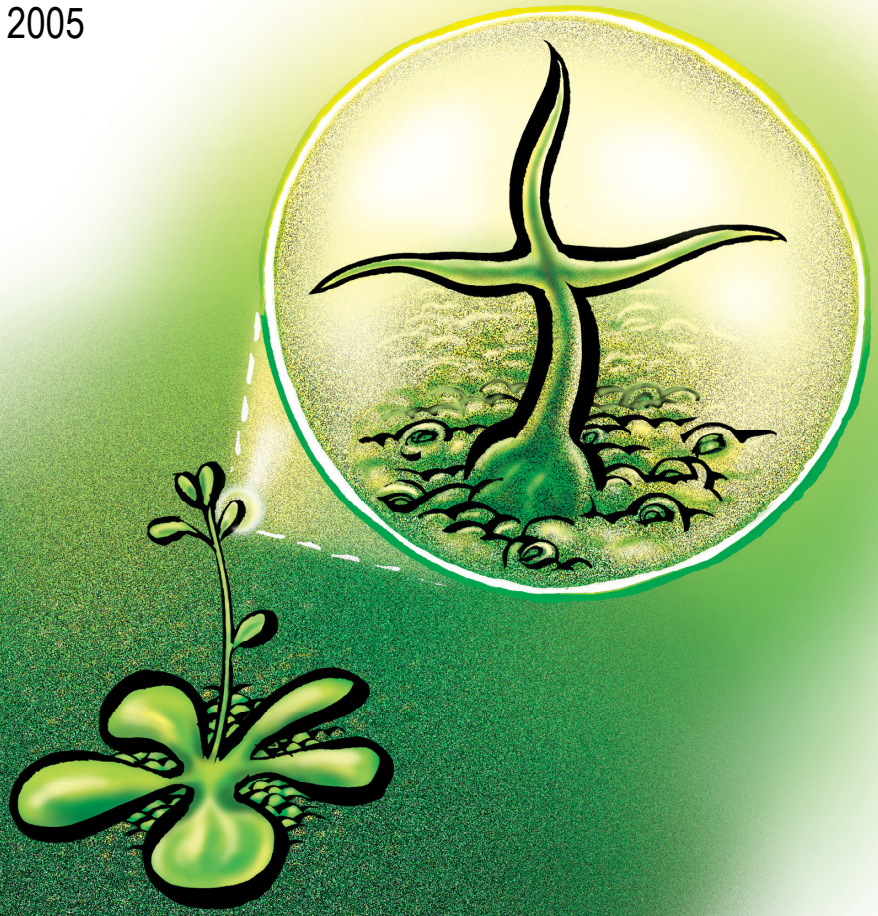
20–21 January 2005



Programme, abstracts & participants

New Phytologist

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Organizing Committee

Alistair Hetherington (*Lancaster University, UK)*
Colin Brownlee (*Marine Biological Association, Plymouth, UK)*
Julie Gray (*University of Sheffield, UK)*
Keith Lindsey (*University of Durham, UK)*
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Acknowledgments

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Programme, abstracts and participant list compiled by Holly Slater. Trichome illustration by Sam Day, www.samday.com

Programme

Thursday 20 January

12:30–13:30	Registration & lunch
13:30–13:40	**Welcome & introductions**, Alistair Hetherington, Holly Slater

Session I

Chairperson: Alistair Hetherington

13:40–14:20	**Colin Brownlee**, Marine Biological Association, Plymouth, UK Interactions between the ECM and polarised signalling machinery during early development in *Fucus* embryos
14:20–15:00	**Paul McCabe**, University College Dublin, Eire Evidence for developmental signals that are essential in controlling somatic embryogenesis in carrot
15:00–15:30	Refreshment break
15:30–16:10	**Julie Gray**, University of Sheffield, UK The link between stomatal development and wax biosynthesis
16:10–16:50	**Robert Pruitt**, Purdue University, West Lafayette, IN, USA Role of the extracellular matrix in regulating epidermal cell interactions
16:50–17:30	**Andy Pereira**, Plant Research International, Wageningen, The Netherlands The SHINE clade of AP2/ERF transcription factors regulate the formation of plant separation layers

Friday 21 January

Session II
Chairperson: Keith Lindsey

09:30–10:10	**Dianne Edwards**, Cardiff University, UK Is the present the key to the past? Thoughts on the evolution of signalling mechanisms
10:10–10:50	**Keith Roberts**, John Innes Centre, Norwich, UK The extracellular matrix and cell elongation
10:50–11:20	Refreshment break
11:20–12:00	**Herman Hofte**, INRA–Versailles, France Coordination of cell expansion with cell wall assembly through cross talk across the plasma membrane
12:00–12:40	**Andrew Fleming**, University of Sheffield, UK Modifying leaf morphogenesis by manipulating the extracellular matrix
12:40–13:00	Discussion & concluding remarks
13:00–14:00	Lunch and depart

Speaker Abstracts

Interactions between the ECM and polarised signalling machinery during early development in *Fucus* embryos

COLIN BROWNLEE
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Following fertilization, zygotes of fucoid algae undergo a well-characterised sequence of events leading to polarization, germination of a rhizoid and the first asymmetric fate-determining cell division. The production of a cell wall is essential for zygote polarization and can influence the fate of the developing rhizoid or thallus cells. However, the mechanisms by which this can occur are still unclear. At least three distinct mechanisms exist though which the cell wall can influence polarity and cell fate.

Components of putative axis stabilisation complexes involving structural interactions between the cytoskeleton and cell wall components have been identified but the way that they function remains uncertain. There is also evidence that releasable cell wall components can signal directly to the underlying cell to influence its developmental pathway. Finally, direct interactions between the cell wall, reactive oxygen production, and membrane channels and the actin cytoskeleton may underlie amplification of localised calcium signals that have been shown to be crucial for localised rhizoid germination and growth.

Evidence for developmental signals that are essential in controlling somatic embryogenesis in carrot

PAUL McCABE
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Somatic embryogenesis is the process whereby cells in liquid culture can redifferentiate and develop into embryos. Carrot is often used as a model species to investigate the control of somatic embryogenesis. However, not all carrot cultures are capable of undergoing embryogenesis. Those that are contain cells that express, in the extracellular matrix, a specific proteoglycan antigen recognised by the monoclonal antibody JIM8.

Single cells expressing this JIM8 antigen can undergo an asymmetric division which gives rise to a sister cell that doesn't express the JIM8 antigen, this sister cell is the embryo initial and will go on to become the somatic embryo. However, if the JIM8 expressing cells are removed from the culture, by immunocapture, the embryo initials fail to become embryos and instead differentiate into callus. Embryogenic development can be restored by feeding the cells with medium that has been 'conditioned' by growing JIM8 expressing cells in it for 1 week. These experiments demonstrate that JIM8 expressing cells produce a signal, essential for somatic embryogenesis, and release it into the culture medium. Identifying this signal may reveal aspects of the role of the extracellular matrix in controlling plant development.

The link between stomatal development and wax biosynthesis

JULIE GRAY, GEOFF HOLROYD, JULIE HUNT, IAN WOODWARD AND ALISTAIR HETHERINGTON
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The *Arabidopsis thaliana HIC* (for high CO_2) gene encodes a putative beta ketoacyl CoA synthase believed to be involved in the synthesis of very long chain fatty acids. Plants carrying a mutation in the *HIC* gene or engineered such that *HIC* gene expression is reduced display an increased number of guard cells when grown under elevated concentrations of carbon dioxide (Gray *et al.,* Nature 1990). As fatty acid elongases are involved in the production of very long chain fatty acids, which are components of the cuticular waxes, the stomatal index of several wax deficient mutants was investigated. *cer1* and *cer6,* which have mutations in decarbonylase and fatty acid elongase encoding genes respectively, were shown to have abnormally high stomatal indices. These results indicate a link between the control of stomatal number and the biosynthesis of cuticular waxes. The results of

recent experiments on the possible involvement of epicuticular waxes in the control of epidermal cell development will be described.

Role of the extracellular matrix in regulating epidermal cell interactions

ROBERT PRUITT
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The epidermal surface of plants serves as the point of contact between the organism and the surrounding environment. Although this surface is exposed to many types of biotic and abiotic challenges, there are relatively few documented cases where the underlying epidermal cells interact with cells that come in contact with their outside surfaces. We have conducted a large-scale genetic analysis of two such systems: pollen-stigma interactions and postgenital organ fusion in *Arabidopsis thaliana*. In each of these cases the genetics strongly indicate that the interaction is regulated at the level of the extracellular matrix (ECM). This has suggested a model in which the properties of the ECM are responsible for controlling the movement of developmental signals both laterally and transversely through the ECM. Cloning of one of the genes identified by mutational analysis, FIDDLEHEAD, has led to the hypothesis that biosynthesis of specific lipid molecules may be key to this regulation. Molecular and phylogenetic analysis of genes related to FIDDLEHEAD has shown that the members of this gene family encode enzymes with differing biochemical specificities and that these biochemical functions probably evolved prior to the divergence of ferns and angiosperms.

The SHINE clade of AP2/ERF transcription factors regulate the formation of plant separation layers

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Plants and the environment are separated by an extracellular interface that plays a dual role as a protective barrier, as well as a medium for the exchange of gases, water and nutrients. The primary aerial plant surfaces are covered by a cuticle, acting as the essential permeability barrier towards the atmosphere. It is a heterogeneous layer composed mainly of lipids, namely cutin and intracuticular wax with epicuticular waxes deposited on the surface. We identified an *Arabidopsis* activation tag gain-of-function mutant *shine* (*shn)* that displayed a brilliant, shiny green leaf surface with increased cuticular wax compared to the leaves of wild type plants. The gene responsible for the phenotype encodes one member of a clade of three proteins of undisclosed function in *Arabidopsis*, belonging to the plant-specific family of AP2/EREBP transcription factors. Overexpression of all three *SHINE* clade genes conferred a phenotype similar to that of the original *shn* mutant. Biochemically, such plants were altered in wax composition (very long fatty acid derivatives), predominantly downstream of the wax decarbonylation pathway. Total cuticular wax levels were increased 6-fold in *shn* compared to the wild type, mainly due to a 9-fold increase in alkanes that comprised about half of the total waxes in the mutant. Chlorophyll leaching assays and fresh weight loss experiments indicated that overexpression of the *SHN* genes increased cuticle permeability, probably due to changes in its ultra-structure. Likewise, *SHN* gene overexpression altered leaf and petal epidermal cell structure, trichome number and branching as well as the stomatal index. Interestingly, *SHN* overexpressors displayed significant drought tolerance and recovery, probably related to the reduced stomatal density. Expression analysis using promoter-GUS fusions of the *SHN* genes provides evidence for the role of the *SHN* clade in plant protective layers, such as those formed during abscission, dehiscence, wounding, tissue strengthening and the cuticle. They are however not expressed predominantly in the epidermis and thus not the prime regulators of epicuticular wax biosynthesis. We propose that these diverse functions are mediated by regulating metabolism of lipid and/or cell wall components in separation layers of the plant. These functions are conserved between dicots and monocots that show a similar mechanism.
Similarly to *SHN*, mutations in the *KCS*, and *FDH* or *HIC* genes result in alteration of stomatal density and trichome number, respectively. The *lcr* mutant showed a dramatically reduced trichome number, while *wax2/yre* had a reduction in stomatal index and reduced trichome size. Both *cer1* and *cer6/cut1* showed also an increase in stomatal index, while *lacs2* was altered in the shape of pavement cells.

Thus, *shn* mutants substantiate the concept that composition of wax in the cuticle effects epidermal cell differentiation, possibly by mediating a transfer of signals for epidermal cell fate (Bird and Gray, 2003).

Is the present the key to the past?: thoughts on the evolution of signalling mechanisms

DIANNE EDWARDS
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The cuticle was arguably the earliest of the great inventions of the land and heralded the suite of characters both anatomical and biochemical that facilitated homoiohydry and the dominance of vascular plants in a wide range of habitats. Limited evidence suggests that the cuticle was probably of similar composition to that in extant plants (although it is impossible to confirm the presence of waxes) and certainly the underlying tissues and their development show remarkable similarity to those today. However the architecture of the earliest land plants, and most notably the absence of leaves, is less familiar and raises questions on the relevance of information gained from extant vascular plants - a research area dominated by a herbaceous angiosperm - to these pioneers, and whether the consequences of signalling mechanisms can be detected in them. Particularly intriguing here would be analysis of patterning in stomata, trichomes and rhizoids. Another approach might be via studies on the somewhat troublesome-to-grow, free-sporing vascular plants - the 'lycopodiums', representatives of which, with stomata-bearing microphylls, are found in the late Silurian and early Devonian, although then growing in an atmosphere and possibly lithosphere quite different from today's. The fossil record of the earliest higher-plant, land colonizers is restricted to their spores, but with further evidence, including molecular phylogenies, indicating affinities with bryophytes. The presence of stomata in extant moss sporophytes pushes back the origin of these structures even further. Today those stomata occur only on the spore capsules, and again studies, on extant representatives, perhaps involving mutants, may have relevance for the origins of signalling mechanisms, although the issue is further complicated by the dearth of information on the extracellular matrix of any members in this group.

The extracellular matrix and cell elongation

KEITH ROBERTS
John Innes Centre, Norwich, NR4 7UH, UK

When plant cells exit from the cell cycle, they usually grow and expand to many times their original volume, often by more than a thousand-fold, but they do not grow proportionately in macromolecular mass. I will explore the different strategies plant cells adopt to increase both their mass and their volume, and the role that DNA content and the cell wall play in this. Generally speaking, cell wall deposition keeps pace with cell growth, but special exceptions exist and I shall discuss three of these. The first is secondary wall deposition during cell differentiation in which deposition continues after growth stops. The second is the elongation of the hypocotyl, a rare example of wall thinning during growth, and the third is the pedicel in which the wall thickens as the cells elongate. Cells seem to have tight genetic and environmental control over the final size a cell attains. Although cells have a very precise mature size, little is known about the molecular mechanisms that such controls feed into. I shall discuss the evidence we have recently obtained to suggest that one of these mechanisms involves regulating the extent to which the pectic polysacharides in the wall are esterified. Lowering ester levels reduces cell expansion, and this throws a new focus on the role of the large family of wall-located pectin esterases.

Coordination of cell expansion with cell wall assembly through cross talk across the plasma membrane

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A central question in plant developmental biology is how chemistry creates architecture outside the cells (Nevins, 1993). Cell walls are highly organized composite materials consisting of oriented fibers embedded in a polysaccharide matrix. Their assembly involves self-organization of macromolecules

assisted by the cellular machinery. Cellulose microfibrils are synthesized by plasma membrane-embedded hexameric complexes. Loss-of-function mutations have identified many genes that are required for cellulose synthesis in primary walls. They encode respectively three cellulose synthase isoforms CESA1,3,6, a membrane-bound cellulase KOR1, novel proteins KOB1, POM1 and COB, at least one expansin and a suite of proteins involved in N-linked protein glycosylation (Robert et al., 2004). The exact contribution of each of those to the different steps in the assembly and regulation of the cellulose synthase complex, the polymerization, extrusion, crystallization, orientation, assembly and rearrangement of cellulose within the wall remains to be determined.

We are studying wall deposition and remodeling during hypocotyl development in *Arabidopsis*. Hypocotyl cells show two growth phases, an initial slow growth phase during which a thick polylamellated wall is deposited and a second rapid growth phase during which the cell wall is extensively remodeled and wall polymers reorient towards an axial orientation. Novel genes encoding putative wall assembly-associated enzymes have been identified through microarray analysis on isolated hypocotyls of seedlings at different growth stages. We also provide evidence for the fine-tuning of cellulose deposition through regulated intracellular targeting of KOR1 cellulase. We finally studied the cross talk between cell wall assembly and cell elongation. The inhibition of cellulose synthesis in mutants or by herbicides, leads to a rapid inhibition of cell elongation. In hypocotyls we observed that administering the cellulose synthesis inhibitor isoxaben during the slow growth phase, inhibited subsequent growth acceleration. This inhibition involves an active process since second site mutants were found that attenuate the growth defect of the cellulose-deficient *cesA6*$^{prc1-}$mutant without restoring the cellulose defect. Microarray analysis showed that growth inhibition by isoxaben was accompanied by rapid changes in gene expression, including those encoding cell wall-related enzymes. One locus (*THE1*) identified by three second site suppressor mutations was cloned and encodes a novel membrane-bound receptor kinase. This kinase may act as a wall integrity sensor.

Nevins, AC. 1993. Biology of Fibrous Composites. Cambridge University Press;
Robert, S., Mouille, G. and Höfte, H. 2004. Cellulose, 11: 351-364.

Modifying leaf morphogenesis by manipulating the extracellular matrix

ANDREW FLEMING
Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Seffield, S10 2TN, UK

Leaves are generated by the shoot apical meristem (SAM). This organ displays a conserved pattern of cell division, leading to the hypothesis that regulation of cell division frequency and orientation plays a causal role in leaf initiation. Using a novel technique to locally manipulate the expression of genes encoding proteins involved in the cell cycle, we have shown that local modulation of cell proliferation in the SAM has no impact on leaf initiation. On the other hand, local induction of a gene encoding expansin (a protein which can modify the extensibility of the extracellular matrix (ECM)) was sufficient to induce leaf formation. Coupled with data showing that specific expansin genes are expressed at the site of leaf formation, these data suggest that expansin-mediated change in biophysical parameters of the ECM is a key event in leaf initiation. Moreover, similar manipulation of expansin gene expression in leaf primordia resulted in altered leaf shape, suggesting that modifying ECM extensibility can be used as a general tool to manipulate organ form. At the same time, manipulation of cell proliferation in the leaf also led to a change of leaf shape, indicating that the influence of cell division on morphogenesis is context dependent and that the relationship between cell division and growth varies during plant development. This relationship is intimately linked with differentiation and our latest data provide an insight into this process.

Wyrykowska, J. & Fleming, A. J. 2003. Proc. Natl. Acad. Sci. USA 100, 5561-5566.
Wyrzykowska, J. et al. 2002. Development 129, 957-964.
Pien, S. et al. 2001. Proc. Natl. Acad. Sci. USA 98, 11812-11817.

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