# 38<sup>th</sup> New Phytologist Symposium

# Colonization of the terrestrial environment 2016



25–27 July 2016 Bristol, UK



Programme, abstracts and participants

### 38<sup>th</sup> New Phytologist Symposium

# Colonization of the terrestrial environment 2016

# Life Science Building, University of Bristol, Bristol, UK 25–27 July 2016

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#### **Acknowledgements**

The 38<sup>th</sup> New Phytologist Symposium is funded by the New Phytologist Trust

#### **New Phytologist Trust**

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Programme, abstracts and participant list compiled by Jill Brooke 'Colonization of the terrestrial environment 2016' logo by A.P.P.S., Lancaster, UK

Contact email: np-symposia@lancaster.ac.uk

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### **Information for Delegates**

#### **Symposium location**

The 38<sup>th</sup> New Phytologist Symposium will be held in the Life Science Building, University of Bristol, Bristol, UK. <a href="http://www.bristol.ac.uk/biology/life-sciences-building/">http://www.bristol.ac.uk/biology/life-sciences-building/</a>

A map showing the location of the venue can be found online at <a href="http://www.bristol.ac.uk/media-library/sites/maps/migrated/documents/precinct-key.pdf">http://www.bristol.ac.uk/media-library/sites/maps/migrated/documents/precinct-key.pdf</a>

All presentations will be given in the Life Science Seminar Room. Posters will be displayed in the Atrium.

#### Catering

Coffee breaks and lunches on Monday, Tuesday and Wednesday will be served in the Atrium.

#### **Excursion to the University of Bristol Botanic Garden and Symposium Dinner**

Buses will leave the Life Science Building at 17:15. There will be a tour followed by drinks at the Botanic Garden. At 19:30 we will walk to Wills Hall (approx. 5 mins walk from the Botanic Garden) where the symposium dinner will be held.

Buses will return to the Life Science Building at 22:00.

#### **Posters**

Posters should be prepared so that they are no larger than A0 size, portrait orientation (118 cm high x 84 cm wide). Posters should be put up during registration (11:00–13:00 on 25 July) and will be displayed for the duration of the meeting. Delegates are welcome to view posters during coffee and lunch breaks; there will also be a dedicated poster session from 16:30 to 19:00 on Monday 25 July. Please stand by your poster for part of this session (we appreciate as poster presenters you will also want to view and discuss the other posters). Please note there will be prizes for the best posters.

#### **Internet access**

The University of Bristol provides access to eduroam and The Cloud wireless services in all campus wireless locations. For more information please go to: https://www.wireless.bris.ac.uk/visitors/

#### Social media

We encourage all attendees to join in discussions on social media sites. Follow @NewPhyt on Twitter and fb.com/NewPhytologist on Facebook for updates before, during and after the meeting. Please use the hashtag #38NPS in all of your tweets.

#### Contact

For further information, and in case of any emergencies, please contact Helen Pinfield-Wells. Email: h.pinfield-wells@lancaster.ac.uk, np-symposia@lancaster.ac.uk; tel: +44 7966 450 389.

### **Meeting Programme**

Monday 25 July		
11:00-13:00	Registration and Lunch	
13:00–13:10	Welcome to the 38 <sup>th</sup> New Phytologist Symposium	
13:10–14:00	<b>Keynote 1 Tim Lenton</b> Chaired by Dianne Edwards Earliest land plants created modern levels of atmospheric oxygen	
Session 1: Interrelations Chair: Dianne Edwards 14:00–16:30	ships	
14:00-14:30	<b>S1.1 Sean Graham</b> Advances and gaps in understanding early land-plant phylogeny based on genome-scale data	
14:30–15:00	S1.2 Cymon Cox Relationships among extant land plants based on chloroplast data	
15:00-15:30	Break	
15:30–16:00	<b>S1.3 Paul Kenrick</b> The early fossil record of land plants and their environment	
16:00–16:15	Selected poster abstract talk Eleanor Vesty: P29 The decision to germinate in spores and seeds is regulated by divergent networks with ancient conserved nodes	
16:15–16:30	Selected poster abstract talk Karl Fetter: P10 Dual reconstruction of paleoecology and whole-plant habit using stable carbon isotopes from dispersed leaves of Laurozamites powellii, an Upper Triassic bennettitalean	
16:30-19:00	Poster reception	
Tuesday 26 July		
09:00-09:50	<b>Keynote 2 Liam Dolan</b> Chaired by Philip Donoghue Development and evolution of land plant rooting systems	
Session 2: Anatomy – developmental genetics Chair: Philip Donoghue 09:50–12:30		
09:50–10:20	S2.1 Brad Olson Peering into the pond for clues to multicellularity	

10:20-11:00	Break
11:00–11:30	<b>S2.2 Jill Harrison</b> Genetic evidence for a multicellular meristem precursor in mosses
11:30–11:45	Selected poster abstract talk  Mark Puttick: P20 Size is not everything: rates of genome size evolution, not C-value, correlate with speciation in Angiosperms
11:45–12:00	Selected poster abstract talk Alexander Hetherington: P13 Unique cellular organisation in the oldest root meristem
12:00–12:30	<b>S2.3 Andrew Plackett</b> Functional genetic analysis in the fern <i>Ceratopteris richardii</i> : a new tool to investigate land plant evolution
12:30-13:30	Lunch
Session 3: Anatomy and species Chair: Harald Schneider 13:30–17:00	d physiology of early land plants – what can we learn from extinct
13:30–14:00	S3.1 John Raven Light on the colonization of the land by photosynthetic organisms
14:00–14:30	<b>S3.2 Julie Gray</b> An ancestral stomatal patterning module in the non-vascular land plant <i>Physcomitrella patens</i>
14:30–15:00	S3.3 Isabel Montanez  Dynamic carboniferous tropical forests: a new view of their paleo-plant function and paleo-ecophysiology
15:00-15:30	Break
15:30–16:00	S3.4 Kevin Boyce Using the constraints of function to understand form in early land plants
16:00–16:15	Selected poster abstract talk Robert Caine: P5 Deep evolutionary conservation of genes involved with stomatal development
16:15–16:30	Selected poster abstract talk Peter Franks: P12 Stomatal control in the first land plants
16:30–17:00	S3.5 Francis Martin Unearthing the roots of mycorrhizal symbioses

17:15	Buses depart to Botanic Garden	
19:30	Symposium dinner, Wills Hall	
Wednesday 27 July		
09:00–09:50	<b>Keynote 3 William (Ned) Friedman</b> Chaired by Chris Hawkesworth The texture of plant evolutionary history: how iterative and unique 'events' shape biodiversity	
Session 4: Refining biogeochemical models to take account of the role of plants and fungi Chair: Chris Hawkesworth 09:50–12:20		
09:50–10:20	<b>S4.1 Derek Vance</b> Reconstructing changes in chemical weathering of the continents associated with the advent of early land plants	
10:20-10:50	Break	
10:50–11:05	Selected poster abstract talk Aisling Cooke: P8 Marchantia paleacea: a new model for arbuscular mycorrhizal symbiosis	
11:05–11:20	Selected poster abstract talk  Katie Field: P11 Symbiotic options for the conquest of land	
11:20–11:50	<b>S4.2 Lyla Taylor</b> Challenges in process-based modelling of cryptogamic weathering	
11:50–12:20	<b>S4.3 Andy Ridgwell</b> Colonization of the terrestrial environment <i>in silico</i>	
12:20–12:30	Closing comments from the organisers	
12:30	Lunch	

### **Speaker Abstracts**

S=speaker abstract; P=poster abstract

Boyce, C. Kevin S3.4 Cox, Cymon S1.2

Dolan, Liam Keynote 2, P4, P13, P27

Donoghue, Philip P20

Friedman, William

Graham, Sean

Gray, Julie

Harrison, Jill

Kenrick, Paul

Keynote 3

S1.1, P2, P9

S3.2, P5

S2.2

S1.3, P25

Lenton, Tim

Martin, Francis

Montanez, Isabel

Keynote 1

S3.5, P7

S3.3

Olson, Brad S2.1
Plackett, Andrew S2.3
Raven, John S3.1
Ridgwell, Andy S4.3

Taylor, Lyla **S4.2** 

Vance, Derek **S4.1** 

### **Speaker Abstracts**



Earliest land plants created modern levels of atmospheric oxygen

TIM LENTON<sup>1</sup>, TAIS DAHL<sup>2</sup>, STUART DAINES<sup>1</sup>, BEN
MILLS<sup>1,3</sup>, KAZUMI OZAKI<sup>4</sup>, MATT SALTZMAN<sup>5</sup>, PHILIPP
PORADA<sup>6</sup>

Keynote 1

13:10–14:00

#### t.m.lenton@exeter.ac.uk

<sup>1</sup>Earth System Science, College of Life and Environmental Sciences, University of Exeter, Exeter, EX4 4QE, UK; <sup>2</sup>Natural History Museum of Denmark, Øster Voldgade 5−7, Copenhagen, Denmark; <sup>3</sup>School of Earth and Environment, University of Leeds, Leeds, LS2 9JT, UK; <sup>4</sup>Center for Earth Surface System Dynamics, Atmosphere and Ocean Research Institute, University of Tokyo, 5-1-5, Kashiwanoha, Kashiwa-shi, Chiba 277−8564, Japan; <sup>5</sup>School of Earth Sciences, The Ohio State University, Columbus, Ohio 43214, USA; <sup>6</sup>Department of Environmental Science and Analytical Chemistry, Stockholm University, Svante Arrhenius väg 8, SE−114 18 Stockholm, Sweden

The progressive oxygenation of the Earth's atmosphere was pivotal to the evolution of life, but the puzzle of when and how atmospheric oxygen (O<sub>2</sub>) first approached modern levels (~21%) remains unresolved. Redox proxy data indicate the deep oceans were oxygenated during 435-392 Ma, and the appearance of fossil charcoal indicates O<sub>2</sub> >15–17% by 420–400 Ma. However, existing models have failed to predict oxygenation at this time. Here we show that the earliest plants, which colonized the land surface from ~470 Ma onwards, were responsible for this mid-Paleozoic oxygenation event, through greatly increasing global organic carbon burial - the net long-term source of O<sub>2</sub>. We use a trait-based ecophysiological model to predict that cryptogamic vegetation cover could have achieved ~30% of today's global terrestrial net primary productivity by ~445 Ma. Data from modern bryophytes suggests this plentiful early plant material had a much higher molar C:P ratio (~2000) than marine biomass (~100), such that a given weathering flux of phosphorus could support more organic carbon burial. Furthermore, recent experiments suggest that early plants selectively increased the flux of phosphorus (relative to alkalinity) weathered from rocks. Combining these effects in a model of long-term biogeochemical cycling, we reproduce a sustained +2% increase in the carbonate carbon isotope ( $\delta^{13}$ C) record, and predict a corresponding rise in O<sub>2</sub> to present levels by 420-400 Ma, consistent with geochemical data. This oxygen rise instigated firemediated negative feedbacks that have stabilised high O2 levels ever since, shaping subsequent evolution.

#### **Session 1: Interrelationships**

Chair: Dianne Edwards



Advances and gaps in understanding early landplant phylogeny based on genome-scale data **S1.1** 

SEAN W. GRAHAM<sup>1</sup>, SHING HEI ZHAN<sup>1</sup>, QIANSHI LIN<sup>1</sup>, GANE K. S. WONG<sup>2</sup>, DENNIS W. STEVENSON<sup>3, 4</sup>

14:00-14:30

swgraham@interchange.ubc.ca

<sup>1</sup>Department of Botany, University of British Columbia, Vancouver, BC, Canada; <sup>2</sup>Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada; <sup>3</sup>Department of Medicine, University of Alberta, Edmonton, AB, Canada; <sup>4</sup>New York Botanical Garden, Bronx NY, USA

Despite considerable advances in early land-plant phylogenetic inference, multiple gaps persist in our understanding of relationships among and within the major lineages (bryophytes, lycophytes, ferns, seed plants), reflected in weakly resolved or strongly conflicting relationships across different studies and analyses. These phylogenetic uncertainties matter for reconstructions of trait evolution, for connecting living and extinct taxa, and for understanding the timing and order of early events in plant evolution, some of which correspond to important transitions in terrestrial plant ecosystems. Here we present the results of recent large-scale phylogenomic analyses, including data derived from the 1000 plants initiative (onekp.com), a comprehensive international collaboration to sequence over one thousand plant transcriptomes that represent the broad diversity of extant plant life on earth. We compare results from different analyses and recent studies of the three plant genomes (nuclear, mitochondrial, plastid), providing an overview of how this advances our understanding of early plant relationships. Although our phylogenetic inferences are generally congruent with studies that use smaller amounts of data, several conflict with what we thought we understood about early plant evolution. A particularly spectacular example includes relationships inferred among the three bryophyte lineages (hornworts, mosses, liverworts) and the vascular plants. We also address the broader implications of our results, and address the sources and consequences of persistent gaps in our knowledge.



### Relationships among extant land plants based on chloroplast data

**S1.2** 

CYMON J. COX

14:30-15:00

cymon.cox@googlemail.com

Centro de Ciências do Mar (CCMAR), Universidade do Algarve, Faro, Portugal

Determining the pattern and timing of morphological changes that accompanied the origin and early diversification of plants on land is fundamental to our understanding the evolution of terrestrial ecosystems. The often cited consensus opinion is that the bryophytes diverged first, with liverworts typically identified as being the earliest-diverging lineage of land plants, and that therefore tracheophytes are derived from bryophyte ancestors. The primary molecular evidence for this conclusion comes from analyses that include chloroplast protein-coding genes which can be shown to possess the greater part of the supporting phylogenetic signal even when included in multigenome data sets. Strikingly, when the protein translations of the same chloroplast genes are analysed, they predict a very different tree; one in which the liverworts and mosses are strongly supported as a monophyletic group, and together they are often grouped with the hornworts. Here we diagnose the main source of the conflict between analyses of chloroplast genes and their implied proteins as being due to the presence of synonymous substitutions in the gene sequences: nonsynonymous substitutions and proteins, when modelled and analysed independently, give largely congruent results. Our analyses suggest that conventional models are unable to adequately account for synonymous substitutions in protein-coding gene data and demonstrate that conflicting results can be attributed to the influence of a directional mutation pressure among synonymous substitutions that drives a composition bias. We find that currently the best supported hypotheses of land plant relationships is that bryophytes are either monophyletic or paraphyletic with mosses plus liverworts forming a monophyletic group. If the latter is correct then it is unclear whether the hornwort clade (nuclear data: c.f. Wickett et al., 2014 PNAS) or the moss-liverwort clade (chloroplast (here) and mitochondrial data: Liu et al., 2014 Syst. Biol.) is the earliest-diverging group of land plants.



The early fossil record of land plants and their environment

**S1.3** 

<u>PAUL KENRICK</u>, CHRISTINE STRULLU-DERRIEN, RIA MITCHELL

15:30-16:00

p.kenrick@nhm.ac.uk

Department of Earth Sciences, The Natural History Museum, London, SW7 5BD, UK

Photosynthesizing microbial communities have existed on land since at least the Neoarchean (2800 to 2500 million years), but fossil evidence indicates that land plants first appeared much later during the mid-Ordovician some 470 million years ago. Although this early evidence is greatly influenced by changes in the rock record and taphonomic bias, it provides unique insights into the initial assembly of terrestrial ecosystems and the organisms that they contained. I will review recent key developments in the field and present our findings on the general relations of early fossil plants, emphasizing the importance of other organisms and especially fungi. The earliest land communities probably comprised varied and mixed associations of bacteria, arthropods, lichens, fungi, green algae and extinct land plants called 'cryptophytes'. Little is known about the cryptophytes, but emerging evidence demonstrates that they were minute sporophytes at the bryophyte level of complexity but with novel combinations of characteristics unseen in living relatives. The fossil evidence of vascular plants is much more extensive with an important record during the Devonian Period (419–359 Ma) that documents the early evolution of key organs, such as rooting system, leaves, vascular system and reproductive structures. Colonization of the land by plants occurred in the context of a co-evolving biota that included lichen-like organisms and diverse fungi and possibly also cyanobacteria that entered into symbiotic relations with the plants. The capacity to form mycorrhizal-like associations is ancient and may have been critical to the evolutionary diversification of plants and their soils. These diverse early assemblages resembled in many respects modern Cryptogamic Ground Covers. One goal of our current research on modern volcanic terrains in Iceland is to identify the physical and chemical imprints that these communities leave in rocks and sediments to better understand their influence on ancient environments and on major geochemical cycles.

# Selected poster talks – Monday 25 July Session 1: Interrelationships

16:00-16:30

16:00–16:15	ELEANOR VESTY  The decision to germinate in spores and seeds is regulated by divergent networks with ancient conserved nodes	Poster No. P28
16:15–16:30	KARL FETTER  Dual reconstruction of paleoecology and whole-plant habit using stable carbon isotopes from dispersed leaves of <i>Laurozamites powellii</i> , an Upper Triassic bennettitalean	P10



Development and evolution of land plant rooting systems

**Keynote 2** 

LIAM DOLAN, HOLGER BREUNINGER, CLEMENCE BONNOT, BRUNO CATARINO, CLEMENCE CHAMPION, ALEXANDER J HETHERINGTON, SUVI HONKANEN, VICTOR JONES, SUSANNA STREUBEL, ANNA THAMM, REKA TOTH 09:00-09:50

liam.dolan@plants.ox.ac.uk

Department of Plant Sciences, University of Oxford, UK

The evolution of the first rooting systems some time before 400 million years was a key innovation that occurred when the first complex multicellular eukaryotic photosynthetic organisms – plants – colonized and diversified on the continental surfaces. Rooting systems are important because they facilitate the uptake of most chemical elements that are required for plant growth. The rooting systems of the earliest diverging group of extant land plants comprise unicellular tip-growing filaments called rhizoids and are morphologically similar to cells that develop at the interface between the plant and the soil in tracheophytes (vascular plants) – root hairs.

An aim of our research is use a variety of approaches to define the regulatory mechanisms that controlled the development of the first land plant root system. We describe fossils and identify genes to define the ancient control mechanism that promoted the formation of rhizoids in the extinct colonizers of the terrestrial environment. A major focus is the comparison of the genetic mechanisms that regulate rhizoid and root hair development in bryophytes and seed plants respectively. The regulatory motifs that are common to both are likely to have been inherited from the common ancestor of liverworts and seed plants – close relatives of the first plants to grow in the dry continental surfaces. Our most recent data suggest that a common mechanism controlled the development of a variety of structures – including rooting cells – that develop from the superficial layer of the common ancestor of land plants.

#### Session 2: Anatomy – developmental genetics Chair: Philip Donoghue



Peering into the pond for clues to multicellularity
BRAD OLSON

**S2.1** 

09:50-10:20

bjsco@k-state.edu

Kansas State University, USA

The evolution of multicellular organisms is a major evolutionary state transition that has occurred at least twenty-five independent times in all domains of life. However, the molecular-genetic and ecological basis of multicellular evolution remains enigmatic. Classically, the Volvocacean algae, which include the well known algae Chlamydomonas reinhardtii and Volvox carteri, have been used as an important model system for multicellular evolution. The Volvocales are an important model of multicellular evolution for many reasons including: 1) they represent the most recent known example of multicellular evolution; 2) because the genomes of the organisms are very closely related, and 3) because they are a tractable molecular-genetic model system. The first step for multicellular organisms to evolve occurs when is when unicells for a collective, termed colonialism. Because colonialism is the first step where organismal selfishness is lost, it is widely viewed to be the rate limiting step of multicellular evolution. In the Volvocacean algae, Chlamydomonas reinhardtii represents the unicellular state, while the closely related alga, Gonium pectorale, represents the transition to colonialism. Significantly, colonialism in the Volvocacean algae evolved by the modification of the cell cycle such that mitotic daughter cells remain attached together after mitosis. Significantly, in the draft genome sequence of Gonium pectorale it is observed that the retinoblastoma tumor suppressor cell cycle regulatory pathways have undergone significant modification compared to Chlamydomonas reinhardtii. Finally, it often assumed the unicellular organisms do not cooperate, however, our recent findings suggest that Chlamydomonas reinhardtii cooperates in the face of environmental challenges, suggesting that the path to cooperation in a multicellular organism may be more simple than originally thought.



### Genetic evidence for a multicellular meristem precursor in mosses

**S2.2** 

**JILL HARRISON** 

11:00-11:30

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Bristol University, Bristol, UK

The radiation of vascular plants over 420 million years ago was underpinned by a suite of developmental innovations including indeterminate shoot growth. Unlike vascular plants, bryophytes such as mosses have gametophyte dominant life cycles, and the sporophyte comprises a single small determinate stem. Whilst vascular plant meristems have juxtaposed stem cell and proliferative zones with specialised functions, in moss sporophytes similar meristematic activities are spatially and temporally distinct. A transiently active apical stem cell sets up the apical basal shoot axis, and a proliferative region termed the intercalary meristem later traverses the midpoint of the sporophyte axis serving to push the reproductive sporangium out of the parent plant. Genetic evidence suggests homology between the intercalary meristem and the proliferative zone of vascular plant meristems.

### Selected poster talks – Tuesday 26 July Session 2: Anatomy – developmental genetics

11:30-12:00

11:30–14:45	MARK PUTTICK Size is not everything: rates of genome size evolution, not C-value, correlate with speciation in Angiosperms	Poster No. P20
11:45-12:00	ALEXANDER HETHERINGTON  Unique cellular organisation in the oldest root meristem	P13



Functional genetic analysis in the fern *Ceratopteris* richardii: a new tool to investigate land plant evolution

**S2.3** 

A. R. G. PLACKETT, E. H. RABBINOWITSCH, J. A. LANGDALE

12:00-12:30

andrew.plackett@plants.ox.ac.uk

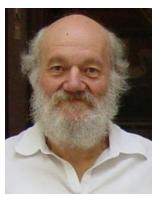
Department of Plant Sciences, University of Oxford, South Parks Road, Oxford, UK

During the colonization of land successive lineages of plants have arisen, each bearing novel developmental innovations that further adapted plants to the terrestrial environment. Understanding the genetic changes underpinning these innovations has been hindered by a restricted number of model species in which genetic transformation allows studies of gene function *in planta*. Genetic models are available within the flowering plants and the bryophytes (mosses, liverworts and hornworts) but these represent the two extreme ends of the land plant phylogeny and there have been no transformable models from the intervening non-seed vascular plant lineages (lycophytes and monilophytes) to bridge this evolutionary gap.

We have recently developed a genetic transformation protocol for a monilophyte species, the fern *Ceratopteris richardii*, and we present our work with this species studying land plant gametophyte evolution. The gametophyte stage of the plant lifecycle has become increasingly specialised for reproduction during successive land plant lineages, reduced from the dominant, indeterminate vegetative structure in bryophytes to only a few reproductive cells in flowering plants. The fern gametophyte represents an intermediate form through which we hope to gain a more detailed understanding of the specialisation it has undergone. To compare with known roles of the plant hormone auxin in bryophyte and flowering plant gametophytes, we have used the *GH3::GUS* reporter gene to map auxin signalling during fern gametophyte development. I will present the results of this work in conjunction with results of auxin manipulation experiments and discuss how the inferred role of auxin during fern gametophyte development relates to auxin signalling in other lineages.

## Session 3: Anatomy and physiology of early land plants – what can we learn from extinct species

Chair: Harald Schneider



Light on the colonization of the land by photosynthetic organisms

JOHN A. RAVEN<sup>1, 2</sup>, PATRICIA SÁNCHEZ-BARACALDO<sup>3</sup>, 13:30–14:00 JOHN BEARDALL<sup>4</sup>

**S3.1** 

j.a.raven@dundee.ac.uk

<sup>1</sup>Division of Plant Sciences, University of Dundee at the James Hutton Institute, Invergowrie, Dundee, DD2 5DA, UK; <sup>2</sup>School of Plant Biology, University of Western Australia, Crawley WA 6009, Australia; <sup>3</sup>School of Geographical Sciences, University of Bristol, University Road, Clifton, Bristol, BS8 1SS, UK; <sup>4</sup>School of Biological Sciences, Monash University, Clayton. VIC 3800, Australia

Primary productivity on land involves oxygenic photosynthetic organisms using photons as energy source with H<sub>2</sub>O as the source of the reductant used in CO<sub>2</sub> assimilation, and the basal oxygenic organism from molecular phylogenies is the terrestrial cyanobacterium Gloeobacter. Oxygenic photosynthesis uses two photochemical reaction in series using chlorophyll a-protein complexes absorbing at 680 and 700 nm and photon harvesting with photochemically silent, chlorophyll aprotein complexes. The ubiquity of chlorophyll a in terrestrial photosynthesis has attracted many hypotheses, the most plausible relating the wavelengths involved in photochemistry to the energy content of the photons, the energy requirements for the observed synthesis of reductant and ATP, and the maximum photon output by the Sun at slightly shorter wavelengths than photons used in photosynthetic photochemistry. Oxygenic photosynthesis must have evolved before the Global Oxygenation Event about 2.3 Ga ago, when the Faint Young Sun had its maximum photon output at a wavelength closer to those involved in photosynthetic photochemistry. An origin of oxygenic photosynthesis deep in H<sub>2</sub>O as a UV-screen in the essential absence of stratospheric O<sub>3</sub> would less readily account for the wavelengths used in photochemistry since water absorbs red and, especially, infrared photons. However, a terrestrial origin of oxygenic photosynthesis would involve substantial UV screening and/or repair of damage caused by UV. Further aspects of such an early origin of terrestrial cyanobacteria will be discussed in the context of extant, and possible earlier, cyanobacterial and green algal components of crytogamic covers and the habitats of the two extant Gloeobacter species.



An ancestral stomatal patterning module in the non-vascular land plant *Physcomitrella patens* 

**S3.2** 

JULIE E. GRAY<sup>1</sup>, ROBERT CAINE<sup>1</sup>, CASPAR C. CHATER<sup>1,2</sup>, YASUKO KAMISUGI<sup>3</sup>, ANDREW C. CUMING<sup>3</sup>, DAVID J. BEERLING<sup>4</sup>, ANDREW J. FLEMING<sup>4</sup>

14:00-14:30

j.e.gray@sheffield.ac.uk

<sup>1</sup>Department of Molecular Biology and Biotechnology, University of Sheffield, Sheffield, S10 2TN, UK; <sup>2</sup>Current address: Departamento de Biología Molecular de Plantas, Instituto de Biotecnología, Universidad Nacional Autónoma de Mexico Cuernavaca, Mexico; <sup>3</sup>Centre for Plant Science, University of Leeds, Leeds, LS2 9JT, UK; <sup>4</sup>Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK

The evolution of stomata almost half a billion years ago, is believed to have aided in the greening of the landmasses of the earth. However, the origin and function of early land plant stomata remains controversial. Recent advances in our understanding of the molecular components that govern angiosperm stomatal function and development has allowed us to begin to explore the ancestral functions and origins of stomata. Mosses belong to one of the most ancient lineages of non-vascular land plant and form rings of stomata around their diploid sporophyte spore capsules. Previously, we have shown that the stomata of *Physcomitrella patens* are able to open and close using signalling components similar to those of the model angiosperm *Arabidopsis thaliana*. Here we present results showing that *P. patens* also controls the formation of its stomata using a similar developmental pathway to angiosperms. In *A. thaliana* a series of Epidermal Patterning Factors (EPF) peptides interact with an array of membrane-localised receptors and affect the activity of transcription factors to control angiosperm stomatal density and distribution. We used molecular genetics to show that the moss *P. patens* has a single conserved EPF homologue which functions to pattern stomata. Our data suggest that the EPF signalling pathway represents an ancient patterning system and provides further support for a monophyletic origin for stomata.



Dynamic carboniferous tropical forests: a new view of their paleo-plant function and paleo-ecophysiology

\$3.3\$

<u>ISABEL P. MONTAÑEZ</u><sup>1</sup>, JONATHAN P. WILSON<sup>2</sup>, JOSEPH 14:30−15:00 WHITE<sup>3</sup>, JENNIFER C. MCELWAIN<sup>4</sup>, WILLIAM DIMICHELE<sup>5</sup> CHRISTOPHER J. POULSEN<sup>6</sup>, MICHAEL HREN<sup>7</sup>

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The radiation of the Earth's most expansive wetland tropical forests occurred during our penultimate icehouse (330 to 260 Myr) under rising atmospheric  $pO_2$  and overall low atmospheric  $pO_2$  concentrations. The unique late Paleozoic atmospheric composition is attributed to atypical rates of organic carbon sequestration in peats (and, ultimately, coals) enabled by a taphonomic window resulting from the interplay of tectonics and tropical climate. Although it is increasingly recognized that repeated restructuring of Carboniferous–Permian tropical forests occurred in response to short- and long-term climate changes, it is generally considered that vegetative feedbacks on the environment were largely limited to carbon sequestration in broad, lowland basins. This paradigm reflects the assumed low photosynthetic rates and gas exchange capacity of these early vascular plants. Here we integrate paleobotanical records, fossil plant anatomy, traits, and stable isotope compositions, with process-based ecological modelling to show that these extinct plants were not merely responding to climate but capable of influencing large-scale fluctuations in atmospheric  $CO_2$  and hydrologic cycling as a consequence of their more dynamic range of physiological functioning than previously considered.

We reconstruct the plant traits of paleotropical floral dominants (e.g.,  $G_{max}$ ,  $A_{max}$ ,  $c_i/c_a$ ) that, coupled with modelling, place constraints on the physiological functioning of late Paleozoic vegetation. Our findings reveal an ecophysiological perspective on these fossil plants that diverges from the conventional view of a low level of function based on their phylogenetic relationship to nearest living relatives. In turn, we utilize this new insight into their physiological functioning to develop an eccentricity-scale record of atmospheric  $CO_2$  for 16 million years of the Carboniferous—Permian, evaluate taxonomic differences in water-use efficiency and the potential for differential ecological competitiveness among late Paleozoic floral dominants, and to investigate the role that  $CO_2$  starvation may have played in the demise of the *Lepidodrendales* at the close of the Carboniferous.



### Using the constraints of function to understand form in early land plants

**S3.4** 

**KEVIN BOYCE** 

15:30-16:00

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Paleoecology is necessarily founded on modern ecology, but that presents a distinct challenge: the modern world is utterly dominated by one highly unique lineage, the flowering plants, that have only been around for a quarter of land plant history. Thus, even when differences in form and structure are expressly recognized in the fossil record, implicit assumptions based on modern angiosperm ecophysiology can lead to very misleading expectations about the Paleozoic origins of vascular plant vegetation. I will present arguments that productivity of non-flowering plants has always been consistently low relative to what is seen among modern flowering plants. The implications of low productivity will then put important constraints on the potential biology of Paleozoic fossil plants. With this context, the early evolution of plant architecture and ecology across the vascular plants will be broadly considered, along with a finer scale dissection of the biology of the Paleozoic arborescent lycopsids.

# Selected poster talks—Tuesday 26 July Session 3: Anatomy and physiology of early land plants — what can we learn from extinct species

16:00-16:30

16:00–16:15	ROBERT CAINE  Deep evolutionary conservation of genes involved with stomatal development	Poster No. P5
16:15–16:30	PETER FRANKS Stomatal control in the first land plants	P12



#### Unearthing the roots of mycorrhizal symbioses

**S3.5** 

16:30-17:00

FRANCIS MARTIN<sup>1</sup>, ANNEGRET KOHLER<sup>1</sup>, DAVID HIBBETT<sup>2</sup>, IGOR GRIGORIEV<sup>3</sup>, MYCORRHIZAL GENOMICS INITIATIVE CONSORTIUM

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The establishment of the mycorrhizal lifestyle represented a critical stage in the history of land plants. Soil-borne mutualistic fungi, such as the arbuscular mycorrhizal and ectomycorrhizal fungi, have helped shape plant communities through a mutualistic relationship with roots. During the diversification of Fungi and the rise of conifer and angiosperm-dominated forests, symbioses formed with ectomycorrhizal fungi have enabled trees to colonize boreal and temperate regions. The evolutionary success of these mutualistic symbioses is evident from the wide range of fungal clades that have established associations with trees and phylogenetic evidence that symbiosis has arisen in saprotrophs on several independent occasions. Recent genomic studies showed that ectomycorrhizal symbioses evolved from ecologically diverse decayer precursors inhabiting decomposing wood and forest litter and radiated in parallel, following the origins of their host-plant lineages. I will discuss the evolutionary histories of mycorrhizal symbioses that have been revealed, including the functions that have been lost by genome erosion and the genes that have been acquired to facilitate mutualistic interactions with host plants. Finally, I will consider how such an intersection of genomics and evolutionary biology can inform our understanding of the biological principles intrinsic to mycorrhizal symbiosis.



### The texture of plant evolutionary history: how iterative and unique 'events' shape biodiversity

**Keynote 3** 

#### **WILLIAM E. FRIEDMAN**

09:00-09:50

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The evolutionary origin of structurally complex terrestrial plants (embryophytes) appears to have been a unique event in the history of life on Earth. In contrast, many evolutionary transitions in the history of life have been highly iterative or homoplasious. In the case of photosynthetic eukaryotes, the origins of secondary plastids and the many origins of multicellularity and/or complex morphology stand out. Once embryophytes were established, the homoplasious origins of leaves (perhaps six or more times), roots (twice), and secondary growth by means of a vascular cambium (seven times) are striking. While many eukaryotic algal lineages are indeed terrestrial, it is clear that only the descendants of one of these clades became anatomically and morphologically complex. This certainly begs the question, why?

## Session 4: Refining biogeochemical models to take account of the role of plants and fungi

Chair: Chris Hawkesworth



Reconstructing changes in chemical weathering of the continents associated with the advent of early land plants

DEREK VANCE<sup>1</sup>, PHILIP POGGE VON STRANDMANN<sup>2</sup>

09:50-10.20

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There is general agreement that the colonization of the continents by plants led to fundamental changes in the long-term carbon cycle. For example, observations in modern environments have suggested that plants drive faster chemical weathering rates, and thus more rapid removal of CO<sub>2</sub> from the atmosphere and its eventual sequestration to carbonate rock in the ocean, both due to the production of organic acids and because they promote longer water-rock contact times in soils. There is debate, however, concerning both the magnitude of the potential chemical weathering rate response, and the extent to which it required large vascular plants with extensive and deep root systems, versus pre-vascular plants like bryophytes or even algae. Here we assess the extent to which records of Paleozoic ocean chemistry can contribute to this debate. Our understanding of how the pattern, rate and intensity of chemical weathering drive changes in marine chemistry has evolved substantially over the past decade. But any attempt to apply that understanding to the Paleozoic runs up against three principal problems. The first is diagenetic alteration of the carbonates used to build the records. The second is the multiplicity of processes that can act together to control any particular geochemical signal, a problem that is particularly relevant to radiogenic isotope systems like strontium. Finally, the records we currently have often lack the time resolution to answer the question at hand. For example, sparse measurements of the stable isotopes of lithium in marine carbonate suggest a fundamental shift in weathering intensity, culminating in oceanic Li stable isotope compositions close to those in the modern ocean, sometime between 400 and 300 Myr ago. These geochemical approaches, whose potential and caveats are reviewed here, will need to be pushed to higher resolution, but also require a multi-dimensional approach to address non-uniqueness in the controls on any one signal.

### Selected poster talks— Wednesday 27 July Refining biogeochemical models to take account of the role of plants and fungi

10:50-11:20

10:50-11:05	AISLING COOKE  Marchantia paleacea: a new model for arbuscular mycorrhizal symbiosis	Poster No. P8
11:05–11:20	KATIE FIELD Symbiotic options for the conquest of land	P11



### Challenges in process-based modelling of cryptogamic weathering

**S4.2** 

<u>LYLA TAYLOR</u> 11:20–11.50

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Department of Animal and Plant Sciences, University of Sheffield, UK

Weathering has profound implications for long-term global carbon cycling because the release of calcium and magnesium from silicate rocks on land, and subsequent deposition of carbonate rocks in the oceans, constrains the concentration of carbon dioxide in the atmosphere over multi-millionyear timescales. Vegetation enhances mineral weathering via mechanisms affecting the chemistry and movement of the soil solution, but not all of these mechanisms seem relevant for cryptogamic organisms which do not penetrate the substrate deeply. The linear dependence of weathering on the reactive surface area of the minerals being weathered suggests that organisms without roots were unlikely to have enhanced landscape-scale weathering to the same extent as deeply rooted vascular plants. This is the basis of the 'Devonian plant hypothesis' proposed by Thomas Algeo and his colleagues in the 1990s, whereby the appearance and spread of late Devonian trees such as Archaeopteris led to the Frasnian-Famennian mass extinction. It also underpins the weathering efficiency function in models of the long-term carbon cycle, and process-based models of plantenhanced weathering. The tacit assumption is that a landscape with a cryptogamic cover is tantamount to a bare landscape. However, the effect of cryptogamic covers as compared to preexisting biofilms or bare ground is difficult to elucidate. Several recent laboratory studies show that poikilohydric plants with or without symbiotic fungi can weather minerals, as can fungi associated with lichens, but the effects of these diverse organisms on weathering in the field today is a subject of debate. Any process-based model of weathering would require parameters describing the regolith as well as the climate and vegetation. What was the state of the Ordovician regolith, and how did the interplay of regolith, climate and vegetation change with time and space?



# Colonization of the terrestrial environment *in silico*ANDY RIDGWELL<sup>1, 2</sup>, TARAKA DAVIES-BARNARD<sup>1</sup>, PAUL 11:20–11.50

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<sup>1</sup>School of Geographical Sciences, University of Bristol, Bristol, UK; <sup>2</sup>Department of Earth Sciences, University of California – Riverside, Riverside, CA, USA; <sup>3</sup>Jet Propulsion Laboratory, Pasadena, CA, USA

The weathering of silicate rocks, and by inference, the efficiency by which atmospheric pCO<sub>2</sub> and climate is regulated via this negative feedback, is purported to be a strong function of primary production on land. The productivity of terrestrial ecosystems, in turn, is a function of its climatic (e.g. pCO<sub>2</sub>, temperature, and precipitation) and physical (e.g. latitude, topography) environment. Moreover, for a given set of environmental conditions, plant productivity is not static through time but will reflect evolutionary transitions and extinctions from the earliest colonisation of land through to the on-going disruption that is the Anthropocene. How can we best assess the importance of some of these non-stationary factors and hence estimate the strength of the silicate weathering feedback in the past? Current (CMIP5 era) models of the terrestrial environment tended to be tightly rooted in a modern-centric view of the Earth system and based on a relatively small set of plant functional types (PFTs) – chosen to reproduce the primary features of observed vegetation distributions. The inherent limitations of such models for geological questions where the boundary conditions and species existing can be very different has thus prompted us to explore the potential for trait (/functional) trade-off based ecosystem models for generating scenarios of past vegetation distributions and primary productivity.

In this talk I'll outline the problem (understanding the terrestrial ecology of the geological past and implications for weathering), summarize the pros and cons of the numerical tools available to us (both traditional PFT and functional trade-off approaches), and present some fun and illustrative preliminary results.

### **Poster Abstracts**

P=poster abstract. Bold=presenting author

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### **Poster Abstracts**

Poster abstracts are ordered alphabetically by presenting author (underlined).

P1 Comparison between an indigenous arbuscular mycorrhizal consortium and a commercial inoculum resistance as affected by vinasse application to soil

<u>V. ARENAS-MONTAÑO</u><sup>2</sup>, D. A. TUESTA-POPOLIZIO<sup>2</sup>, L. V. HERNÁNDEZ-CUEVAS<sup>3</sup>, E. E. QUIÑONES-AGUILAR<sup>2</sup>, G. DÁVILA-VÁZQUEZ<sup>1</sup>, S. M. CONTRERAS-RAMOS<sup>1</sup>

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Arbuscular mycorrhizal fungi found in a field irrigated with vinasse might be adapted to this disturbed environment. Vinasse is a residue generated from alcohol production from sugarcane, beet, agave (for tequila production), among others, with high organic matter (2.2–3.9%) and cation concentration (6.3 ± 0.13 mg/L) and acid pH (3.5 to 4.2). A greenhouse experiment was conducted for three months to evaluate the resistance of an indigenous consortium (NC: *Claroideoglomus etunicatum, Funneliformis geosporum* and *F. mosseae*) compared to a commercial inoculum (CI: *Glomus intraradices*) in symbiosis with *Zea mays* to two acid pH levels (3.5 and 4.5) and two tequila vinasse concentrations (30% and 60%) using water as control. Spore density, colonization percentage and intensity, soil pH, electrical conductivity (EC), and plant growth were evaluated. The vinasse application promoted an increase in soil pH and EC which were negatively correlated with spore density and plant height. Plants inoculated with NC grew significantly more than with CI, mainly at 60% vinasse treatment. NC spore density was less affected by vinasse amendments than CI. The indigenous consortium was more resistant and provided more benefits to maize plants when it was subjected to stress conditions than the commercial inoculum.

### Plastid-genome evolution in an 'early' moss lineage, *Buxbaumia* (Buxbaumiaceae)

#### D. BELL, W. GERELLE, Q. LIN, V.K.Y. LAM, Y. CHANG, S.W. GRAHAM

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The small genus *Buxbaumia* (Buxbaumiaceae) is the sister group of the rest of Bryopsida, which is by far the largest class of bryophytes. It is also notable as one of few putatively mycoheterotrophic bryophytes. Mycoheterotrophic plants obtain some or all of their nutrition from fungal partners (partial mycoheterotrophs are photosynthetic; full mycoheterotrophs are non-photosynthetic). *Buxbaumia* is chlorophyllous, but like other mosses appears to be non-mycorrhizal. We discovered during a plastid genome survey of mosses that *Buxbaumia aphylla* has reading frame interuptions in at least one plastid NAD(P)H dehydrogenase (*ndh*) subunit gene, and characterize this further using a transcriptome available for this species through the 1KP project. This possible loss is intriguing, as the NAD(P)H dehydrogenase complex has consistently been lost in partially or fully mycoheterotrophic plants. We incorporate the plastid genome of *Buxbaumia* in a backbone phylogeny that includes a broader range of bryophyte species, compare its plastid genome to relatives for evidence of structural change, and test for shifts in selective regime in its uninterrupted plastid genes.

### Global biogeography of the bipolar moss *Polytrichum juniperinum* reveals origin in Antarctic region

#### E. M. BIERSMA, J. JACKSON, K. LINSE, H. GRIFFITHS, P. CONVEY

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Bipolar distributions are frequently encountered in bryophytes, even being the most common distribution pattern (~45% of species) in Antarctic bryophytes, the dominant flora on the continent. However, the origin, timing and underlying mechanisms (ancient vicariance, long distance or 'stepping stone' dispersal) of inter-hemispheric distributions are not well understood. Here, using the nuclear Internal Transcribed Spacer (ITS) and the plastid trnL-F region combined with population genetic and molecular dating methods, we examine past dispersal patterns and timings of inter-hemispheric movements in the moss Polytrichum juniperinum. The analyses suggest that P. juniperinum originated in the Antarctic region (Antarctic, sub-Antarctic and southern South America). From the Antarctic region it dispersed into Australasia (twice), South Africa and low latitude regions in South America, as well as the entire Holarctic region. Subsequently, a separate trans-equatorial dispersal event occurred from the Holarctic back to the Antarctic region. This study suggests long-distance dispersal is the main driver of the inter-hemispheric disjunction in P. juniperinum. All arrivals to the Antarctic region were well before the Last Glacial Maximum, suggesting that, despite the harsh climate during past glacial maxima, plants have had a much longer presence in the region than assumed.

### P4 Functional PTB phosphate transporters are present in streptophyte algae and early diverging land plant

<u>C. BONNOT</u>, H. PROUST, B. PINSON, F. COLBALCHINI, A. LESLY-VEILLARD, G. MORIERI, B. BREUNINGER, C. CHAMPION, A. J. HETHERINGTON, S. KELLY, L. DOLAN

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Plants absorb inorganic phosphate (Pi) through Pi-transporters located in the plasma membrane of cells at the interface between the plant and the external environment. PHOSPHATE TRANSPORTER 1 (PHT1) proteins are H+/Pi-symporter responsible for Pi-uptake from the environment in angiosperms. PHT1 sequences are present in early diverging land plant and streptophyte algae suggesting that PHT1 proteins function in these taxa. However, Pi-uptake requires sodium (Na+)influx in streptophyte algae suggesting that Na+/Pi-symporters are involved in Pi-uptake in some streptophytes. In chlorophytes algae, PHOSPHATE TRANSPORTER B (PTB) proteins have been hypothesised to be Na+/Pi-symporters responsible for Pi-uptake. Our work shows that PTB transporters are present in streptophytes. The higher steady state levels of mRNAs of most PTB genes of the early diverging land plant M. polymorpha and streptophyte algae C. nitellarum in low-Pi than in replete-Pi growth conditions support the role of streptophyte PTB proteins in Pi-uptake. Expression of three PTB proteins of the early diverging land plant M. polymorpha in the Saccharomyces cerevisiae pho2 mutant, defective in high-affinity Pi-transport, rescues growth in low-Pi environments confirming their Pi-transport function. These data suggests that two Pitransport mechanisms – mediated by PTB and PHT1 proteins – operate in parallel in streptophyte algae and early diverging land plants.

### P5 Deep evolutionary conservation of genes involved with stomatal development

R. S. CAINE<sup>1‡</sup>, C. C. CHATER<sup>2‡</sup>, Y. KAMISUGI<sup>3</sup>, A. CUMING<sup>3</sup>, M. TOMEK<sup>4</sup>, D. LANG<sup>4</sup>, R. RESKI<sup>5</sup>, A. FLEMING<sup>6</sup>, J. E. GRAY<sup>1</sup>, D. J. BEERLING<sup>6</sup>

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Stomata are ancient structures that together with other adaptations have assisted land plants in colonising the earth. Normally consisting of two microscopic guard cells that surround a central pore stomata are often associated with the uptake of CO<sub>2</sub> and the release of H<sub>2</sub>O. Whilst much is known about how these structures develop in vascular land plants, in non-vascular land plants little is known and it is unclear whether stomatal developmental mechanisms are conserved between these anciently diverging groups of land plants. Using the model organism and moss *Physcomitrella patens* we illustrate that keys genes involved in stomatal development and patterning are conserved in an extant non-vascular land plant representative. Such genes include key stomatal development bHLH transcription factors orthologues of Arabidopsis *SPEECHLESS* (*SPCH*), *MUTE* and *FAMA* and *ICE1/SCREAM* (*SCRM*) and *SCRM2*. Furthermore, we also show that key stomatal patterning orthologues of Arabidopsis *EPF1* and *TMM* are also retained and utilised by *P. patens* to correctly space stomata. Taken together our findings imply that a genetic module of genes and associated proteins has been conserved in land plants since prior to the divergence of the mosses from the ancestral land plant lineage around 450 million years ago.

### P6 Rhizoid-like structures in green filamentous alga – a possible adaptation to the terrestrial environment

#### L. CAISOVA

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Algae are one of the most diverse forms of life on Earth. Despite the fact that they do not dominate land ecosystems, several algal lineages adapted for successful survival in the terrestrial environment. Here, I report about the semi-terrestrial green alga (*Draparnaldia* sp., Chaetophorales, Chlorophyceae) that forms, in addition to upright green filaments, structures that morphologically resemble rhizoids of moss. Since a formation of such rhizoid-like structures is a rare event across green algae, I studied this phenomenon in more detail. I found that: (1) These 'rhizoids' are multicellular, often branched, and show apical growth. However, in contrast to moss rhizoids, they do still contain remnants of a chloroplast. (2) In liquid medium, 'rhizoids' grow down and anchor the alga to the substrate. On solid medium (liquid phase absent), 'rhizoids' grow towards the light and their chloroplasts get enlarged. Whether they can give rise to new upright green filaments needs to be investigated. In conclusion, my current findings indicate that 'rhizoids' show two different modes of behaviour depending on the environment where the alga grows. Further investigation of their function(s) and molecular origin can provide new insights into evolutionary processes that have shaped adaptations (and colonization) of earliest photosynthetic organisms to the terrestrial habitat.

### Phylogenomic analyses suggest early origins of major fungal clades and independent diversifications to break down cellulose-rich cell walls

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The vast majority of extant fungi are closely associated with plants or plant material. However, little is known regarding the origin and evolution of this association. We approached these questions by studying the evolutionary patterns of plant-cell-wall-degrading enzymes (PCWDE) across the Kingdom Fungi. We sampled whole genome data from 352 taxa (338 fungi, 14 outgroups). We reconstructed a phylogeny and performed dating analysis based on 434 singlecopy proteins. We examined the distribution of 36 PWCDE families across all sampled taxa. We reconstructed gene genealogy for each enzyme family and reconciled with the species phylogeny to investigate the evolutionary patterns of these enzymes. Our results resolved the common ancestors to the phyla of fungi as being older than land plants and that many fungal PCWDE families also have an ancient origin that predates the origin of land plants. We identified multiple, independent episodes of diversification of PCWDE associated with the origins of several higher fungal taxa. The timing of and the fungal taxa involved in these diversification events suggest that major fungal clades were present in terrestrial environments prior to land plants and that they interacted with early terrestrial life forms that contained cellulose-rich cell walls (e.g., streptophytes, microbial mats).

### Marchantia paleacea: a new model for arbuscular mycorrhizal symbiosis

#### AISLING COOKE, GURU RADHAKRISHNAN, PIERRE-MARC DELAUX, GILES OLDROYD

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The majority of land plants form arbuscular mycorrhizal (AM) symbioses with soil fungi, including the earliest diverging and most primitive clade, the liverworts. The emerging model liverwort, *Marchantia polymorpha*, does not form AM symbioses, but a closely related species, *Marchantia paleacea* is readily colonized and forms a functional AM symbiosis.

*M. paleacea* has a simple genome structure, is easily propagated and can be transformed rapidly, in contrast with existing symbiosis models such as model legumes and cereal crops. It also shares several characteristics with the earliest land plants, such as a gametophyte dominant life cycle, unicellular rooting structures and lack of true vasculature. This makes this species ideal for studying the molecular mechanisms of AM symbiosis in land plants generally, and in primitive land plants particularly.

Phylogenetic studies indicate that the *M. paleacea* genome contains homologues of many genes known to be involved in arbuscule development and fungal infection. In some cases, direct gene homologues do not exist but gene expression studies indicate that paralogous genes perform a similar function.

### P9 Early land plants and their resilience to future dry conditions

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The origin of stress-related genes is crucial for clarifying our understanding of the early adaption of plants to different terrestrial environments. Here I report on a project to characterize the transcriptomes of 10 representative early land plants (bryophytes). Our main goal is to measure transcriptional responses to major in situ stressors, to provide a comparative framework for studying the evolution of stress-related genes in early land plants. Stressful situations will be generated by using experimental translocations. We will compile transcriptome data under these conditions for the (vegetative) gametophyte stage of five liverworts: Asterella africana (Aytoniaceae), Exormotheca pustulosa (Exormothecaceae), Saccogyna viticulosa (Geocalycaceae), Plagiochila maderensis (Plagiochilaceae) and Porella canariensis (Porellaceae); three mosses: Echinodium spinosum (Echinodiaceae), Isothecium prolixum (Lembophyllaceae), and Homalia lusitanica (Neckeraceae); and two hornworts: Anthoceros caucasicus (Anthocerotaceae) and Phymatoceros bulbiculosus (Phymatocerotaceae). These species are all threatened in Portugal and are expected to suffer from the negative effects of future climate change in this region. They therefore provide phylogenomic case studies for predicting stress responses in other early land-plant lineages. Such predictions are essential for developing conservation actions, and may give insights into understanding the general mechanisms associated with stress responses in situ, including desiccation tolerance. Our long-term goal is to identify whether these are core stress-response toolkits in early land plants, providing novel phylogenomic resources for studying bryophyte ecology, behaviour and bryophyte evolutionary diversification.

**P10** 

Dual reconstruction of paleoecology and whole-plant habit using stable carbon isotopes from dispersed leaves of *Laurozamites powellii*, an Upper Triassic bennettitalean

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Stable carbon isotopes are a powerful tool for examining ecological processes across landscapes and time. Isotopic fractionation of atmospheric carbon into plant tissue occurs during photosynthesis, and the magnitude of the  $\delta^{13}C$  difference is related to variation of photosynthetic rates. As available light in forest canopies decreases, so too does photosynthetic rate and  $\delta^{13}C_{leaf}$ ; the so-called canopy effect. We apply the canopy effect to interpret the paleoecology and habit of the bennettitalean Laurozamites powellii, based on abundant and well-preserved leaves collected from Upper Triassic strata near Fort Wingate, NM, USA. Leveraging the mean and variance of  $\delta^{13}C_{leaf}$  measurements at different canopy heights from modern forests, evidence from fossil  $\delta^{13}C_{leaf}$  suggests an open canopy with strong, homogeneous sunlight conditions. Measurements of leaf physiognomy and epidermal cell shape, indicative of positional changes within a crown, covary with  $\delta^{13}C$ , suggestive of a divaricate habit. The application of empirical observations of changing light conditions and its effect on  $\delta^{13}C$  and morphology from modern systems to the fossil record demonstrates the potential of this approach for paleoecological reconstructions in deep time, and may provide significant insight into the evolution of terrestrial ecosystems.

## P11 Symbiotic options for the conquest of land

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The colonisation of Earth's continental land masses by plants >475 Ma marked a turning point in the development of the terrestrial biosphere, with widespread consequences for the future of terrestrial life. It has long been hypothesised that the terrestrialisation of plants was facilitated by nutritional symbioses with Glomeromycota fungi to form arbuscular mycorrhiza-like associations. The establishment of this symbiosis would likely have enhanced access to mineral nutrients for early, rootless plants in exchange for carbon fixed through photosynthesis. Our recent discoveries that the earliest diverging clade of land plants (Haplomitriopsida liverworts) forms mutualistic symbioses with partially saprotrophic Mucoromycotina fungi challenge this long-standing paradigm. Using a combination of microscopic, molecular and isotope tracer techniques, we have shown that other lineages of early-diverging liverworts form simultaneous mutualistic associations with both Glomeromycota and Mucoromycotina fungi. Together with recent fossil evidence, these findings bring into question the identity, biology and functioning of the fungal symbionts of the earliest land plants. Here, we suggest that there were symbiotic options available to the earliest land plants and that such relationships may have been far more varied and transient than hitherto assumed.

## P12 Stomatal control in the first land plants

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Considerable debate has emerged on whether stomata of the first land plants and all non-seed plants lack key active (metabolically-driven) stomatal responses to atmospheric  $CO_2$  concentration and water stress. One hypothesis posits that stomata of the first land plants were little more than passive hydraulic valves and persisted in this limited functional form until the emergence of seed plants. It further posits that the subsequent evolution of seed plants brought monumental advances in stomatal function, including the gain of stomatal sensitivity to elevated  $CO_2$  and, crucially, active response to water stress. If this hypothesis withstands testing it will reshape molecular, physiological and evolutionary models of stomatal function and their application at multiple scales. Here I present new data showing active stomatal responses to  $CO_2$  and the water stress hormone abscisic acid in non-seed plants. The results, combined with molecular evidence, form the basis of a proposed universal model of stomatal control in land plants and its evolution. In this model all of the core active and passive stomatal control elements were present in some form in the common ancestor of stomata-bearing land plants, and were conserved through more than 410 million years of stomatal evolution.

## P13 Unique cellular organisation in the oldest root meristem

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Roots and shoots of plants develop from meristems – cell populations that self-renew and produce cells that undergo differentiation. We report the discovery of the first fossilized remains of an actively growing root meristem from permineralised Carboniferous soil with detail of the stem cells and differentiating cells preserved. The cellular organisation of the meristem is unique. The position of the Körper–Kappe boundary, discrete root cap and presence of anticlinal cell divisions within a broad promeristem distinguish it from all other known root meristems. This indicates that the same general cellular dynamics are conserved between the oldest extinct and extant root meristems. However, its unique cellular organisation demonstrates that extant root meristem organisation and development represent a subset of the diversity that has existed since roots evolved.

## P14 Three key sub-leaf modules and the diversity of woody angiosperms

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Earth harbors a dazzlingly diversity of leaf designs. These diverse leaf types seem to fall into two modes of global distribution: 1) contrasting leaves run across different functional groups and different biomes, forming a leaf economics spectrum; 2) numerous leaves with similar leaf economics traits concentrate within the same functional group or habitat, forming 'trait hotspots'. Leaf economics spectrum is valuable for explaining vastly different leaf designs at larger scale, yet the mechanisms underlying 'trait hotspots' remain unknown. Here, we propose a 'modularized leaf design' perspective to explain 'trait hotspots' or the coexistence of woody angiosperm leaves with similar economics traits but potential differences in other leaf trait dimensions in species-rich communities. We show that woody angiosperm leaves have at least three key sub-leaf modules: light capture module near the upper surface, gas exchange module at the bottom, and waternutrient flow module in the middle, with each module contributing to a trait dimension relatively independent of leaf economics axis. Different combinations of these trait dimensions thus allow for the trait 'hotspots' in species-rich communities and deciphering these traits combinations should offer critical insights into the evolutionary trajectories of diverse leaf structures and functioning worldwide.

# P15 Arbuscular mycorrhizal community composition across 21 potato cultivars from a conventionally managed field

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The rapidly increasing global food demand leads to higher usage of synthetic fertilizers and pesticides. Potato (*Solanum tuberosum* L.) as one of the largest food crops in the world has one of the heaviest demands for fertilizers of all vegetable crops. Therefore, there is an urgent need to find novel approaches to sustainably increase agricultural productivity. Arbuscular mycorrhizal fungi (AMF) might be the key component of sustainable crop production. Although AMF are holding a wide host range, some AMF—plant host combinations are more preferred than others. The aim of current study was to get new knowledge about AMF—plant genotype incompatibility. In total 315 soil and root samples were collected in the year 2014 from field experiment site in Reola, Estonia. AM fungal community composition was assessed by using Illumina MISeq sequencing of ITS region. Results showed that the richness of arbuscular mycorrhizal fungi varies throughout the growing season. Comparing the community composition between potato cultivars was found that roots of different cultivars were colonized by relatively different communities of Glomeromycota. Thus, our study demonstrates that the community composition and richness of arbuscular mycorrhizal fungi was affected by cultivar, and as well as plant growth stage.

### **P16** Did a blind watchmaker construct the first stomata?

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Stomata are the gateway for terrestrial gas exchange with the atmosphere and are critical to the survival of land plants. Currently, debate rages as to how the stomata of different land plant groups respond to environmental signals and how these responses are controlled at a molecular level. Evidence suggests two incompatible hypotheses either that stomatal behaviour has been exposed to significant selective pressure and evolution over time or none at all. While this debate remains unresolved, the primary goal of stomatal physiologists and modellers of land plant behaviour is the ability to accurately predict plant responses to the environment. Using multiple, independent methods I show that functional atmospheric gas exchange is highly predictable based on the knowledge of the land plant clade. Under both controlled and field settings the gas exchange responses of the major vascular plant clades: lycophytes, ferns, conifers and angiosperms, can all be effectively and accurately modelled. These results indicate huge functional shifts in plant behaviour and gas exchange across land plant lineages that may account for the increased success and competiveness of progressive clades through time. Further understanding of these major evolutionary differences in functional gas exchange both between and within land plant lineages provides an exciting opportunity to further explore ecological adaptation and competition in the present and over geological time.

# P17 The genetic control of sex determination in ferns and the origin of abscisic acid signalling in land plants

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Gametophytes of ferns develop either as males or hermaphrodites under the control of phytohormones. Antheridiogen (an analogue of gibberellin) promotes the development of male gametophytes while abscisic acid (ABA) blocks this response. Single-gene mutants insensitive to ABA as gametophytes have been described in the model fern species *Ceratopteris richardii*. Using a candidate gene approach and recently developed expressed sequence database for *Ceratopteris* we aimed to molecularly characterise these mutants. In three allelic mutants we identified significant null mutations in a *Ceratopteris* homologue of the core ABA signalling gene *Open Stomata 1 (OST1)*. We found that functional ABA signalling through OST1, plays a central role in regulating the sex determination of fern gametophytes, as well as the maintenance of spore dormancy; yet appears to play no role in the development of the fern sporophyte or stomatal function. Our results indicate that ABA signalling first evolved to regulate sex determination then transitioned to control transpiration in the earliest seed plants. Given the importance of the fern gametophyte to the reproductive, ecological and evolutionary success of this lineage, our study highlights the significant role ABA signalling has played in the colonisation of land by plants.

## P18 Modelling early fungal symbioses and climate instability in the Paleozoic

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Since plants first colonised land, the terrestrial biosphere has amplified global weathering fluxes indirectly through nutrient extraction. This biological mediation of chemical cycling creates a stabilizing mechanism that buffers against changes in atmospheric CO<sub>2</sub> and global surface temperature. But the existence of these strong stabilizing feedbacks require that environmental stresses on the land biosphere directly limit its effect on chemical weathering. Recent investigations into fungal symbioses of early diverging lineages of plants have revealed greater complexity in terms of fungal diversity and functioning than previously thought. This is particularly pertinent in the case of liverwort symbioses with partially saprotrophic Mucoromycotina fungi, showing no reduction in nutrient uptake under lower CO<sub>2</sub> concentrations despite reduced host photosynthate supply. These findings contrast with liverwort–Glomeromycota symbiotic functioning.

Here, we construct an idealised Paleozoic terrestrial biosphere with Mucromycotina symbioses within a simple Earth system model. This biosphere shows significantly less buffering capacity against low atmospheric CO<sub>2</sub> and global temperature than a comparative Mesozoic land biosphere dominated by angiosperms with obligately biotrophic fungal partners (Glomeromycota). We propose that evidence for multiple glacial 'icehouse' climate periods in the Paleozoic, as opposed to the comparatively warm Mesozoic, points to a terrestrial biosphere with less ability to regulate climate.

## P19 Visualization of sieve tube function in Brown Algae: evolutionary implications

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Kelps (Laminariales, Phaeophyceae) possess sieve tubes that are evolutionarily unrelated but structurally similar to the tubes in the phloem of vascular plants. Comparative functional studies therefore can help to identify biophysical principles that governed the evolution of vascular land plants. In fully functional, intact Bull Kelp (*Nereocystis luetkeana*), we were able to (i) directly visualize sieve tube transport, (ii) determine transport velocity in individual tubes, (iii) demonstrate the pressure-induced reversal of flow direction across sieve plates, and (iv) characterize a unique, reversible wall-swelling reaction involved in the response of the sieve tube network to wounding. While (i) to (iii) provide strong direct support for Münch-flow as the mechanism of translocation in kelp sieve tubes, (iv) calls for a re-evaluation of published anatomical data and questions the validity of current ideas about the development of individual tubes. Most importantly, the comparison of kelp and angiosperm sieve tubes allows the distinction of structural features that are necessary and sufficient to enable Münch-type long-distance transport, from non-essential features that represent peculiarities of specific clades. Examples will be discussed.

## P20 Size is not everything: rates of genome size evolution, not *C*-value, correlate with speciation in Angiosperms

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Angiosperms represent one of the key examples of evolutionary success, and their diversity dwarfs other land plants; this success has been linked, in part, to genome size and phenomena such as whole genome duplication events. However, while angiosperms exhibit a remarkable breadth of genome size, evidence linking overall genome size to diversity is equivocal, at best. Here, we show that the rates of speciation and genome size evolution are tightly correlated across land plants, and angiosperms show the highest rates for both, whereas very slow rates are seen in their comparatively species-poor sister group, the gymnosperms. No evidence is found linking overall genome size and rates of speciation. Within angiosperms, both the monocots and eudicots show the highest rates of speciation and genome size evolution, and these data suggest a potential explanation for the megadiversity of angiosperms. It is difficult to associate high rates of diversification with different types of polyploidy, but it is likely that high rates of evolution correlate with a smaller genome size after genome duplications. The diversity of angiosperms may, in part, be due to an ability to increase evolvability by benefiting from whole genome duplications, transposable elements and general genome plasticity.

## P21 Symbiosis signalling in early land plants

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Bryophytes, the earliest known extant land plants, are among the many plant species that are able to host Arbuscular Mycorrhizal (AM) fungi. The sequencing of the *Marchantia polymorpha* genome and the recently developed genetic tools makes this liverwort an emerging model plant. But as *M. polymorpha* does not form AM symbiosis, we sequenced the genome of *Marchantia paleacea* to look for symbiosis signalling genes. Although symbiosis orthologs from bryophytes have been used to complement mutants in their *Medicago truncatula* counterparts, an extensive survey of symbiosis genes has not been carried out in a bryophyte.

Through phylogenetics, we found that for most symbiosis signalling genes, orthologs exist both in *M. polymorpha* and *M. paleacea*. A few genes did not have orthologs in *M. polymorpha* but did so in *M. paleacea*. The loss of these genes could explain why *M. polymorpha* does not form AM symbiosis, while *M. paleacea* does. Although AM symbiosis occurs in different tissues in bryophytes and higher plants, the presence of orthologs of the SYM pathway suggests that these genes might function in similar ways across all plants.

## P22 Changing views on the origins of plant–fungal symbiosis

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The liverworts are phylogenetically the most ancient of the extant land plants and therefore their fungal symbioses represent the best modern homologs of the first symbiosis to form between plants and fungi. It is now believed that symbiosis with arbuscular mycorrhizal fungi (Glomeromycota) may have been predated by a symbiosis with Mucoromycotina fungi which are known to enter into an intimate mutualism with Haplomitriopsida (the earliest branching liverworts). Recently, Glomeromycota and Mucoromycotina have been discovered to enter into a dual symbiosis in one complex and one simple thalloid liverwort. Simultaneous colonisation by both fungal lineages is proportionally more beneficial than being colonised by only one. To test how widespread throughout the liverworts are Mucoromycotina and dual colonisation we analysed over 750 globally-collected complex and simple thalloid liverworts. We found that diverse Mucoromycotina fungi occur throughout the complex and simple thalloid liverworts and the majority of liverwort species were able to associate with Glomeromycota or Mucoromycotina and in many cases both. The presence of Mucoromycotina throughout the early-branching liverworts supports the notion of this symbiosis forming very early during land plant evolution and reveals the hitherto unrecognized significance of present day Mucoromycotina—plant symbioses worldwide.

# P23 Unexpected environmental conditions: suggest Paleozoic plant morphological gas conductance models

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The importance of plants in regulating Earth's greenhouse gases has been debated. We address the relationship between the morphological and physiological response of extant Lycophytes to changing oxygen concentration, affecting atmospheric pressures, changing plant carbon and water balance. At atmospheric pressures of ~5kPa over current conditions *Huperzia lucidula* was found to change leaf shape – significantly increasing in length to width ratio, markedly decreasing in stomatal density, but increasing in stomatal index. Gas conductance models demonstrate that paleo-plant stomatal indices are by themselves not accurate measures of atmospheric gas dynamics, as the closely related *Selaginella kraussiana* was found to have a different sensitivity to morphological traits. Consequently, we have characterized the effects of a possible 307Mya Carboniferous 30%O<sub>2</sub> & 118kPa atmosphere in increasing stomatal density, internal CO<sub>2</sub>, PLUE, and WUE, while decreasing the overall ETR. We suggest *H. lucidula* as an early vascular plant model, the reexamination of geological atmospheric conditions as paleo-plant gas exchange can be influenced by atmospheric conditions other than carbon dioxide composition. This data provides evidence for Middle–Late Carboniferous transitional climate conditions and the influence of hyperbaric induced increases in plant primary productivity at the expense of reduced plant water loss.

## Molecular diversity of fungal communities in conventional arable soil

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Population growth and changing consumption habits have led to an intensification of arable land, which is evidently a threat to biodiversity. Simplification of farming systems along with continuous monocropping, have caused a decline in many species. Plausibly also changes have occurred in the regulation of root exudates, which affects both biologically and biochemically soil microbial communities. To maintain species richness and diversity even at small scales farming systems including the right choice of crop varieties that maintain or even enhance diverse microbial community should be preferred. Therefore, in 2014 soil samples were collected three times during the growing season from plants of 21 different potato varieties grown in a conventionally treated soil. The field site was located in Reola, Estonia. Fungal community composition was assessed by using Illumina MiSeq sequencing of ITS region. Soil fungal richness was the lowest in midseason. During that time the agricultural treatment is most intensive. At the end of the growing season soil, fungal community demonstrated a rapid recovery. Potato variety, on the other hand, didn't exhibit any considerable effect on soil fungal community. The results suggest that fungi are resilient organisms, who are capable of restoring their community even after a severe disturbance.

## P25 Fungal interactions in early fossil freshwater environments

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Sometime at the beginning of the Palaeozoic (ca 500Ma) the nature of terrestrial ecosystems changed radically with the evolution of embryophytes (land plants). These changes occurred in the context of developing interactions with other eukaryotes, among them Fungi. Molecular phylogenies are converging on an origin of Fungi in freshwater environments involving partnerships with algae and animals. One unique early fossil site where organims are preserved together under exceptional conditions – the 407 million year old Rhynie Chert (Scotland) – enables further testing and exploration of this hypothesis. Association between the freshwater alga *Palaeonitella* and parasitic chytrids are already known. Here we report a new association between Chytridiomycota and freshwater organisms likely of animal affinity. We used Confocal Laser Scanning Microscopy, a technique that is proving to be a powerful tool for 3-D documentation of fossil Fungi. The new Chytridiomycota closely resembles living species in the Rhizophydiales. It forms probable parasitic associations with possible animal remains, playing a mycoloop role as in modern systems (i.e., releasing otherwise locked up nutrients to the food web). Our results add to knowledge of fungal interactions in early freshwater environments, which seem to be predominantly parasitic.

# P26 Stomatal immunity involves guard cell type-specific and non-autonomous signalling events

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Stomatal closure is a mechanism by which pathogen infection is prevented. The guard cells forming the stomatal pore perceive bacterial flagellin (flg22) and EF-Tu (elf18), and this induces the closure of stomata. Stomatal regulation to abiotic stresses is well studied, but we know little about guard cell signalling that is activated through pathogen perception. We show that flg22-induced stomatal closure is independent of both ABA biosynthesis and ABA receptors but requires the guard cell-specific OST1 kinase. This suggests that flg22-induced guard cell signalling converges with the central stomatal response pathway to activate stomatal immunity. To investigate the role of cell-autonomous signalling events, we expressed or silenced the cognate receptors for flg22 and elf18 in a guard cell-specific manner. Flg22-induced stomatal closure was impaired when MAMP perception or ROS production was restricted to guard cells. Limiting the leaf expression of EF-Tu RECEPTOR (EFR) from guard cells showed that stomata closed normally in response to elf18 trigger. Silencing the reactive oxygen species producing NADPH oxidase in guard cells did not affect elf18-induced stomatal closure. Our data reveal that aspects of stomatal immunity involve guard cell-specific signalling components as well as non-symplastic cell-to-cell signalling events.

# Phosphatidylinositol 4-kinase regulates cell fate establishment in earliest stage gametophyte development in the liverwort *Marchatia polymorpha*

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The colonization of land by plants was accompanied by the development of increasingly complex bodies. This required establishment of cell lineages with different cell fates, which is often associated with an asymmetric cell division. Here we describe the development of the *Marchantia polymorpha* gametophyte from a spore. The first cell division is asymmetric, forming an apical cell that divides to generate photosynthetic cells and a smaller basal cell, which doesn't divide, and differentiates as a tip-growing rhizoid. We isolated T-DNA insertion mutants with defective rhizoid differentiation that are mutated in the gene encoding *PHOSPHATIDYLINOSITOL 4-KINASEa1* (*PI4Ka1*). We found that the basal cell frequently undergoes additional cell divisions in Mppi4ka1 mutants or in wild type treated with a PI4K inhibitor. This suggests that MpPI4K activity is required for repression of cell division in the basal cell. PI4Ka is an enzyme that catalyzes the production of a signaling phospholipid called phosphatidylinositol 4-phosphate (PI4P), which is important for formation and identity of membrane domains. Based on treatment with inhibitor at different times during development, we propose that PI4K activity regulates the cell fate establishment of the basal cell before and/or during the asymmetric cell division possibly by affecting cell membrane polarity.

# P28 Evaluation of vinasses' usage as fertilizer on maize crop growth and arbuscular mycorrhizal fungi (AMF) from soil

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Vinasses are wastewaters from spirits or alcohol production, and usually are disposed of into soil as fertilizers. However little is known regarding growth of crops and their association with AMF from soil when vinasses are amended. An experiment was established in a greenhouse with maize plants to evaluate the weekly irrigation with three different concentrations of tequila vinasses (V-25%, V-50% and V-75%), water (W), without (-F) and with (+F) fertilizer at 150 kg ha<sup>-1</sup>. The growth of plants was recorded with height, chlorophyll index, fluorescence rate (F690/F740), number of leaves and leaf area every month during 3 months. Biomass, AMF colonization and number of spores was determined at the end. The height of plants with vinasses irrigation +F or –F was not significantly different compared with W treatment, although with +F was taller than –F. The same behavior was observed in the other parameters, however a reduction was observed after 2 months. The biomass in V-50%+F and V-75%+F was significantly lower than W or V-25%+F treatments. The colonization and the number of spores did not show significant differences. Results suggested that the use of vinasses as fertilizer in maize crop had not negative effect in plant and AMF.

### **P29**

## The decision to germinate in spores and seeds is regulated by divergent networks with ancient conserved nodes

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Plants first colonised the land almost half a billion years ago. In a relatively short space of time they inhabited ecological niches across the globe. How were the first plants able to 'move' and distribute themselves, whilst evolving into new species?

Spores were key to early-evolving land plant distribution as they establish a new plant at a greater distance from the parent plant than vegetative growth alone, and also enable variation, being the products of meiosis. In later-evolving plants, the functionally equivalent 'dispersal units' are seeds. We have defined the signals and genes that regulate how quickly a spore germinates, using the model moss *Physcomitrella patens*. We show that moss spores, unlike seeds, do not show primary dormancy, but that germination-competent spores can have secondary dormancy imposed by environmental signals. We suggest that a completely novel hormone-signalling network mediates environmental responses in spores, which is not conserved in seeds. We show that conserved 'nodes' exist within the germination-regulatory network, as ancient proteins regulate responses to abscisic acid (ABA) in both spores and seeds.

Our research raises key questions about the signaling networks that regulate responses to the environment in spores, and hence control early-diverging species' spread and survival.

### **P30**

#### SEC6 subunit of the exocyst complex in moss

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Octameric exocyst complex is an evolutionary conserved tethering factor and effector of Rho and Rab GTPases contributing to the polarized secretion in yeast, animals and plants. Polarized cell growth plays an important roles in plant morphogenesis and has been studied mostly in pollen tubes and root hairs. In moss there are three types of tip growing cells – chloronema, caulonema and rhizoids. Unlike other exocyst subunits, genomes of *Arabidopsis* and *Physcomitrella* encode only one SEC6 paralogue. In A.t SEC6 loss-of-function is gametophytically lethal. Here we show, that it is the same in moss – despite repeated efforts we were unable to get moss SEC6 null mutant. However by chance we recovered two partial-knockout lines displaying severe developmental changes - shift in the proportion between chloronema vs. cauolnema protonema types in growth rate and inability to form gametophores. Complementation of mutant lines by PpSEC6 cDNA and as well as At SEC6 cDNA successfully restored function including development of sexual organs and producing viable spores. These results demonstrate the crucial role of moss SEC6 subunit in polarized growth and transition from filaments to three-dimensional body form.

Acknowledgement: This work is supported by the CSF/GACR proj. GA15-14886S.

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