25th New Phytologist/Colston Research Society Symposium

Colonization of the terrestrial environment

Clifton Hill House, University of Bristol, UK
21–22 September 2010

Programme, abstracts and participants

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Organizing committee

David Beerling *(University of Sheffield, UK)*
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Liam Dolan *(University of Oxford, UK)*
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'Colonization of the terrestrial environment' illustration by A.P.P.S., Lancaster, U.K.

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Speaker Abstracts

Session 1: The early terrestrial environment
Chair: *Chris Hawkesworth*

1.1 Creating habitable zones

EUAN NISBET
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A better name for our planet would be Ocean. In the Hadean aeon (about 4.5 – 4 Ga ago, where 1 Ga = 10^9yr) Earth has had surface water since prior to 4.4 Ga ago. Most of the early surface was probably ocean. However, zircon minerals of this age imply granitoid rocks existed in a few places, and thus probably some aluminous clay minerals occurred. Under the water, the early surface, however, may have been mainly covered by high-Mg ('komatiitic') lava.

The onset of life was perhaps about 4 Ga ago, at the onset of the Archaean aeon (about 4-2.5 Ga ago). Whether life was itself born in the mud of a warm little pond remains hot debate, but the arrival of replicating cells would instantly have altered the face of the planet. Life is adept at extracting cations from minerals, and would have accelerated and changed the breakdown of the surface rocks, by its selective action. The key biochemical reactions that sustain the biosphere depend on metals characteristic of hydrothermal systems around volcanoes – e.g. MoFe and Ni for the nitrogen cycle, Mg for photosynthesis, Ni in hydrogen processing, Cu and Zn in many reactions. These metals must have been readily available – indeed, intrusive – to the first replicating cells, which lacked the sophisticated metal-gathering processes of modern life. Early life would have formed biofilms, managing redox gradients. Above, the influence of sunlight would have sourced relatively oxidised chemical species such as sulphate. Below, reduced material existed, either from rock or from organic waste, with a highly focussed redox transition between top and bottom. This boundary between heaven's nutrient above and the excrement below is the habitat of life, which has built its home on its faeces.

The early atmosphere was of inorganic origin. The geological record implies the existence of liquid oceans at least since the early Archaean (3.8 Ga ago) and likely throughout the Earth's history. But the young Sun was fainter than today. This poses a challenge – why didn't the ocean surface freeze? Perhaps in the Hadean it was indeed frozen, though the deep water would have been kept liquid by the geothermal heat flux.

Since 3.5 Ga ago, or earlier, the atmosphere has been manipulated on a large scale by life, to the extent that the air has become a biological construction, regulating the planetary climate. Methanogens may be of great antiquity, with methane emission helping to maintain liquid Archaean oceans, despite a faint young Sun. Anoxygenic photosynthesis may date back to 3.5 Ga or earlier. Oxygenic photosynthesis may have begun around 2.9 Ga ago. This is the date of the first appearance of large-scale carbonate reefs, and from this date begins the distinctive partitioning of carbon isotopes between carbonate and organic carbon. Transition from the anoxic to the oxic state risks glaciation. CO_2 build up during a global snowball may be an essential precursor to a CO_2-maintained greenhouse with high levels of atmospheric O_2.

After photosynthesis began, the supply of reduced waste and dead organic matter below would have increased sharply. The excreted sulphate and later oxygen and nitrogen would have collected above, allowing the development of the modern biosphere. Most biochemical reactions were probably in place as early as late Archaean, though there may have been episodes when the system was inverted, with oxidised species below and methane-rich air above. By the late Archaean, the mud was probably host to massively complex consortia of microbial life, both archaea and bacteria, cycling and recycling redox power and available nutrients.

1.2 Effects of plant–fungal co-evolution on the terrestrial environment

JONATHAN R. LEAKE
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Mutualistic symbiotic soil fungi co-evolved with land plants even before the advent of roots over 400 million years ago, co-evolving with roots as plants invaded the land to form mycorrhizal associations that still remain ubiquitous in over 80% of plant species today. The crucial role of arbuscular mycorrhizal fungi (AMF) in early land plant evolution is supported by congruent evidence gained from paleontological, molecular clock and molecular genetic analyses. Recent experimental studies have now established the beneficial mutualistic basis of mycorrhiza-like associations in root-less lower land plants, and the enhancement of these benefits under elevated CO_2 conditions similar to those of the early Palaeozoic when terrestrial ecosystems started to develop. The evolution of mutualistic AMF are now thought to have been a vital step that enabled plants to colonise the terrestrial environment by overcoming the extreme constraint of low phosphorus availability in most terrestrial sediments. Through enhancing the mobilization and uptake of phosphorus, AMF increases biomass and productivity of land plants leading to increasing plant stature, and greater biogeochemical cycling of elements. These effects appear to have driven major changes in the terrestrial environment through the formation of pedogenic clay minerals, enhancement of weathering of calcium and magnesium silicates on the continents, and increasing the losses of these base cations to the oceans where they sequestered CO_2 from the atmosphere in carbonate sediments. The co-evolution of plants and AMF appears to have been the opening move that put in chain a sequence of events that greened the surface of the Earth with terrestrial plants of increasing biomass and complexity. These developing ecosystems enhanced weathering processes that have fed-back, via effects on atmospheric CO_2 concentrations, in regulating Earth’s climate and biogeochemistry over the past 400 million years.

1.3 The role of arthropods in the early evolution of terrestrial ecosystems

CONRAD C. LABANDEIRA
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Some of the earliest, well documented terrestrial ecosystems provide evidence for food webs consisting of a variety of nutritional types, including photosynthetic plants, heterotrophic fungal or fungal-like organisms, and arthropods of varied dietary strategies. In addition, recent evidence for early ecological relationships consists of an increasing number of bilateral associations among these three nutritional groups of organisms. For plant–fungal associations, mycorrhizal symbioses provide documentation that intimate nutritional reciprocity originated very early in land ecosystems. In addition, parasitic associations occurred between these two groups of organisms. Fungal–arthropod associations recently have been investigated and include distinctive, coprolite-containing borings in the enigmatic organism, Prototaxites, a possible ascomycete fungus. These borings, occurring in a two specimens from the Early and Late Devonian, also exhibit fungal reaction rims also contain chewed but undigested mycelial fragments. The most intriguing associations are the plantarthropod associations of two feeding types, based on dispersed coprolites, plant-damage, and arthropod mouthpart structure. The first feeding type is spore consumption, either as (nearly) monospecific assemblages or more eclectic diets consisting of admixtures of other reproductive and vegetative material. Most of this type of feeding was detritivory, although limited herbivory existed. The best case for herbivory can be found in various lesions on plant stems with reaction tissue and other types of evidence for healing. Associational data for early terrestrial ecosystems can be summarized by placing the times of origin of major plant structures available for herbivores, versus when they are first herbivorized. Two patterns are evident. First are those organs, such as stems and sporangia that become herbivorized almost as soon as they appear. The second pattern consists of organs such as roots, leaves, seeds and wood, which have major lags, ranging from 54 to 98 million years, sometimes into the Carboniferous, before they become live food for arthropods. These differences in lags suggest that there were impediments to arthropod herbivory throughout the Devonian and into Carboniferous, after this feeding type was established during the Early Devonian.

Session 2: Early land plants
Chair: ***Mike Benton***

2.1 Palaeontological evidence for the origin and early evolution of land plants

CHARLES H. WELLMAN
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The land plants (embryophytes) are a monophyletic group that evolved as an adaptive response to the invasion of the land. Fossil evidence for the earliest land plants consists of dispersed spores and dissociated fragments (enigmatic cuticle-like and tubular structures). Actual megafossil remains are extremely rare, most likely because these plants lacked recalcitrant (e.g. lignified) tissues and were consequently of low fossilization potential. Nonetheless, fossil and other evidence suggests that plants invaded the land in the Mid Ordovician and consisted of basal embryophytes believed to have been of a ‘bryophyte-like’ grade of organization. These plants were probably generalists that tolerated a wide range of environments and were cosmopolitan. A similar flora appears to have persisted for at least 30 million years. The emergence of polysporangiophytes (vascular plants and their immediate predecessors) is shrouded in mystery. However, by the Late Silurian it appears that vascular plants dominated the vegetation and the ‘bryophyte-like’ plants had been outcompeted and relegated to subsidiary components. This talk will critically review the fossil evidence for the earliest land plants. A number of current controversies will be examined including: (i) the affinities of Cambrian palynomorphs purported to represent land plant spores; (ii) suggestions that the dissociated fragments represent disarticulated bryophytes; (iii) discrepancies between the fossil record and evidence provided by molecular clocks.

2.2 Early land plant evolution

PAUL KENRICK
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Sometime during the late Neoproterozoic or early Palaeozoic terrestrial ecosystems changed fundamentally with the colonization of the land by plants. Evidence comes from a variety of sources, but currently these present a conflicting and very incomplete picture in terms of the relative timing of events, the organisms involved, and the pattern of diversification of various groups. The record of dispersed spores indicates that land plants originated during the mid Ordovician, and that there was an initial diversification of groups related to bryophytes. Evidence from body fossils (i.e., stems, leaves, roots, etc.) appears much later, during the latter part of the Silurian Period, and documents a well known and widely analysed radiation of simple vascular plants in the apparent absence of bryophytes. The topology of molecular phylogenetic trees is consistent with the evidence from fossil spores supporting a bryophyte-first hypothesis, but calibrations of these phylogenies produce results that fall into two categories: those that are broadly consistent with the picture derived from spores and those that are very much older. These inconsistencies are attributable to biases operating in the early fossil record and to assumptions underpinning tree calibration. Circumventing these biases to obtain a clearer perspective on the plant colonization of the land requires a better understanding of the nature of the early Palaeozoic terrestrial rock record and would benefit from additional geochemical and sedimentological indicators.

Session 3: Emerging resources
Chair: *David Beerling*

3.1 The moss *Physcomitrella patens*: a model to study how land plants adapted to an arid aerial environment

RALPH S. QUATRANO, AUDRA CHARRON, ABHA KHANDELWAL, HEATHER MARELLA, YOICHI SAKATA
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The descendants of the earliest land plants evolved two general mechanisms for survival in the relatively arid aerial environment. While the vascular plants developed tissue specializations to transport and retain water, examples of the other main lineages of land plants (e.g. bryophytes such as mosses) retained a simple, nonvascular morphology. As a result, mosses continually undergo a co-equilibration of their water content with the surrounding environment and rely on intrinsic gene regulatory networks to reduce damage due to water stress. We will focus on the cellular and molecular responses to dehydration and rehydration in the moss *Physcomitrella patens* to determine if the networks regulating this response in moss are similar to those found during seed desiccation in vascular plants.

The phytohormone abscisic acid (ABA) and the transcriptional regulator ABI3 play a central role in regulation of desiccation tolerance in seeds. The ABA-response pathway and ABI3 genes are present in *P. patens*. Using both a deletion and over-expression strain of *PpABI3*, ABA regulated gene expression and ABA inhibition of colony growth, were dramatically affected. We have also shown that *PpABI3* is required for ABA-induced desiccation tolerance in *P. patens*. Based on these and other results, we suggest that the control of desiccation tolerance by ABA and ABI3 in *P. patens* is similar to their role in seeds.

3.2 Clues to genetic innovations for terrestrialization emerging from the *Selaginella* genome

JODY BANKS
Department of Botany and Plant Pathology, Purdue University, West Lafayette Campus, West Lafayette, IN 47907-2054, USA

Selaginella is a lycophyte, which is a monophyletic and ancient group of land plants with a rich fossil record. Lycophytes diverged from all other land plant lineages not long after plants evolved vascular tissues and is thus a critical taxon for understanding and inferring the early evolution of land plants. *S. moellendorffii* has a very small genome (110Mbp) and was recently sequenced; the unusual features of its compact genome will be described. Comparing the proteomes of the green algae *Chlamydomonas*, the moss *Physcomitrella*, *Selaginella* and several angiosperms has allowed us to examine how gene number has changed during land plant evolution as well as correlate gene gains and losses with evolutionary innovations and losses that have occurred throughout land plant evolution. Examples of such changes in developmental and metabolic genes will be described.

Session 4: The evolution of the plant body
Chair: *Phil Donoghue*

4.1 The evolution of plant roots

LIAM DOLAN
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Land plants colonized the continental surfaces of the Earth some time before 460 million years ago and the evolution of rooting structures was one of the keys to the success of this underlying the success of this invasion. The first rooting systems were relatively simple and became progressively more complex as subsequent groups of land plants evolved. Fossil and microfossil evidence indicates that the first land plants were bryophytes and the root systems of extant liverworts mosses and hornworts consist of a mass of tip-growing filaments (rhizoids). Further complexity evolved in species with specialized root organs that consist of axes covered with unicellular tip-growing filaments; modified shoot axes (rhizomes) bear tip-growing filamentous cells called rhizoids and roots bear tip growing filamentous cells called root hairs. We identified a group of basic helix loop helix transcription factors that control the development of filamentous rooting cells in the relatively recently evolved flowering plants and the relatively ancestral mosses. This indicates that the genetic mechanism regulating the development of rooting systems is ancient. We are characterizing the regulatory networks in flowering plants and mosses to determine if the changes in regulation over the past 460 million years can account for the diverse morphologies of rooting structures that have evolved in that time.

4.2 The evolution and development of leaves

JANE A. LANGDALE
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The morphology of most extant land plant species is generated through the production of leaves in ordered patterns from shoot apical meristems. However, primitive plants had neither organized meristems nor leaves. Using a combination of lineage analysis, live cell imaging and mutagenesis, we are elucidating how shoot development occurs in a range of plants. Recent data will be presented and will be discussed in the context of how developmental mechanisms evolved to elaborate different shoot forms.

4.3 The Emerald Planet: how plants “greened the Earth”

DAVID BEERLING
Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK

The colonization of the continents by land plants over 450 million years was one of the most far-reaching chapters in the history of life on Earth. It fundamentally changed the ecology and climate of the planet. In this lecture, David Beerling will discuss new findings explaining how it all came about. He will draw on exciting new findings that implicate the symbiotic relationship between plants and soil-dwelling fungi as a mechanism fuelling the evolution of terrestrial plant life and the atmosphere.

4.4 The significance of the sequence in which embryophytes acquired nutritional attributes

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Knowing the sequence in which embryophytes acquired attributes related to nutrition is necessary for understanding how land plants functioned with a particular suite of characters, what biogeochemical outcomes could have occurred at that stage, and to set the stage for considering EvoDevo of a particular attribute. The first method that was used in this quest was the fossil record, recording the earliest occurrence of particular structures. The fossil record has uneven coverage of clades and of structures, variable and often limited temporal resolution, and frequently restricted palaegeographic cover at a particular time. An example of restricted temporal definition is the lack of resolution of the sequence in which xylem (as tracheids) and stomata evolved: this is an important consideration in the evolution of homoiohydry. Restricted fossilization of structures is illustrated by symbioses related to nutrition: arbuscular and ecto-mycorrhizas are found in the fossil record, while diazotrophic bacterial symbionts are not, e.g. the absence of coralloid roots and their cyanobacterial symbionts in fossils of cycad root systems which have well-preserved arbuscular mycorrhizas. Cladistic phylogeny helps to give a temporal sequence to the occurrence of the various attributes, though this depends on the fossil record for providing calibration and the inclusion of extinct clades in cladograms. While the sequence of attributes suggested by such analyses can be accommodated in ecophysiological models of plants with a particular combination of attributes, the absence of extant examples of plants with some character combinations means that there can be no direct analysis of the fitness attributes of such combinations. Despite this, it has been possible to provide some relatively sound conclusions as to the influence on global biogeochemistry of Palaeozoic vascular plants whose combination of characters has parallels in today's vegetation.

Raven JA, Andrews M (2010) Evolution of Tree Nutrition. Tree Physiology 30: 1050-1071.

Session 5: The inception of the oxygen cycle and the evolution of key biochemical and physiological processes
Chair: ***Ian Woodward***

5.1 Support for a mid-Paleozoic rise in atmospheric oxygen

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The radiation of oxygen-demanding, marine metazoans during the Cambrian and Ordovician occurred during a time of extensive black shale deposition and where modeling indicates low levels of atmospheric oxygen. To understand the evolution of the chemical environment during this time, we investigated Paleozoic sediments with geochemical proxies using iron and molybdenum. Iron speciation was used to identify sediments deposited under anoxic and sulfidic (i.e. euxinic) water columns, and these were subsequently analyzed for molybdenum concentration and isotopic composition. Euxinic sediments provide a record of the abundance and isotopic composition of seawater molybdenum. A significant increase in Mo/TOC and δ^{98}Mo is observed in the early Devonian, reflecting a decrease of global euxinia and an increase in bottom water oxygenation. We infer that this shift was driven by a substantial increase in atmospheric oxygen. This mid-Paleozoic rise in atmospheric oxygen likely resulted from the evolution of vascular plants. The addition of lignin, the low carbon to phosphorous (C/P) ratio of plant material and increased terrestrial weathering all contributed to enhanced organic burial which allowed the atmosphere to stabilize at a higher pO_2 state. The transition to a more oxygenated state of the global ocean is also correlated with increased size maxima of marine vertebrates and the evolution of large predatory fish. Therefore, we show that increased atmospheric oxygenation, likely promoted by plant evolution, gave way for the nektonic revolution in the Devonian.

5.2 The evolution of nitrogen–fixing symbioses

J. ALLAN DOWNIE, JEREMY D. MURRAY
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The nitrogen-fixing symbioses that occur between plants and bacteria (rhizobia and *Frankia* spp.) evolved about 90 million years ago, and are limited to the Rosid I clade of plants. Infection leads to an intimate association of symbiont and host such that bacteria are taken up into root cells. Genetic analyses of *Rhizobium*- and *Frankia*-induced nodule formation in legumes and *Casuarina* respectively have revealed a conserved signalling pathway. Several components on this pathway are also required for establishment of the arbuscular mycorrhizal symbiosis that leads to mineral uptake in roots. This mycorrhizal symbiosis was probably important for the evolution of land plants and nodulation signalling appears to be an adaptation of this more ancient signalling pathway. The acquisition of symbiotic nitrogen fixation presumably enabled plants to colonise environments low in nitrogen. A rapid diversification of legumes occurred shortly after the KT extinction boundary event and this was probably enhanced by (a) their ability to colonise nitrogen-poor soils, (b) a genome wide duplication and (c) horizontal gene transfer amongst soil bacteria allowing many bacteria to interact with legumes and activate the nodulation signalling pathway.

5.3 The fossil record of tracheophyte physiological evolution

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Continuity with modern photosynthetic function is the most reasonable first assumption when considering the early plant fossil record. Individual fossil plants are treated as pared down versions of modern plants and original evolutionary succession as a scaled up version of modern ecological succession. However, morphological and anatomical details of early fossil plants require a more complicated picture. First, the anatomy and minute size of the earliest *Cooksonia*-like sporophytes indicate physiological dependence on an unpreserved gametophyte generation. Thus, the tracheophyte relatives making up the earliest preserved terrestrial macrofloras had bryophyte-like physiology with important implications concerning both early ecosystems and the evolution of an independent sporophyte. Second, although vascular plants of a more modern aspect—including the presence of roots, leaves, and arborescence—were diverse by the Carboniferous, physiological function still lagged behind what would be expected from the modern world. Assimilation and transpiration rates are both closely correlated with leaf vein density and that vein density was drastically lower in all Paleozoic plants relative to the flowering plants that have evolved since the Cretaceous. As a result, the impact of Paleozoic vegetation on climate and the carbon cycle was substantially less than today. Furthermore, the much narrower range of photosynthetic capacities also suggests that the function of early ecosystems would be unfamiliar to modern plant ecologists.

Session 6: Colonization and associated challenges–lessons from the present day
Chair: *Liam Dolan*

6.1 Plant diversity and the carbon cycle

F.I. WOODWARD
Department of Plant and Animal Sciences, University of Sheffield, Western Bank, Sheffield, S10 2TN, UK

Contemporary patterns of plant diversity are the result of environmental and evolutionary changes extending over millions of years, while these current patterns of diversity broadly follow the global distribution of terrestrial primary production. An important question for contemporary ecology is how future changes in climate and carbon dioxide might influence the carbon cycle and the distribution of diversity. Combinations of field observations, experiments and modelling will be presented to show the intimate interlinking of the carbon cycle and diversity. It emerges that primary production can be used to predict diversity, while also driving micro-evolutionary change but with an uncertain dependency on future increases in carbon dioxide concentration.

6.2 Evolutionary consequences of colonization and species range expansion

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When individuals from a species colonize a new territory and spread, large evolutionary changes take place in a short time span of just a few generations. These changes leave a long-lasting footprint in the genetic structure of species. Such signatures of past expansions form the bread-and-butter of most phylogeographic surveys. During the last 5-10 years, spatially explicit modeling approaches, which are particularly relevant for sessile organisms such as plants colonizing terrestrial ecosystems, have unraveled some of the underlying processes. In particular, 'surfing events' take place 'in the wave', i.e. at the advancing margin of the expanding species. 'Surfing' is the rapid fixation and spread of genetic variants that takes place during the early phase of colonization, as a result of intense genetic drift coupled with rapid demographic growth. Even maladapted alleles can surf, allowing populations to move from one adaptive peak to another across a valley. In fact, during long colonization, the populations at the expanding margin experience not one but a succession of intense drift events followed by rapid demographic rebound that considerably accelerate the pace of evolution, allowing increasingly derived alleles to appear and producing long branches on phylogenetic trees. In the specific case when one species colonizes a region already occupied by a partly interfertile species, massive introgression can take place with genes typically flowing from the resident towards the expanding species. All these results point to the same direction: colonization can result in rapid evolution, both for neutral and for selected characters. Conversely, there is little or *no change without movement*, an expression used by the French sociologist Pierre Bourdieu in another context.

Poster Abstracts

Listed alphabetically by first author, presenting author is underlined.

1. Mesocosm-scale experimental quantification of mineral weathering by mycorrhiza and its implications for terrestrial biogeochemistry

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The rise of vascular land plants in the Paleozoic is hypothesized to have driven lower atmospheric CO_2 levels through enhanced weathering of Ca and Mg bearing silicate minerals. However, this view overlooks the co-evolution of roots and mycorrhizal fungi in early land plants, since many of the weathering processes ascribed to plants are potentially being driven by the combined activities of roots and fungi. Here we present results from plants grown under ambient and elevated CO_2 concentrations in which carbon allocation through roots and mycorrhizal fungi and their effects on weathering can be distinguished and measured.
Plant species were chosen to address the impact of evolutionary trends in mycorrhizal association and rooting depth on silicate weathering. More deeply rooted *Sequoia sempervirens (*arbuscular mycorrhizal, AM*) and Pinus sylvestris* (ectomycorrhizal, EM) were contrasted with a shallowly rooted fern, *Osmunda regalis* (AM) in mesocosms with horizontally inserted mineral-containing mesh-covered cores. Preliminary results indicate differences in 1) growth responses to elevated CO_2, 2) solution chemistries, and 3) magnitude and timing of ^{14}C-labelled photosynthate flux from plant to fungal partner. Ongoing measurements will characterize the extent of fungal colonization on basalt and granite, assess mineral weathering, and quantify biomass element uptake in these systems.

2. Do direct temperature responses by arbuscular mycorrhizal fungi influence plant growth and nutrition

G.E. BARRETT[1,3], C. CAMPBELL[2], A. FITTER[1], A. HODGE[1]
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Plants typically form symbiotic relationships with mycorrhiza, yet plant temperature responses are typically measured with little consideration for these fungi. Arbuscular mycorrhizal (AM) fungal associations are ubiquitous in terrestrial ecosystems and provide a range of benefits to plants including improved nutrient uptake efficiency. Little is known however, about how these fungi respond directly to changes in soil temperature. To address this, plants colonised with AM fungi were grown in two-compartment microcosms where the soil dwelling extra-radical mycelium (ERM) of the fungus could be separated from the roots. The ERM was then grown under a range of temperature regimes whilst associated host plants remained at uniform temperature. The ERM was supplied with a labelled organic nitrogen (^{15}N) source and its growth and ^{15}N capture ability were measured. AM fungi showed positive responses to increasing temperature which tended to enhance their nutrient capture ability. Furthermore, temperature indirectly affected the growth of host plants through its impact on the fungal partner. This research indicates that the benefits provided to plant hosts by mycorrhizal fungi may be strongly influenced by soil temperature. It also highlights the need to consider mycorrhizal fungi when assessing plant responses to temperature.

3. Stomatal ABA signalling conserved across 450 million years of land plant evolution

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The evolution of stomata enabled land colonisation by sporophyte-dominant plants over 400 million years ago. The oldest fossil stomata appear on tracheophytes, but phylogenetic evidence suggests that gametophyte-dominant bryophytes are the most ancient surviving lineage with stomata. Crucially, it is unknown whether stomata, as environmentally responsive gas-exchange systems, evolved once or whether they have multiple evolutionary origins. Comparative molecular and physiological studies of *Physcomitrella* moss with the model angiosperm *Arabidopsis* provide evidence that stomata are monophyletic. Our results indicate that the core regulatory genetic module involved in guard cell ABA signalling has been conserved since the divergence of seed plants and mosses from their common ancestor over 450 million years ago.

4. The functional and evolutionary significance of fungal associations in 'lower' land plants.

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The arbuscular mycorrhizal (AM) association is the most widespread plant-fungal symbiosis on Earth, coevolving with terrestrial plants over 400 million years ago. Today, most land plants have this mutually beneficial fungal symbiosis in which plants receive soil nutrients in exchange for photosynthates. However, this view is based almost exclusively on investigations of higher plant AM associations, whereas virtually nothing is known about their functionality in the 'lower', more evolutionarily ancient land plants. We supplied $^{14}CO_2$ to the plant and ^{33}P to the fungal partners to quantify and characterize the carbon-for-mineral nutrient exchanges in AM associations in key lower plant clades and in a modern higher plant; providing the first comparative analysis of AM functioning in higher and lower plant groups. The symbiosis is shown to provide benefits in the lower plants, and the carbon-cost to nutrient gain benefit across plants at different stages of evolutionary advancement provides the first experimental support for the longstanding assumption that mycorrhizas co-evolved with lower-land plants to the mutual benefit of the plant and fungal partners. These findings strengthen the evidence that AM have played a crucial role in the development of the terrestrial biosphere from over 400 million years ago to the present day.

5. Evolution of wall-remodelling enzyme activities from charophytes to embryophytes

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Charophyte and embryophyte cell walls consist of cellulose, pectins and hemicelluloses. Unlike many land plants, charophyte walls contain little if any xyloglucan or MLG – abundant in grasses, cereals and *Equisetum*. Much remains to be discovered about charophyte wall-modifying enzymes, information that would promote our appreciation of the 'primordial' plant cell wall. In our work we are exploring the changes in cell wall biochemistry which took place during plant evolution focusing on the modern charophytic algae, the closest extant relatives of land plants. We tested the ability of embryophytes to graft xyloglucan- and mannan-based oligosaccharides using various polysaccharides as donor substrates. We detected novel homo- and hetero-transglycosylation activities in diverse enzyme extracts prepared from pteridophytes and charophytes. In contrast to pteridophytes, charophytes possess significant mannan endotransglycosylase activity suggesting that the mannan-based polymers of algal walls might be being modified and covalently linked to other wall polysaccharides by the action of enzymes catalysing trasnglycosylation. The discovery of MXE (a novel 'heterotransglycosylase' recently described for *Equisetum)* in charophytes was surprising because these algae appear to lack the appropriate substrates. These and similar *in-vivo* and *in-vitro* experiments with diverse [3H]- and fluorescent oligosaccharides will be reported, providing new information on the biology of charophytic walls. We thank the Leverhulme Foundation for funding.

6. In Search of Meaning: Mathematical Analysis and Modeling of Calcium Signals

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Fluctuating calcium concentrations are important in many signaling pathways, such as the establishment of symbioses between plants and microbes. Signal molecules released by both mycorrhizal fungi and nitrogen-fixing bacteria in the soil activate a common symbiotic signaling pathway in the plant roots. This leads to nuclear and cytosolic calcium oscillations, but downstream events diverge and result in drastically different symbioses. The calcium oscillations are predicted to confer specificity, and we aim to understand how the signals are being distinguished. However, the data presents several challenges in the form of high noise levels and biological variability. Therefore we have developed a novel set of methods to analyse these calcium oscillations, including efficient detection of key frequencies with Bayesian Spectrum Analysis and characterisation of phase space dynamics using attractor reconstructions. Mathematical modeling with ODEs describing the underlying machinery allows for further insights into the system's behaviour and for predictions of relevant components. Ongoing work is investigating how different calcium signatures could relate to the evolution of the symbiotic signaling pathway. Taken together, this extensive analysis will shed light on the meaning of different calcium signals.

7. F129L mutation in net blotch of barley *Pyrenophora teres*

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The evolution of resistance to fungicides is a serious problem in agriculture. Resistance of plant pathogenic fungi towards QoI (Quinon Outside inhibitors) fungicides is mainly caused by two mutations in the cytochrome *b* gene, the F129L and G143A mutations, and the latter is seems to be the main mechanism of resistance in QoIs. There are some reports mentioning that control of net blotch of barley *Pyrenophora teres* Drechsler affected to some extent by F129L mutation.

Molecular methods using PCR has been used to detect mutant (F129L) isolates of *P. teres* using allel-specific primers. The PCR product was sequenced aligned and analyzed showing that a range of isolates were carrying the F129L mutation. Results showed that change in codon TTC (coding for phenylalanine of the wild type) is changed to TTG, CTC and TTA in mutant isolates (all coding for leucine in the mutant types).

In vitro studies to determine fungicide sensitivity of *P. teres* isolates showed that pyraclostrobin and epoxiconazole still have a strong inhibitory effect on the growth of mutant isolates. However, *in planta* results showed that there was variation in disease control.

It is concluded in this study that F129L mutation is reduced *in planta* performance of fungicides.

8. Parallel lives: how seaweed genomes help to understand why macroalgae stayed in the seas

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The green, red and brown macroalgae, being increasingly distant marine cousins of land plants, have long provided morphological, physiological, and developmental yardsticks against which to compare the terrestrial adaptations and evolution of embryophytes. The recent acceleration of sequencing technology is now allowing genomic comparisons to be added to this list. We have carried out a preliminary annotation and classification of the protein kinase superfamily – one of the largest regulatory gene families in eukaryotic genomes - in the red macroalga, *Chondrus crispus*, and the brown macroalga, *Ectocarpus siliculosus*, and discuss how expansions and losses in protein kinase sub-families compare to those seen in green plants, and how these may reflect algal life cycles and development. We also consider current progress in potential green macroalgal genome projects.

9. Cloning and functional characterisation of Armadillo-related genes in moss

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Armadillo-related proteins play important roles in cellular processes both in animals and plants. In *Arabidopsis*, ARABIDILLO-1 and ARABIDILLO-2 (‘*Arabidopsis* Armadillos’) control lateral root development. Three *Arabidillo* homologues have been identified in the *Physcomitrella* genome; *Physcodillo-1*, *-2* and *-3*. The current draft of the genome contains an incomplete version of *Physcodillo-2* and a truncated version of *Physcodillo-3*. Using cloning, sequencing and Southern blotting approaches, a full characterisation of the *Physcodillo* loci was completed. We found that *Physcodillo-2* resides alone on scaffold 13 whereas full-length *Physcodillo-1* and *-3* genes, including their promoter sequences exist as identical inverted repeats on scaffold 91. *Physcodillo-1/-3* and *Physcodillo-2* appear to be 84% identical at the protein level. Full promoter sequences of the three respective genes have been cloned and stable *Physcodillo* promoter::GUS lines generated successfully. Specific gene expression patterns and promoter activities have been supported by tissue-specific expression analyses by RT-PCR. A stable *Physcodillo-2* knockout line has been generated. Attempts have also been made to delete the entire *Physcodillo-1/-3* locus via gene targeting by homologous recombination, in order to obtain both double and triple knockout mutants. Studies using *Physcomitrella* will inform our understanding of how this seemingly important gene family has evolved from the ‘early pioneers’ to modern day flowering plants.

10. Small is beautiful: new investigations into Lower Devonian plant mesofossils and their *in situ* spores

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Much of our understanding of the anatomy of the earliest land plants comes from well-preserved charcoalified mesofossils. Whilst representing only a facet of early land vegetation, initial studies indicate that these minute axes with terminal sporangia continue to make a significant contribution to the understanding of biodiversity and development of terrestrial ecosystems during the Lower Devonian. As well as exceptional anatomical preservation, many sporangia contain *in situ* spores, many of which represent new taxa (both cryptospore and trilete), whilst some have been recognised in the dispersed spore record, but not previously been recorded *in situ*. A new investigation aims to obtain detailed morphological, anatomical and ultrastructural data on both the mesofossils (particularly the axes) and their *in situ* spores, predominately using SEM and TEM techniques. With this data it is hoped that the affinity of these mesofossils may be elucidated, and their taxonomic relationship with the early tracheophytes and bryophytes can be explored. Recent evidence of highly-branched mesofossil sporophyte axes suggests that at least some of these minute plants may represent stem-group embryophytes with bryophytic characters.

11. The transition from gametophyte to sporophyte: a transcriptomic analysis of the moss *Physcomitrella patens*

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Bryophytes (liverworts, mosses and hornwort) represent the earliest lineage of plants to colonise the terrestrial environment some 450 million years ago. The subsequent 'greening of the Earth' was marked by a switch from the gametophyte dominate phase of this group to the sporophyte-dominant phase of vascular land plants. Due to the wealth of molecular, genetic tools and data available, the moss *Physcomitrella patens*, provides a powerful model to study this key lifecycle transition in early plants. We undertook a transcriptomic profiling of *P. patens* undergoing the transition from a gametophytic phase to the sporophytic phase, isolating RNA from both the predominant gametophyte protonema, but also from carefully dissected and staged sporophytes. This RNA was then hybridised to custom made *P. patens* Agilent microarrays and the resulting data analysed to identify significantly differentially expressed genes. Our analysis has found that a large change does occur in the transcriptome of the moss between the gametophyte and the sporophyte phases, as well as during sporophyte development. These data provide a valuable resource to both test classical theories on the developmental, physiological and structural elements proposed to be important for conquest of the land by plants, as well as allowing the identification of novel gene leads which may be involved in the gametophyte/sporophyte transition. Comparison with model angiosperms (Arabidopsis) provides a means of establishing the functional significance of conserved genetic elements.

12. Using *Selaginella* to investigate stomatal evolution

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Stomata first appear in land plants in the fossil record some 410Mya (Edwards, Kerp & Hass, 1998) this acquisition by terrestrial plants is regarded as one of the 'five key innovations' underpinning the success of the embryophytes (Raven, 2002). Each stoma is formed by a pair of specialised cells (guard cells) that surround a central stomatal pore. As the guard cells increase or decrease in turgor the aperture of the pore changes. This in turn controls the uptake of carbon dioxide into the leaf for photosynthesis and the loss of water vapour from the plant during transpiration. Guard cell turgor is under the control of a range of exogenous (light, carbon dioxide concentration, atmospheric relative humidity) and endogenous (hormonal) signals. The guard cells integrate this information to 'set' the optimum aperture to best suit the prevailing environmental conditions. Research in 'higher plants', especially *Arabidopsis thaliana* has revealed that a complex intracellular signal transduction network is responsible for coupling extracellular stimuli to alterations in guard cell turgor (Hetherington and Woodward, 2003).
In order to gain insights into the evolution of stomata we have been investigating the control of stomatal function in a 'lower plant' – the lycophyte
Selaginella uncinata. We will compare stomatal responses to a range of stimuli in *S. uncinata* and *A.thaliana*. We shall also report on progress in understanding the signalling transduction pathway underlying ABA-mediated closure in *S. uncinata*.

13. Armadillo repeat proteins in the moss *Physcomitrella patens*: structure, stability and subcellular localisation.

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Armadillo/β-catenin proteins contain tandem repeats of a 42-amino acid sequence motif (Arm repeat) that form a conserved superhelical protein-binding surface. Animal Armadillo proteins are involved in various important developmental processes, including cell differentiation, intracellular signalling and cytoskeletal regulation[1]. Recent genome sequencing efforts have revealed that Arm-repeat containing proteins exist in all plants, but the majority are uncharacterised. To gain an insight into the ancestral roles of Armadillo proteins, we investigated the function of Arabidillo[2]-like proteins in the moss *Physcomitrella patens*. Structure, subcellular localisation and stability of *Physcomitrella* proteins were compared to their higher plant counterparts.

Although their amino acid sequence is highly similar, *Physcomitrella* proteins appear to be more stable than their *Arabidopsis* homologues. Analyses of the subcellular localisation of full length and truncated versions of these proteins suggest that, unlike in Arabidopsis, *Physcomitrella* proteins have both nuclear and cytoskeletal functions. Different strategies to achieve high expression levels have been adopted to allow the identification of Arm-repeat interacting partners in moss.

The understanding of how Armadillo proteins have evolved will help reveal more about the evolution of plants from ancestral unicellular cells to successfully colonise the terrestrial environment.

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14. Biotrophic relationships between fungi, fungi-like and plants in early terrestrial environments.

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A fungal way of life is shared by several major living groups of organisms, notably Fungi (Eumycota) and Oomycetes (Straminipila). Many of these organisms develop biotrophic (i.e. parasitic and symbiotic) relationships with plants. Here we describe such relationships by working on thin sections of petrified fossils made during the 19–20th centuries and currently housed in University or Museum collections. Mycorrhizae are mutualistic associations between plants and fungi; they are present in ancestral forms (Paramycorrhizae) in Devonian and Lower Carboniferous plants. Eumycorrhizae (modern forms) appear later; we documented the oldest occurrence of this type in the roots of the cordaitalean gymnosperm *Radiculites reticulatus* from the Upper Carboniferous rocks from Grand'Croix (Central Massif, France). Oomycetes have been recognised within the leafy branches of a lycopod from the Carboniferous Period, and have also been described in the Devonian Rhynie Chert. Our recent research shows evidence of Oomycetes in the extinct seed fern *Lyginopteris*, a key element of the Upper Carboniferous mire environments (seed ferns or pteridosperms). Morever, we provide the earliest evidence for a biotrophic parasitic mode of life in the Oomycete group. These discoveries indicate that biotrophic relationships involving fungi or Oomycetes were established in early terrestrial ecosystems.

15. Evidence of oil bodies in Paleozoic liverwort fossils

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One of the unifying characters of the morphologically diverse liverwort clade, the sister group to the remaining embryophytes, is the presence in most taxa of unique organelles called oil bodies. These true, membrane-bound organelles contain complex mixtures of lipophilic compounds. Found in some or all of a plant's cells, they are highly diverse in shape, size, and number per cell and are well-documented taxonomic characters; yet, their function remains unknown. As part of an exploration of oil body evolution and function, we test the homology of the small, scattered, dark cells found in nearly all Paleozoic liverwort fossils with the specialized oil body cells of some extant representatives of early-diverging lineages of liverworts. Fluorescence and SEM microscopy, GC-MS, morphometric analyses and statistical methods will be used to compare representatives of Paleozoic liverwort taxa with extant taxa. Preliminary results suggest that the dark, scattered cells found in Paleozoic liverwort fossils are homologous with the oil body cells of extant taxa, providing evidence for specialized oil body cells as the plesiomorphic state in liverworts.

16. The influence of phylogeny on element concentrations in plants

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Recent publications show that the concentration of many elements in angiosperms is influenced by phylogeny. There have been no meta-analyses of these effects or analyses using APGIII. Such analyses are presented here for 20+ elements down to the ordinal level and the implications for colonisation of the land discussed. REML models with species as a fixed factor and dataset as a random factor were used to estimate relative concentrations for several hundred species from greenhouse experiments and the literature. Hierarchical ANOVAs based on the APGIII phylogenetic classification showed that concentrations were significantly influenced by phylogeny. At the superorder level for almost all elements the Lilianae had the lowest concentration (in particular the commelinid orders) and for many elements there were significant differences between the Rosanae and Asteranae. For alkali and alkali earth metals, and a number of other elements, the Caryophyllanae had the highest relative concentrations. There were significant differences at the ordinal level and an increasing concentration of almost all elements from orders in the Lilianae to orders in the Asteranae. Preliminary meta-analyses suggest significant mineralogical and stiochiometric patterns across major groups of angiosperms that might enrich the understanding of the colonisation of the land by angiosperm groups.

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