14th *New Phytologist* Symposium

Programme, abstracts & participants

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New directions in plant ecological development

23–24 January 2006
The Royal Society, London, UK

Organizing Committee

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Programme, abstracts and participant list compiled by Holly Slater. Symposium logo, cartoon plant showing eco-devo response to low- and high-light environments, by Sam Day, www.samday.com

Programme

Monday 23 January	
09:00–10:00	Registration – tea and coffee
10:00–10:10	**Welcome & introductions**, Holly Slater, Sonia Sultan, David Ackerly
10:10–10:35	**Keynote remarks: Anthony D Bradshaw,** Liverpool, UK Unravelling phenotypic plasticity – why should we bother?
10:35–11:20	**Rens Voesenek,** University of Utrecht, The Netherlands Submergence-induced shoot elongation: from floodplain communities to genes
11:20–12:05	**Angela Hodge,** University of York, UK Plastic plants and patchy soils
12:05–12:50	**Ariel Novoplansky,** Ben-Gurion University of the Negev, Israel Amelioration of competitive responses in plants
12:50–13:50	Lunch
13:50–14:35	**Johanna Schmitt,** Brown University, Providence, RI, USA Adaptive evolution of seasonal timing in *Arabidopsis thaliana*
14:35–15:20	**Kathleen Donohue,** Harvard University, Cambridge, MA, USA Developmental phenology, morphological plasticity, and habitat selection in plants
15:20–15:50	Refreshment break
15:50–16:35	**Jack Schultz,** Penn State University, University Park, PA, USA The transcriptional intersection of plant development and defense responses to insects
16:35–17:20	**André Kessler,** Cornell University, Ithaca, NY, USA Ecological consequences of induced plant responses to herbivory: a solanaceae example
17:30–19:30	Posters and drinks reception

Tuesday 24 January	
09:00–9:45	**Harry Smith,** University of Nottingham, UK Signals and sensitivities in plant responses to density
9:45–10:30	**Candace Galen,** University of Missouri-Columbia, MO, USA Rooted in the blues: a novel role for blue light signaling in the foraging ecology of plants
10:30–11:00	Refreshment break
11:00–11:45	**Fernando Valladares,** CSIC Madrid, Spain Why plants differ in the extent of their phenotypic plasticity? An ecophysiological perspective

11:45–12:30	**Cynthia Weinig**, University of Minnesota, St Paul, MN, USA Genetic sources of adaptation and evolutionary constraint in heterogeneous competitive environments.
12:30– 12:35	**Introduction to breakout discussions**
12:45–13:45	Lunch
13:45-14:45	**Breakout discussions** (1) Genetic mechanisms and molecular tools – chaired by Hilary Callahan (2) Environmental heterogeneity and plant development – chaired by Alastair Fitter (3) Eco-devo and community/ ecosystem processes – chaired by Peter Curtis
14:45-15:00	Break (15 minutes for discussion group leaders to collect thoughts)
15:00-16:00	**Discussion group reports and final discussion**
16:00–17:00	Closing reception – traditional afternoon tea

Speaker abstracts

Listed in programme order

Keynote speaker:

Unravelling phenotypic plasticity – why should we bother?
BRADSHAW, ANTHONY D
Liverpool, UK

The ability of a genotype to change its phenotype was once considered rather a nuisance – making it difficult to define a genotype. This lead to the idea there was a problem called instability. But quite early it was recognised that stability was under genetic control, and was a character like other attributes of an individual.

From this came the idea that there were two sides to this, and that the ability to change could be important – and given the title of plasticity. Once recognised, it became clear from surveys of different species and populations that plasticity i) can be a complex character, ii) can be selected to fit species to the particular demands of different environments.

For plants, which cannot meet variations in environment like animals by behavioural responses, phenotypic plasticity can be very important. Besides their role in unravelling mechanisms, plants should therefore be valuable in demonstrating its contribution to fitness experimentally. We ought also be able to demonstrate that appropriate genetic variability is available by which complex responses can be built up by selection. Genes must not only exist to determine character means, but also to determine character response, which adds interesting complexity to our ideas about evolution.

Speakers:

Submergence-induced shoot elongation: from floodplain communities to genes
VOESENEK, LAURENTIUS A.C.J.
Plant Ecophysiology, Department of Biology, Utrecht University, Sorbonnelaan 16, 3584 CA Utrecht, The Netherlands

Complete submergence is an environmental perturbation with a severe impact on plant growth. However, some species have the capacity to minimize submergence time through upward bending of petioles (hyponastic growth) and fast elongation of the entire petiole. The combined effect of these two responses hastens the emergence of leaf tips above the water surface; the tips then functioning as 'snorkels' to restore aerial photosynthesis and impeded gas exchange with the atmosphere.

Several plant hormones play an important role in the perception and transduction of the submergence signal. Ethylene accumulation in submerged plants is the sensing system that reliably signals the switch from an aerial into a submerged environment. Further downstream ethylene interacts with the hormones abscisic acid (ABA) and gibberellins (GA). This signal-transduction cascade is elucidated using experimental studies with *Rumex palustris* and *Arabidopsis thaliana.* Furthermore, shade-induced elongation is also used as a tool because we assume that it has a similar downstream transduction route as ethylene-induced elongation.

Plant species differ strongly in their growth response upon ethylene; some species show an inhibition of growth whereas others like *R. palustris*, are stimulated by ethylene. Elongation data of 22 river floodplain species are superimposed on a vegetation-environment relationship using 84 vegetation surveys from floodplains along the river Rhine in the Netherlands. We conclude that the capacity to elongate upon ethylene accumulation is an important trait in field distribution patterns of plants in flood-prone environments. Fast shoot elongation under water seems to be a favourable trait only in environments with shallow and prolonged flooding events, while costs associated with this response prevent its expression in sites with deep floods and in sites with floods short in duration.

Plastic plants and patchy soils

HODGE, ANGELA
Department of Biology, University of York, Area 14, PO Box 373, York, YO10 5YW, UK

The distribution of nutrients in soil is heterogeneous or 'patchy'. It is well established that when roots encounter such nutrient-rich patches they can proliferate within it, often spectacularly so. However, while the benefit of root proliferation to immobile ions such as phosphate is relatively easy to interpret, it has been more difficult to explain in terms of highly mobile ions such as nitrate. We have shown that when plants were grown as individuals there was no relationship between root proliferation in an nitrogen-rich patch and the amount of nitrogen (N) captured from the patch by the plant. In contrast, when two different plant species were grown together in competition for a common N-rich patch then root proliferation did confer an advantage: the plant species which proliferated the most captured the most N from that patch. Plants also have an additional nutrient acquisition mechanism namely, mycorrhizal symbiosis. We have demonstrated that when only arbuscular mycorrhizal fungi (AMF), had access to a complex organic patch, the AMF enhanced decomposition of, and acquired N from, the patch. AMF may therefore have an important role in accessing N from complex organic patches to which the plant may not have direct access.

Amelioration of competitive responses in plants

NOVOPLANSKY, ARIEL
Mitrani Department of Desert Ecology, Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, 84990, Israel.

Competition usually involves the allocation of limiting resources to non-reproductive functions. Natural selection is expected to favor mechanisms that increase competition with nonself neighbors and limit wasteful competition with self. Recent studies have demonstrated that plants are able to limit allocation to roots that are confronted by roots of the same plant. Although the specific mechanism of root self/nonself discrimination is not clear, the findings demonstrated that the amelioration of competition with self is based on physiological coordination between roots that belong to the same physiological individual rather than immune-like allochemical recognition. New findings suggest that competition between roots can be ameliorated by mycorrhiza. Preliminary experiments have shown that mycorrhiza hyphae might facilitate communication and developmental coordination between neighboring plants, regardless of their physiological or genetic relatedness, that are otherwise fierce competitors. These findings suggest new exciting directions in the study of plant signaling and communication and their ecological and evolutionary implications.

Adaptive evolution of seasonal timing in *Arabidopsis thaliana*

SCHMITT, JOHANNA
Brown University, Providence, RI, USA

The transition to flowering is regulated by diverse environmental cues such as photoperiod, vernalization, and ambient temperature, which mediate several different signaling pathways. Plants must integrate information from all of these pathways in order to flower at the appropriate time under dynamic real-world conditions. Both the environmental signals and the ecological factors that exert selection on the resulting phenotypes vary in space and time, so the optimal flowering response may vary geographically or across seasons. *Arabidopsis thaliana* is an ideal

model system for investigating the functional and evolutionary significance of natural variation in the converging signaling pathways regulating reproductive timing. Ecotypes of *A. thaliana* from diverse climates exhibit considerable natural variation in developmental timing and its sensitivity to different environmental signals. Natural molecular polymorphisms at several key flowering time genes are associated with natural variation in developmental timing, as well as fitness under field conditions, and display geographic patterns suggesting adaptation to climate.

Developmental phenology, morphological plasticity, and habitat selection in plants
DONOHUE, KATHLEEN
Harvard University, Department of Organismic and Evolutionary Biology 22 Divinity Ave. Cambridge, MA, 02138 USA

Plants have several ways whereby they can determine the environment to which they are exposed at different life stages and as such can effect a sort of habitat selection. This paper discusses three examples of habitat selection through which plants alter the environment experienced by themselves or their progeny: seed dispersal, flowering timing, and germination timing. It reviews pathways through which habitat selection alters evolutionary and ecological trajectories by altering the selective environment to which organisms are exposed, the phenotypic expression of plastic characters, and the expression of genetic variation. Theoretical and empirical results show that habitat selection can create positive or negative feedbacks between phenotypes and environments, which in turn cause novel evolutionary constraints and novel life-history expression.

The transcriptional intersection of plant development and defense responses to insects
SCHULTZ, JACK C., & WITIAK, SARAH MELISSA.
Plant Physiology Program and Chemical Ecology Center, Chemical Ecology Lab, Orchard Rd, Pennsylvania State University, University Park, PA 16802 USA

Induced plant defenses are an ecologically-important component of plant phenotypic plasticity that varies with tissue development, indicating that defense and development interact to produce the appropriate phenotype. Both development and defense responses are transcriptionally-regulated, complex programs. Whole-genome transcriptional profiling of Arabidopsis responding to attack by 4 insect species identified hundreds of genes normally known to be involved in development and/or regulated by ‘developmental hormones’ such as brassinolide and auxin. This transcriptional link probably arises for several reasons and suggests more overlap between developmental and defense programming than previously recognized.

Insect-elicited plant galls represent the ultimate intersection of defense response and development. Galling is an ancient and important ecological interaction in which the galler manipulates plant defenses and development to produce a chemically-benign structure in which its offspring develop. We present evidence that grape phylloxera (*Daktulosphaira vitifoliae*) elicits ectopic expression of flower and fruit genes in grape leaves, producing a structure comprising elements of those organs and specifically designed to house the insect. Ectopic organogenesis via transcriptional reprogramming is the likely basis of all gall development, and provides clues about the kinds of signals galling insects may use to manipulate their hosts.

Ecological Consequences of Induced Plant Responses to Herbivory: A Solanaceae Example

KESSLER, ANDRÉ
Ecology & Evolutionary Biology, Cornell University, 445 Corson Hall, Ithaca, NY 14853, USA

The past decades have seen an intense development of organismic biology and genomics of individual species on one hand and population biology and evolutionary ecology on the other hand. While the great discoveries made in these systems will continue over the next decades, more and more discoveries will occur in the interface between different biological disciplines. It is through such integrative approaches that the mechanisms of evolution and adaptation will be revealed. The study of plant-insect interactions is exemplary among the integrative research fields and succeeds by unifying the research efforts on the cellular and organismal level with those on the whole plant and community level.

The Solanceae family provides a series of examples for such integrative study system which are increasingly and likewise used in genetic, physiological and ecological research. Recently launched initiatives such as the Solanaceae Genome Network will only accelerate this process and will create new opportunities for integrative research, in particular to study the mechanisms of plant-insect interactions. I will discuss these future potentials by presenting our current research on induced responses to herbivore damage and their consequences for plant fitness and arthropod community composition of the wild tobacco plant *Nicotiana attenuata* and wild tomato species (*Solanum* spp.). The examples emphasize both, the usefulness of genetic and molecular tools in ecological research and the importance of a detailed understanding of the natural history of species when studying plant-insect interactions.

Signals and sensitivities in plant responses to density

SMITH, HARRY
Division of Plant Science, University of Nottingham, Sutton Bonington Campus, Loughborough, LE12 5RD, UK

Few plants live alone; most cohabit, and compete vigorously for resources. Anticipation of competition is an important element of cohabitation and plants have evolved a sophisticated sensory system that allows for the detection of the presence, proximity and competitive threat of neighbours. Thirty-five years ago I began what has turned into a life-time obsession to understand how plants detect and respond to neighbours. Three strategic steps can be recognised in any stimulus-response system; first, an unambiguous signal is required; secondly, a sensory device capable of detecting, again unambiguously, that signal; and finally, a mechanism for translating the information perceived into an appropriate response. In crowded communities there is likely to be a plethora of signals. We concentrated on light-signals, linking what was already known about the interaction of light with vegetation to the spectral sensitivities of the phytochromes. During the late 1970s and 1980s we showed: 1), a systematic relationship existed between spectral changes and community density; 2), that these spectral changes were detected by the phytochromes; and 3), that elongation responses in simulated vegetative shade could be directly related to the strength of the perceived signal. I will briefly summarise these findings, which essentially describe what has become known as the *shade avoidance syndrome*. Shade avoidance has since being followed up in many different approaches by groups all over the world. Mutant studies have told us which members of the phytochrome family are responsible. Micro-array analyses, QTL identification and association genetics are illuminating the pathways leading from perception to response. At the other end of the scale, the adaptive significance of shade avoidance has been investigated in depth in natural communities. In the second half of my talk I will discuss recent observations, which indicate that plants not only have varied sensitivities to shade signals, but through the distribution and density of leaves they can also generate quantitatively different signals. These notions may eventually lead to a more comprehensive model of plant-plant interactions in crowded communities.

Rooted in the blues: a novel role for blue light signaling in the foraging ecology of plants

GALEN, CANDACE. [1], RABENOLD, JESSICA J.[1], COLEMAN, JAMES S.[1], LEUNG, JEFFREY.[2] & LISCUM, EMMANUEL.[1].
[1]*Division of Biological Sciences, 105 Tucker Hall, University of Missouri, Columbia MO 65211 USA*. [2]*Inst Sci Vegetales*, *1 Avenue De La Terrasse, Bât. 23. Urp2355 Cnrs. Gif-Sur-Yvette 91198, France*.

Many plant photoreceptors are sensitive to dim light, more characteristic of root than shoot environments. Yet, the ecological significance of root-mediated light sensing is largely unknown. Here we address the impact of phototropin-1 (phot-1) a blue light photoreceptor, on root growth and drought tolerance of *Arabidopsis thaliana*. Under natural conditions in open environments, lack of phot-1 dramatically decreases fitness. Growth of *phot1* mutant plants is similar to wild-type in wet soil, but reduced in dry soil. Leaf functional traits cannot account for this effect. Thermal imaging of cotyledons and gas exchange measurements of mature leaves suggest that rates of transpiration and photosynthesis are similar for *phot1* and wild-type individuals throughout the lifecycle. However, phot-1 is also expressed in primary and lateral roots. Mutants lacking or with strongly reduced phot-1 protein level (respectively, *phot1-5* and *phot1-1* genotypes) exhibit meandering root growth characterized by non-directional 'wiggling'. Root wiggling accounts for the reduced growth rate of *phot-1* plants under drought. Our findings suggest that in *A. thaliana*, a species of disturbed, open habitats in nature, the adaptive significance of phototropism is conferred via the light avoidance behavior of roots instead of the light 'seeking' behavior of shoots.

Why plants differ in the extent of their phenotypic plasticity? An ecophysiological perspective

VALLADARES, FERNANDO
Instituto de Recursos Naturales. CCMA-CSIC, Serrano 115 E-28006 Madrid, Spain

Plants, as sessile organisms in changing environments, should always benefit from a high degree of phenotypic plasticity. But plants clearly differ in the pattern and amount of their plastic responses to the environment, revealing the existence of limits to plasticity. Two main kinds of limits are imposed to the maximization of phenotypic plasticity, internal and external limits. Internal limits include trade-offs among traits and functional limitations on plasticity expressed in more than one trait. Phenotypic inertia induced by propagule size was explored with cuttings of Buxus sempervirens. The size of the cuttings exerted a significant influence on the phenotypic responses to light, although the responses varied with the trait: thick stems rendered highly plastic leaves in terms of chlorophyll content but plasticity in response to light was higher in thin cuttings in term of leaf thickness. External limits include risks of plasticity in terms of reduced survival under certain environmental conditions. Some plants from stressful environments exhibit a reduced plasticity, which has been linked to a conservative resource use strategy. But plants coexisting in stressful environments exhibit contrasting plasticities, revealing the potential for alternative strategies involving different levels of plasticity even in these environments. This possibility is analysed by exploring fitness costs of plastic responses to shade in woody Mediterranean seedlings simultaneously exposed to either drought or freezing temperatures.

Genetic sources of adaptation and evolutionary constraint in heterogeneous competitive environments

WEINIG, CYNTHIA
University of Minnesota, Department of Plant Biology, 250 Biosciences Center, 1445 Gortner Avenue, St. Paul, MN 55108

Evolutionary biologists have traditionally used statistical genetic approaches to predicting phenotypic evolution. The strength of these approaches, however, is also their greatest weakness: namely, it is possible to understand evolutionary dyanmics without understanding the underlying genes. My lab is focused on identifying genes targeted by selection in heterogeneous competitive settings, as well as how the phenotypic effects of specific genes vary across environments. We use both genetic model plant, *Arabidopsis thaliana*, as well as the wild, near-relative *Brassica rapa*.

In recent studies, we mapped QTL for competitive ability in both *Arabidopsis* and *Brassica*. We observed that several QTL had environment-specific effects on fitness. In addition, a large number of QTL affected the expression of plastic competitive traits (stem elongation) at both early and late developmental stages, suggesting significant evolutionary constraints over ontogeny. Further studies suggest the genetic locus, *GIGANTEA*, may underlie natural variation in petiole elongation, a second characteristic response observed among crowded plants in many species. Using the genome synteny between *Arabidopsis* and *Brassica*, we will ultimately test whether similar or different genetic mechanisms underlie competitive success in these two species and other members of the mustard family.

Poster Abstracts

Listed alphabetically by first author; the presenting author is underlined

1. Induced systemic resistance to herbivory in ramets of a clonal plant network

GÓMEZ, S. & STUEFER, J.F.
Department of Experimental Plant Ecology, Radboud University Nijmegen, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands

Herbivory acts as an important selective pressure in many environments. As opposed to herbivores, plants lack the advantage of mobility to escape their enemies. Instead they can cope with their attackers by expressing defensive phenotypes. Producing constitutively defended phenotypes is assumed to be costly, and therefore plant defense theory presumes inducible defensive phenotypes have evolved to save costs allowing allocation of finite resources to other important functions when defense is not needed.

We investigated the presence of induced resistance after herbivory in potentially independent but physiologically integrated ramet populations of *Trifolium repens*. Our main questions were:

- Is *Trifolium repens* able to induce a defensive phenotype after herbivory?
- Which traits are involved in the induced resistance and are these associated to costs?
- Does clonal integration lead to induced resistance in interconnected but undamaged ramets?
- What are the ecological and evolutionary consequences of systemic expression of induced resistance in a clonal plant network?

Through a series of greenhouse experiments and bioassays (choice tests) we have found that undamaged ramets of clonal plant networks of *T. repens* are able to respond to local herbivore attack by changing morphological and presumably chemical traits. This potentially allows interconnected individuals of clonal plant networks to activate an 'early warning system' when herbivores are present allowing undamaged ramets from the same clonal fragment to switch on their defense system before the actual herbivore attack happens.

2. Plastic and constant developmental traits contribute to adaptive differences in co-occurring *Polygonum* species

GRIFFITH, TIMOTHY M. & SULTAN, SONIA E. [1]
Department of Biology, Wesleyan University, Middletown, CT 06459, U.S.A. [1]Corresponding author

Adaptive differences among species are often thought to result from developmentally constant trait differences. However, functionally related constant and plastic traits may interact to determine the phenotype's adaptive value in particular conditions. We compared shade avoidance traits for two annuals (*Polygonum persicaria* and *P. hydropiper*) that co-occur in pastures with varying plant density and used selection analyses to test trait contributions to fitness in alternative density treatments. Both species expressed plasticity for internode elongation in response to density; *P. persicaria* plants increased internode length and height more in high density than did those of *P. hydropiper*. By contrast, node numbers were relatively constant across density treatments in both species: *P. hydropiper* seedlings consistently produced more nodes than *P. persicaria* seedlings. Increased height was adaptive in high density stands, so *P. persicaria* plants had higher fitness in this environment. However, constant differences in node number contributed to *P. hydropiper's* greater relative fitness at low density, where more nodes and hence leaves enable plants to better exploit light. These differences between species did not result from evolutionary constraints. We discuss how adaptive differences in both plastic and constantly expressed traits may jointly contribute to ecological distribution, including coexistence in patchy habitats.

3. Ecological selection and speciation in sunflowers

GROSS, BRIANA L., LAI, ZHAO, & RIESEBERG, LOREN H.
Department of Biology, Indiana University, Jordan Hall 142, 1001 East Third Street, Bloomington, IN 47405, USA

The homoploid hybrid *Helianthus deserticola* inhabits the desert floor, an environment that is both extreme and divergent compared to those of its two parental species, *H. annuus* and *H. petiolaris*. I am exploring the role of ecological selection in the origin of this species using phylogenetic, quantitative genetic, and genomic techniques. A phylogenetic study indicates that *H. deserticola* may be the product of multiple hybrid speciation events, emphasizing the importance of deterministic forces, perhaps ecological selection, in the speciation process. An analysis of phenotypic selection documented strong selection acting on early generation hybrids between the parental species grown in the *H. deserticola* habitat. Selection on several traits was in the direction of *H. deserticola*, suggesting that ecological selection shaped the morphology and life history of the hybrid species. Genotyping the BC_2Pet cross from the field experiment showed that the strength of selection on individual QTL would allow divergence in the face of gene flow. Finally, I have collaborated in a microarray-based analysis of gene expression in the hybrid species relative to its two parents. Five differentially expressed genes were tested for potential adaptive value, and one was significantly associated with fitness in the BC_2Ann cross from the *H. deserticola* habitat.

4. Understanding the link between environmental heterogeneity and seed dispersal in the invasive annual, *Erodium cicutarium*.

BAYTHAVONG (nee JACOBS), BROOKE S., STANTON, MAUREEN L. & RICE, KEVIN J.
Population Biology Graduate Group, UC Davis, One Shields Avenue Davis, CA USA 95616

Plant distributions are in part determined by environmental heterogeneity on both large (landscape) and small (several meters) spatial scales. Plant populations can respond to environmental heterogeneity via genetic differentiation between large distinct patches, and phenotypic plasticity in response to heterogeneity occurring at small scales relative to dispersal distance. *Erodium cicutarium* has partially invaded serpentine soils in Northern California, which impose harsh and variable abiotic stress on plants growing there. We collected seeds of *E. cicutarium* from dense patches of *Erodium* in spring 2004 and subsequently dispersed them to one of four distances from their maternal homesite (0, 0.5, 1 or 10 m) to examine the relationship between dispersal distance and offspring fitness on serpentine and non-serpentine soils. Preliminary analyses indicate a distinct fitness peak when seeds are dispersed 0.5 meters from their maternal homesite on serpentine patches, while in non-serpentine patches fitness is uniformly higher any distance away from the maternal homesite. These results indicate the potential for differential selection on dispersal distance both on small spatial scales (0.5 meters) and large spatial scales (50 to 100 meters) between patches of serpentine and non-serpentine soils. Ongoing field research is focused on addressing the relationship between phenotypic plasticity and fitness in *E. cicutarium* on small and large spatial scales.

5. Limited costs of wrong root placement in *Rumex palustris* in heterogeneous soils

JANSEN, CORIEN[1], VAN KEMPEN, MONIQUE[1], BÖGEMANN, GERARD M. [1], BOUMA, TJEERD J.[2] & DE KROON, HANS[1]
[1]*Department of Experimental Plant Ecology, Radboud University Nijmegen, Toernooiveld 1, PO Box 9010, 6500 GL Nijmegen, The Netherlands.* [2]*Center for Estuarine and Coastal Ecology, Netherlands Institute of Ecology, PO Box 140, 4400 AC Yerseke, The Netherlands*

Many studies have focused on root proliferation in heterogeneous soils, and the benefits in terms of nutrient acquisition are often limited. Benefits may not necessarily be high if also the costs of ‘wrong’ root placement in patches of limited duration are limited, but these costs are still underexposed in studies of root foraging. We assessed short-term costs that may arise when a nutrient-rich patch induces root proliferation, but then rapidly disappears while a different patch appears at another location.

Rumex palustris plants were grown with a homogeneous or a heterogeneous nutrient application, with the same overall nutrient supply. After roots had proliferated in a nutrient-rich patch, nutrient supply was switched from homogeneous to heterogeneous and vice versa, or a patch appeared at a different location. After a switch in nutrient application, the relative growth rates of the roots were adjusted quickly to the novel pattern of nutrient availability. However, the changes in local root biomass lagged behind the rapid shift in nutrient supply, because of the realized root mass caused by the nutrient pattern before the switch. Despite this slow relocation of root biomass to the new patches, *R. palustris* did not exhibit costs of switching in terms of biomass or nitrogen uptake. One explanation is that the uptake rate per unit root length was increased in new patches. Furthermore, we have indications that redistribution of nitrogen within the plant lowered the costs of strong root growth considerably.

6. How does root morphology and response to nutrients relate to life history traits in ecotypes of *Capsella bursa-pastoris*?

KARLEY, A.J., VALENTINE, T.A., GREIG, J., IANNETTA, P.P.M., SQUIRE, G.R.
Scottish Crop Research Institute, Invergowrie, Dundee, DD2 5DA

Within-species variation in the physiology and life history traits of weeds could be an important component of ecological diversity, particularly in intensively managed arable systems. Using *Capsella bursa-pastoris* as a model arable weed, we have characterised the extent of intra-specific diversity for above- and below-ground traits that could impact on resource allocation and, therefore, interactions with other trophic groups.

Shepherd's purse, or *Capsella bursa-pastoris*, is a common weed of arable fields in the UK and Northern temperate regions. Twenty-one accessions collected from parental lines sourced from arable sites across the UK have been grown *ex situ* and significant within-species variation has been demonstrated in plant development, biomass and leaf production, shoot architecture and nitrogen nutrition. The hypothesis that variation in root architecture and responses to soil nutrients contributes to these differences has been tested in a subset of accessions. Significant variation between eight accessions in seedling root length, lateral branching and root hair production could be partially related to differences in rates of plant development and nutrient acquisition. Border cell production varied between accessions and in response to nitrogen and phosphorus deficiency. The potential impact of within-species variation on foliar herbivores and soil trophic groups is currently being explored.

7. Interactive effects of mechanical stress and shade on plasticity of ten genotypes in *Potentilla reptans*

LIU, YUN.[1,2] & ANTEN, NIELS P.R.[1]
[1]Department of Plant Ecology, Utrecht University, P.O. Box 800.84, 3508 TB, Utrecht, the Netherlands; [2]College of Agronomy and Life sciences, College of source and environment, Southwest University, Chongqing, 400716, China

It has been argued that responses to mechanical stress (such as wind) should be suppressed in dense vegetation since the resultant shorter stature would lead to lower fitness. But this point has been debated. We therefore investigated the interactive effects of canopy shading (15% of daylight with a red-to-farred ratio, R/FR, of 0.3 vs. 50% daylight and R/FR = 1.2) and mechanical stress (0 or 40 daily brushes with a duster) on the growth and allocation of 10 genotypes of the clonal plant *Potentilla reptans*. All genotypes exhibited typical 'shade avoidance' responses under low R/FR, such as the production of fewer leaves with longer petioles, and reductions in petiole diameter, stolon growth and root allocation. Brushed plants produced more leaves with shorter petioles, more stolons and greater root allocation. All responses to brushing occurred independent of light treatment indicating that responses to mechanical stress were not suppressed under canopy shading. Interestingly the responses to mechanical stress were opposite in nature to the responses to light quality, in other words, low mechanical stress induced responses similar to low R/FR. It is possible therefore that in dense vegetation, wind shielding by neighbours provides an additional cue that induces shade avoidance.

8. Spatial heterogeneity in nutrient supply drives plant nutrient and biomass responses to multiple global change drivers in model grassland communities

MAESTRE, FERNANDO T. & REYNOLDS, JAMES F.
Department of Biology, Duke University, Phytotron Building, box 90340, Durham, NC 27708, USA

The spatial pattern of nutrient supply (nutrient heterogeneity) influences the productivity of plant communities, but it is virtually unknown how nutrient heterogeneity and global change drivers interact to affect plant performance and ecosystem functioning. We conducted a microcosm experiment to evaluate the effect of simultaneous changes in the atmospheric concentration of CO_2 ([CO_2]), nutrient heterogeneity (NH), nutrient availability (NA) and species evenness (SE) on the biomass and nutrient content of assemblages formed by *Lolium perenne*, *Plantago lanceolata* and *Holcus lanatus*. NH modulated the effects of NA on biomass production and aboveground nitrogen content (interaction NH x NA), and of elevated CO_2 on biomass production (interaction NH x CO_2). SE had limited effects on the response of most of the assemblages evaluated. Assemblage biomass was stimulated by elevated [CO_2] only under high NA conditions. Such increase was more pronounced when nutrients were heterogeneously supplied. Under this circumstances, assemblages exhibited precise root foraging patterns, and had higher total, above- and belowground biomass. For a given increment in NA, the assemblages had higher biomass and nitrogen content when the nutrients were heterogeneously supplied. Our results show that NH has the potential to influence the response of plant assemblages to simultaneous changes in [CO_2], NA and biodiversity.

9. Adaptive radiation of photosynthesis and life-history traits in the Hawaiian lobeliads

MONTGOMERY, REBECCA A., GIVNISH, THOMAS J. & GOLDSTEIN, GUILLERMO
Department of Botany, University of Wisconsin, 430 Lincoln Dr. Madison, WI 53706, USA

Six endemic genera/sections of lobeliads (Campanulaceae) occupy the full range of light environments on moist sites in the Hawaiian islands, from open alpine bogs to densely shaded rainforest interiors. The group displays an incredible range of leaf morphology (simple to pinnately-lobed leaves), stature (0.3-14 m tall) and growth form (shrubs to trees; unbranched, palm-like and branched; terrestrial, epiphytic or stem succulent). Lineages vary in dispersal, seed size (0.3-3 mm) and growth rates. In addition, species have diverged in photosynthetic adaptations across the sun-shade continuum. Here we give an overview of physiological and life history trait variation across the Hawaiian group, highlighting our physiological research in field populations and common gardens. We argue that the Hawaiian lobeliads have undergone a radiation in photosynthetic adaptations to sun vs. shade involving (1) shifts in gas exchange under both static and fluctuating light conditions (2) differences in resistance to photoinhibition and (3) changes in leaf morphology. These shifts in traits result from both environmental and genetic differences among taxa and appear to be adaptive, enhancing C gain in their habitat of origin. Limitations in response of certain taxa to the light environment are hypothesized to result from the influence of multiple limiting resources.

10. Genetic differences in patterns of growth, development, and plastic response to environmental quality in a perennial plant

MORIUCHI, KEN S. & WINN, ALICE A.
Department of Biological Science, Florida State University, Tallahassee, FL, U.S.A. 32306-1100

The natural environments of plants comprise many factors that can vary independently, and plants must integrate development over these factors to produce an appropriate phenotype. Theory for plant response to stress suggests that plants may integrate multiple environmental variables by responding to overall quality of environments defined as the average growth rate in an environment. In previous work we showed that individuals of *Viola septemloba* (Violaceae) alter their phenotype in response to environment quality and the observed responses are consistent with the predictions of stress response theory. Differences in traits of plants grown in low- and high-resource environments were not simply the result of differences in size, but arose because plants followed different developmental trajectories in the two environments. Here we compare the developmental trajectories among eight inbred lines of *V. septemloba* grown in low- and high-resource environments. We report variation among lines and significant line by environment interactions for several traits indicating genetic variation for developmental trajectory and for the pattern of alteration of development in response to the environment. Lines with distinct developmental trajectories and flexibilities permit dissection of the genetic basis of developmental response to the environment and the developmental integration of multiple trait responses to complex environments.

11. Long-term interactions of two desert shrubs

O'BRIEN, ERIN E. & MAHALL, BRUCE E.
Ecology, Evolution and Marine Biology, University of California, Santa Barbara, Santa Barbara, CA 93106-9610, USA

Larrea tridentata and *Ambrosia dumosa* co-dominate many parts of the Mojave Desert to the virtual of exclusion of other perennials, and they both display root communications that influence root growth of neighbors. *L. tridentata* produces an indiscriminant allelopathic root exudate that slows root growth in nearby plants and likely contributes to the regular spacing of this species. *A. dumosa* displays self and population level recognition and segregates roots among intra-population but not inter-population individuals. Nearly three decades ago, a removal experiment was initiated and short-term effects indicated that inter-specific interference was stronger than intra-specific interference. 28 years later we surveyed all plants in the experimental plots to determine the community level effects of the removal treatments. The size and density of *L. tridentata* were not significantly affected by the removal of *A. dumosa*. However, *A. dumosa* showed a significant increase in density with the removal of *L. tridentata*, despite *L. tridentata* representing a much smaller fraction of the number of plants and aboveground biomass present in a plot. These results suggest that, where present, *L. tridentata* may dictate community structure in the Mojave due to its longevity and potent interference mechanisms.

12. Changes in leaf biomechanics and photosynthesis in response to different light and nutrient availability

ONODA, YUSUKE[1], ANTEN, NIELS P. R.[1], SCHIEVING FEIKE[1] & PONS, THIJS L.[2]
[1]Department of Plant Ecology and [2]Department of Plant Ecophysiology Utrecht University, PO box 800.84, 3508TB Utrecht, The Netherlands

Leaf mechanical properties are important to maintain photosynthesis for a long time. In the present study, we studied the effects of light and nutrient availabilities on leaf biomechanics and photosynthesis. We analysed force-displacement curves that were obtained by punch-and-die tests, and strength (maximum force to penetrate per unit area), toughness (total energy to penetrate) and an indicator of leaf rigidity (initial slope of force-displacement curve) were evaluated. High light increased strength, toughness, rigidity and Pmax (light saturated rate of

photosynthesis). The relative increases in strength and toughness with light availability were greater than the increase in Pmax. High nutrient availability did not change strength and toughness, but slightly reduced leaf rigidity and increased Pmax. Therefore Pmax was not correlated with strength or toughness across different nutrient availabilities. Across both light and nutrient treatments, strength (or toughness) was strongly correlated with LMA (leaf mass per area), but its relationship was not proportional. Strength/LMA decreased with high light irrespective of nutrient availabilities, which suggests that mass use efficiency for strength was higher in low light plants and independent from nutrients.

13. Growth and plasticity in dense canopies; molecular integration of multiple signals

PIERIK, RONALD, DJAKOVIC, TANJA & VOESENEK, LAURENTIUS A.C.J.
Department of Biology, Section Plant Ecophysiology, Utrecht University, Sorbonnelaan 16, 3584 CA Utrecht, the Netherlands

Plants growing in dense vegetations ensure light capture through so-called shade avoidance responses to neighbors which include upward leaf movement and increased shoot elongation. Although shade avoidance is a well-known phenomenon, information about its mechanistic basis is still limited. We show here that the gaseous plant hormone ethylene stimulates these responses in dense tobacco stands, leading to enhanced light capture and thus competitive power. Ethylene may act as a chemical neighbor detection signal, but also modulates signaling cascades induced by other canopy signals, including blue light intensity and red:far-red (R:FR) ratio. Ethylene and light-induced shade avoidance responses further involve the hormones auxin and gibberellic acid (GA). This web of signals seems to, at least partly, converge at one molecular point; the DELLA proteins. These are growth-inhibitory transcription factors that are destabilized upon GA signaling. We used DELLA-GFP reporter lines in Arabidopsis to show that DELLA abundance is decreased in accordance with increased shoot elongation under low R:FR or low blue. This is related, not only to GA itself, but also to auxin and possibly ethylene as well as the light signals directly. Suggestively, DELLA proteins act as integrators of different canopy and hormone signals to regulate shade avoidance responses.

14. Plastic responses to mechanical stress: adaptive significance of morphological and architectural adjustments.

PUIJALON, S., BORNETTE, G. & SAGNES, P.
UMR CNRS 5023, Ecology of Fluvial Hydrosystems, Université Claude Bernard-Lyon1, 43 boulevard du 11 novembre 1918, 69622 Villeurbanne cedex, France

Plants permanently encountering mechanical stimulation (wind, water movements) often exhibit morphological changes that can hardly be inferred from results concerning resource stresses. Moreover, the adaptive value of these changes is poorly studied, particularly for higher plants submitted to flow stress. This work aimed at measuring plastic adjustments to plant morphology and clonal architecture, as well as their adaptive value, observed in two aquatic plant species (*Berula erecta* and *Mentha aquatica*) exposed to current stress. The morphological variations, hydrodynamic performances (drag and drag coefficient) and fitness-related traits (vegetative growth and clonal multiplication) were measured on plants sampled in situ along a flow velocity gradient. *B. erecta* displayed size reduction and low plant drag at higher flow velocities, which probably expresses escape strategy. The clonal growth pattern contributes to reducing the damage risk, through biomass reallocations: one tall ramet at low velocity, but shorter individuals with many interconnected stolons at high velocity. For *M. aquatica*, morphological differences along the gradient did not lead to greater hydrodynamic performance, suggesting tolerance strategy. Plant size increased with increasing velocities, suggesting an indirect effect of current favouring growth. For both species, these changes were not associated to lower plant fitness at high velocities.

15. How plants respond to mechanical stress: from *Arabidopsis* to the real world of complex growth forms

ROWE, N.[1], & PAUL-VICTOR, C.[1,2]
[1]*Botanique et Bioinformatique de l'Architecture des Plantes, UMR 5210 CNRS, TA40/PS2, Boulevard de la Lironde, F-34398 Montpellier, France;* [2]*Institut of Environmental Sciences, University of Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland*

Plant development is strongly influenced by mechanical perturbation and the 'mechanical environment' of a plant. Different growth forms have evolved different ways of adapting to different mechanical conditions. This study analyses the effects of mechanical perturbation on the biomechanics of plant growth forms. We studied the response of *Arabidopsis thaliana* to mechanical perturbation under controlled laboratory conditions. The response included a significant reduction in length, flexural stiffness and Young's elastic modulus of the inflorescence axis. Surprisingly, variation in mechanical properties occurred without modification in diameter but with changes in the proportions and densities of tissues within the stem. In the real world, especially in the tropics, diverse growth forms can have extremely wide-ranging mechanical properties of the stem. Different growth forms such as trees, lianas and epiphytes respond to the mechanical environment in different ways and can show remarkable differences in mechanical properties both during ontogeny and under differing mechanical environments. We discuss how phenotypic plasticity of mechanical architectures can be studied in the laboratory, with model plants such as *Arabidopsis* as well as in the field with far less control over potential environmental effects and where growth forms and development can be far more complex than a laboratory model.

16. Which phenotypes are adaptive? Insights from nearly-dead *Arabidopsis* plants

SHAKOOR, AQSA, PATTERSON, ANGELICA E. & CALLAHAN, HILARY S.
Biological Sciences, Barnard College, Columbia University, 3007 Broadway, NY, NY 10027 U.S.A.

Many plant studies have documented how trait variation influences lifetime fitness. Although lifetime fitness estimates involve scoring both reproductive output and survivorship, few studies link survivorship itself with a variable trait or traits. Presumably, rapid decay of dead plant tissues has hindered application of a straightforward technique employed in animal studies — scoring traits in survivors and corpses. We have developed and continue to develop protocols for imposing lethal and sub-lethal stresses at various developmental stages in the *Arabidopsis thaliana* life cycle. Coupling these with appropriate control protocols, we test for co-variation between survivorship and functional traits. Recently, our lab has conducted studies involving lethal and sub-lethal water deprivation imposed upon recombinant inbred lines (RILs) from the Bay-Shahdara population. Our first study documented variation among RILs in rosette root traits but not in survivorship. A larger study then examined whether survivorship differences among RILs co-varied with previously documented seedling root architecture traits. We discuss how our approach will be useful in future studies examining not only whether and how stress-induced phenotypes affect survival, but also more complete investigations of whether stress-induced plasticity is adaptive, because such a question must examine trade-offs between survival and reproduction.

17. CO_2-mediated effects of foliar sugar concentration and developmental timing in *Arabidopsis*

SPRINGER, CLINT J. & WARD JOY K.
Department of Ecology and Evolutionary Biology, University of Kansas, 8028 Haworth Hall, 1200 Sunnyside Avenue, Lawrence, KS 66045, USA

Elevated atmospheric CO_2 has been shown to both delay and accelerate the developmental timing of plants, and is often associated with increased foliar sugar concentrations. Recent studies indicate that sugars may play a role as signaling molecules that may influence floral timing. We investigated the role of CO_2-induced changes in foliar sugars on developmental timing by growing four closely related genotypes of *Arabidopsis* at three concentrations of CO_2 (270 ppm, pre-industrial; 380 ppm, present; 700 ppm, future). The four genotypes included: one previously selected for high seed production at elevated CO_2 (SG); a control genotype randomly selected at elevated CO_2 (CG); and two parental genotypes initially crossed to produce SG and CG (P1 & P2). Foliar sugar concentrations increased between 270 and 700 ppm CO_2 for all genotypes. In addition, all genotypes exhibited delayed floral initiation between 270 to 380 ppm, as sugars increased. However, only SG exhibited delayed floral initiation between current (380 ppm) and future (700 ppm) CO_2 concentrations. Thus, CO_2-mediated changes in floral timing that are associated with increased sugars may only occur at CO_2 concentrations below the current value, and may only occur above the current CO_2 value if effects of selection are considered.

18. Root growth responses to soil physical properties.

VALENTINE, T.A., BINNIE K., HANS J., MCKENZIE, B.M. & BENGOUGH A.G.
Scottish Crop Research Institute, Invergowrie, Dundee, DD2 5DA.

During growth through soil, roots are often physically constrained, by mechanical impedance, water stress, and oxygen deficiency. The strength of soil depends not only on the soil type, but also its water content. Insufficient water may result in soil becoming too hard for roots to penetrate, whilst excess water can result in hypoxia. Variability within soil structure also affects how roots penetrate a particular soil, as roots may use cracks and continuous pores to penetrate even very hard soils. Plants have several mechanisms for overcoming physical constraints for example, increasing exudation and production of border cells to decrease frictional resistance, forming aerenchyma to transport oxygen to root tips, and changing root and root system morphology. We use a suite of techniques to investigate these responses in both controlled (lab) and more variable field conditions. Field investigations include soil physical constraints throughout the growing season under different soil managements, and how these affect root growth and root gene expression. In the laboratory we are developing methods for detailed analysis of the mechanisms controlling root growth, for example, using confocal microscope images of agar grown roots, and screening for root mutants which have altered border cell complement.
Funding Acknowledgements: BBSRC and SEERAD

19. Genotypic differences in light capture characteristics in a 5 year old competition experiment of the clonal plant *Potentilla reptans*

VERMEULEN, P.J.[1], ANTEN, N.P.R.[1], STUEFER, J.F.[2] & DURING, H.J.[1]
[1]Department of plant ecology, Utrecht Univerisity, P.O box 800.84 NL-3508 TB Utrecht, The Netherlands. [2]Department of Ecology, Radboud University Nijmegen, Toernooiveld 1 6525 ED, Nijmegen ,The Netherlands.

Much research has focused on the ability of plants to change their phenotype to different light conditions. Few studies however have linked the plasticity of different genotypes with their ability to compete with other genotypes for light in dense vegetation. Here we present the shoot characteristics of the genotypes that have remained in the vegetation after 5 years of competition between 10 genotypes of the clonal plant *Potentilla reptans*, linked with their light capture within the vegetation.

We harvested 100 individual leaves in each of the 8 competition plots, measured leaf and petiole characteristics and identified the genotype by genetic analysis. Within each plot light distribution was measured and used to calculate the relative light availability for each height. Light capture was calculated for each individual leaf using the height and leaf area of the individual leaf.
We will address the following questions: Do the genotypes differ in the way they adjust their leaf morphology in the vegetation? Do the differences between genotypes allow them to utilize different positions in the vegetation by efficiently capturing light per unit invested aboveground biomass (Φ_{mass})? Does the genotype that has the highest frequency of leaves in the vegetation also capture the most light?

20. Petiole length differences in *Trifolium repens*: Cell size or cell number?

WEIJSCHEDE, JELMER., ANTONISE, K., & HUBER, H.
Radboud University Nijmegen, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands

Many plants show typical shade-avoidance responses when they encounter shaded conditions. Two processes, cell elongation and cell division can contribute to shade induced elongation processes. It is still unclear, however, whether selection acts on both processes separately or in concert.
We studied shade induced petiole elongation in 36 *Trifolium repens* genotypes which all differed in constitutive petiole length as well as in their ability to express shade induced elongation processes. Epidermal prints of the petioles subjected to simulated canopy shade and control conditions were made and cell length and total cell number were assessed to answer the following questions:

- How do cell size and cell number explain the differences in constitutive petiole lengths?
- How do changes in cell size and cell number contribute to shade induced petiole elongation?

Our results show that different mechanisms contribute to constitutive petiole length and shade induced elongation. In addition, there was a trade-off between cell-elongation and cell-division in the shade induced petiole elongation response. While some genotypes elongate their petioles by elongating the cells, others simply produce more cells.
Anatomical processes underlying shade induced petiole elongation will enhance our knowledge of the mechanisms involved in the evolution of shade avoidance responses.

Participants

Name	Establishment	Country	Email	Research Interests
Ackerly, David	University of California, Berkeley	USA	dackerly@berkeley.edu	Organizer
Aphalo, Pedro J.	University of Jyväskylä	Finland	pedro.aphalo@cc.jyu.fi	Photobiology, neighbours, shade-avoidance, red:far red ratio, ultraviolet radiation, trees, growth analysis, statistical applications, mineral nutrition, drought
Baythavong (nee Jacobs), Brooke	University of California, Davis	USA	bsjacobs@ucdavis.edu	Dispersal, phenotypic plasticity, maternal environmental effects, local adaptation, environmental heterogeneity
Bornette, Gudrun,	UMR CNRS 5023 Ecology of fluvial hydrosystems	France	bornette@avosnes.univ-lyon1.fr	Community ecology, disturbances, adaptations, plant strategies, phenotypic plasticity, floods
Bothwell, John	Marine Biological Association	UK	jhbot@mba.ac.uk	Algae, Development, Calcium, Ectocarpus, Polarity, cell cycle
Bradshaw, Tony	Liverpool University	UK	tonybradshaw@blueyonder.co.uk	See speaker abstract
Brauns, Mascha	University of Göttingen	Germany	mbrauns@gwdg.de	Biodiversity, litter bags, deciduous forest ecosystem, litter traps, biomass production, mono and mixed species stands, nutrient cycles, forest canopy research
Breuker, Casper	University of Manchester	UK	casper_j_breuker@yahoo.co.uk	Evo-devo, plant defences, insect-plant interactions, resistance, morphometrics, adaptation, functional evo-devo
Buggs, Richard	Gateshead	UK	richard.buggs@cantab.net	Ecology, plant science, evolution, sexual systems, polyploidy, *Mercurialis annua*, environmental selection, hybid zones, range boundaries, biogeography
Callahan, Hilary	Barnard College, Columbia University	USA	hcallahan@barnard.edu	Ecological genetics, phenotypic plasticity, natural selection, *Arabidopsis thaliana*, evolutionary functional genomics
Curtis, Peter	Ohio State University	USA	curtis.7@osu.edu	Discussion leader
de Kroon, Hans	Radboud University Nijmegen	The Netherlands	h.dekroon@science.ru.nl	Plasticity, roots, foraging, fitness, costs and benefits, allocation, evolution
Donohue, Kathleen	Havard University	USA	kdonohue@oeb.harvard.edu	See abstract
Fitter, Alastair	University of York	UK	ahf1@york.ac.uk	Discussion leader
Galen, Candace	University of Missouri at Columbia	USA	GalenC@missouri.edu	See speaker abstract
Gómez, Sara	Radboud University Nijmegen	The Netherlands	s.gomez@science.ru.nl	Induced plant defenses, plant-insect interactions, plant-plant communication, clonal integration
Gray, Julie	University of Sheffield	UK	j.e.gray@sheffield.ac.uk	
Griffith, Timothy	Georgetown College	USA	tgriffi0@georgetowncollege.edu	Phenotypic plasticity, ecological specialization, geographic range limits, photomorphogenesis, light cues, photoperiodism, population genetics
Gross, Briana	Indiana University	USA	brgross@indiana.edu	Speciation, genetics, evolution, ecological genetics, hybridization

Gruntman, Michal	Ben-Gurion University	Israel	gruntman@bgu.ac.il	Developmental plasticity in plants, evolutionary ecology, plant ecophysiology, plant reponses to herbivory, self/nonself discrimination, physiological coordination
Hetherington, Alistair	Lancaster University	UK	A.Hetherington@lancaster.ac.uk	Stomata, signalling, development, physiology, calcium
Hodge, Angela	University of York	UK	ah29@york.ac.uk	See speaker abstract
Huber, Heidrun	Radboud University	The Netherlands	H.Huber@science.ru.nl	Phenotypic plasticity, adaptation, selection, ontogeny, development, reproductive allocation, maternal effects, evolutionary ecology, costs & benefits of plasticity
Hutchings, Mike	University of Sussex	UK	M.J.Hutchings@sussex.ac.uk	Plant ecology, clonal plants, responses to environmental heterogeneity, root ecology, competition, conservation ecology, restoration ecology
Jansen, Corien	Radboud University Nijmegen	The Netherlands	C.Jansen@science.ru.nl	Plasticity, root morphology, selective root placement, flood tolerance, soil heterogeneity, costs of plasticity
Karley, Alison	Scottish Crop Research Institute	UK	akarle@scri.ac.uk	Nutritional physiology, plant development, architecture, insect herbivory, trophic interactions, nutrient transport
Kessler, Andre	Cornell University	USA	ak357@cornell.edu	See speaker abstract
Lake, Janice	University of Sheffield	UK	j.a.lake@sheffield.ac.uk	Ecology, physiology, stress responses, signalling systems, Arabidopsis
Liu, Yun	Utrecht University	The Netherlands	Y.Liu@bio.uu.nl	Allometry, allocation, biomechanics, fitness, growth, plasticity, R/FR, thigmomorphogenesis
MacCallum, Catriona	Public Library of Science	UK	cmacallum@plos.org	ecology, evolution, conservation
Maestre Gil, Fernando T	Universidad Rey Juan Carlos	Spain	fernando.maestre@urjc.es	Plant-plant interactions, global change, environmental heterogeneity, spatial ecology, ecosystem function, arid environments, plant-soil interactions, restoration ecology
McConnaughay, Kelly	Bradley University	USA	kdm@bradley.edu	Allocation theory, plasticity, chemical defense, physiological ecology, global change ecology
Montgomery, Rebecca	University of Minnesota	USA	rebeccam@umn.edu	Ecophysiology, tropical ecology, evolutionary physiology, forest ecology, plasticity, woody plants, adaptive radiation
Moriuchi, Ken	Florida State University	USA	moriuchi@bio.fsu.edu	Life history, heterogeneous environments, stress response, allocation, resource acquisition
Mukherjee, Jayanti	Utah State University	USA	jayanti@cc.usu.edu	Plant development, drought tolerance, phenotypic plasticity, evolution and consequences of plasticity, plant ecophysiology, plant eco-genetics, molecular basis of drought tolerance, herbivory, competition and plasticity
Novoplansky, Ariel	Ben-Gurion University of the Negev	Israel	anovopla@bgumail.bgu.ac.il	See speaker abstract
O'Brien, Erin	University of California, Santa Barbara	USA	eobrien@lifesci.ucsb.edu	Root growth, plant interactions, root communication, plant signalling, root tropisms
Odling-Smee, John	Oxford	UK	john.odling-smee@anthro.ox.ac.uk	Niche construction, evolution, ecology
Onoda, Yusuke	Utrecht University	The Netherlands	y.onoda@bio.uu.nl	Acclimation, biomechanics, photosynthesis, light, nutrient, leaf anatomy, Plantago major, toughness
Paul-Victor, Cloé	University of Zurich	Switzerland	cloepv@uwinst.unizh.ch	Evolution, development, biomechanics, growth form, phenotypic plasticity, ecology, coexistence

Pierik, Ronald	Utrecht University	The Netherlands	r.pierik@bio.uu.nl	Canopy, signal transduction, hormones, light signaling, crosstalk, shade avoidance, growth, ecophysiology
Piola, Florence	Université Claude Bernard Lyon1	France	piola@univ-lyon1.fr	
Puijalon, Sara	University Lyon1	France	puijalon@avosnes.univ-lyon1.fr	Phenotypic plasticity, stress, ecomorphology, clonality, hydrodynamics, submerged aquatic vegetation, fitness
Pujol, Benoit	University of Oxford	UK	benoit.pujol@plants.ox.ac.uk	Quantitative genetics, phenotypic plasticity, sex-limited gene effects, genetic correlations, population admixture, range expansion, reproductive systems, phenotypic evolution, microevolutionary responses
Rowe, Nick	University of Montpellier	France	nrowe@cirad.fr	Plant growth forms, biomechanics, evolution, ecology, phenotypic plasticity, development
Rubio de Casas, Rafael	Universidad Complutense de Madrid	Spain	rrubioca@bio.ucm.es	Plant Ecology, phylogeography, evolution
Schmitt, Johanna	Brown University	USA	Johanna_Schmitt@brown.edu	See speaker abstract
Schultz, Jack	Pennsylvania State University	USA	ujq@psu.edu	See speaker abstract
Slater, Holly	Lancaster University	UK	h.slater@lancaster.ac.uk	Organizer
Smith, Harry	Nottingham	UK	harry.smith@nottingham.ac.uk	See speaker abstract
Springer, Clint	University of Kansas	USA	cjs@ku.edu	Elevated CO_2, plant developmental timing, evolution
Stenøien, Hans K.	Norwegian University of Science and Technology	Norway	stenoien@bio.ntnu.no	Population genetics, molecular ecology, molecular evolution, Arabidopsis, primitive plants, epigenetics, gene expression
Storkey, Jonathan	Rothamsted Research	UK	jonathan.storkey@bbsrc.ac.uk	Agro-ecosystems, plant competition, ecosystem function, modelling, plant-invertebrate interactions
Sultan, Sonia	Wesleyan University	USA	sesultan@wesleyan.edu	Organizer
Taylor, Gail	University of Southampton	UK	gt1@soton.ac.uk	
Valentine, Tracy	Scottish Crop Research Institute	Scotland	TVALEN@scri.sari.ac.uk	Roots, soil, physical properties, border cells, barley, exudation, Fluorescence imaging
Valladares, Fernando	CSIC Madrid	Spain	valladares@ccma.csic.es	See speaker abstract
van Tienderen, Peter	University of Amsterdam	The Netherlands	tienderen@science.uva.nl	Hybridization, cold adaptation, self incompatibility, polyploidy, flooding tolerance
Vermeulen, Peter	Utrecht University	The Netherlands	p.j.vermeulen@bio.uu.nl	Plasticity, evolution, canopy analysis, game theory, clonal plants, modelling, competition
Voesenek, Rens	University of Utrecht	The Netherlands	L.A.C.J.Voesenek@bio.uu.nl	See speaker abstract
Vogel, Johannes	The Natural History Museum	UK	Natalie.Bell@nhm.ac.uk	Population biology, conservation of biodiversity, evolutionary biology, phylogeny, ferns, bryophytes, dna barcoding, science in society

Weijschedé, Jelmer	Radboud University Nijmegen	The Netherlands	j.weijschede@science.ru.nl	Plasticity, shade avoidance, genotypic variation, evolution, anatomical mechanism, Trifolium repens, selection, plant-environment interactions, evolutionary ecology
Weinig, Cynthia	University of Minnesota	USA	cweinig@umn.edu	See speaker abstract
Woodward, Ian	University of Sheffield	UK	f.i.woodward@sheffield.ac.uk	New Phytologist
Young, Jayne	University of Sheffield	UK	j.young@sheffield.ac.uk	New Phytologist