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**iGRAD-Plant – An International
Graduate Program for Plant Science
„The Dynamic Response of Plants
to a Changing Environment“**

Introduction

The International Graduate Program for Plant Science (iGRAD-Plant) is offering a structured PhD program with excellent research possibilities for young scientists. iGRAD-Plant is a joint program with the Jülich Research Center (ICG-3 Phytosphere) and the Genetics Program of the Michigan State University (MSU), East Lansing, USA. The Graduate Program was established in June 2009 with the financial support of the German Research Council.¹ Since then, the iGRAD-Plant program offers an excellent scientific training in modern plant sciences, interdisciplinary research projects, and an innovative Transferable Skills program to 17 excellent graduate students coming from seven different countries. The iGRAD-Plant faculty consists of 11 junior and senior faculty members at HHUD and the Jülich Research Center, and 15 faculty members at MSU, one of the strongest plant research groups in the United States. The partners at MSU contribute complementary expertise in genomics, bioinformatics, cell biology, and biochemistry. In addition, the international collaboration provides a rich environment for graduate training and promotes mobility and integration of graduate researchers into the international research community. The long-term goal of the iGRAD-Plant program is to evolve the partnership between HHUD and MSU into a joint degree program, through which a student will be able to earn a PhD degree granted cooperatively by both universities.

Research

In contrast to most animals and microorganisms, plants are sessile organisms, and thus are not able to evade unfavorable environmental change by migration or flight. Instead, plants have evolved multiple complex mechanisms to cope with environmental change. These range from the production of dormant stages such as seeds, which enable plants

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to outlast adversarial growth conditions through the seed bank and distribution over long distances to explore new terrain, to rapid responses at the cellular level, such as the hypersensitive response to pathogen attack or production of antioxidants to cope with oxidative stress. In addition, due to allelic variation, many genetic traits show considerable plasticity in natural populations, thus defining a broad reaction norm (coping range) within which selection can operate to enable the fittest to survive. Consequently, the study of plant adaptation to changing environments is a broad field, ranging from population dynamics to cell biology. Within this broad context, the specific focus of iGRAD-Plant Graduate Program is on the dynamic molecular changes in response to environmental cues at the cellular and tissue levels, such as signal transduction pathways, metabolic and physiological responses, and biochemical adaptation. This focused approach is complemented by exploring the effects of allelic variation on specific cellular traits, such as the antioxidant defense system and by a comprehensive set of non-invasive and destructive phenotyping tools that have been developed and contributed by our partners at the Jülich Research Center (ICG-3 Phytosphere) and at Michigan State University. Under the umbrella of the common research theme, the scaffold of iGRAD-Plant is built by three parallel and complementary research thrusts; (i) Photo-oxidative stress and anti-oxidative defense; (ii) Intrinsic and extrinsic control of plant growth in response to environmental cues; (iii) C4 photosynthesis as an adaptation to abiotic and biotic stress (Fig. 1).

Fig. 1: Diagram depicting the three major research thrusts forming the iGRAD-Plant Graduate Program. All groups have access to the joint project platforms and will actively participate in the structured PhD training program.

Photo-oxidative stress and anti-oxidative defense

Photo-oxidative stress is related to the light-induced formation of reactive oxygen species (ROS) in the chloroplast and represents one of the most important stress factors for land plants. Photo-oxidative stress emerges from the limitation of photosynthetic light utilization and is thus not only restricted to high light intensities, but will be generated under all conditions that limit productive use of harvested light energy. The photo-oxidative potential of photosynthesis is buffered by the chloroplast antioxidant defense system. A combinatorial network of enzymes and low molecular weight antioxidants detoxifies ROS inside chloroplasts and diminishes the risk for photo-oxidative damage. In response to unfavorable conditions, such as fluctuating light and temperature conditions, the antioxidant defense system is activated: Gene expression is induced and low molecular weight antioxidants accumulate. Three projects at HHU in the groups of Prof. Magarete Baier, Prof. Peter Jahns and Dr. Nicole Linka are centered on photo-oxidative stress and the plant anti-oxidative defense system; these projects are closely interfaced with ongoing research in the several groups at MSU. Thereby, the projects range from the characterization of Quantitative Trait Loci (QTLs), which are involved in adaptation/acclimation of the chloroplast antioxidant system in different plant ecotypes (Prof. Baier), over the analysis of mutant plants affected in the xanthophyll cycle activity or energy dissipation mechanisms exposed to different light and temperature regimes (Prof. Jahns), to the role of plant peroxisomes in the oxidative stress response (Dr. Linka).

Intrinsic and extrinsic control of growth in response to environmental cues

Three projects at the Jülich Research Center and HHU are examining the relation between environmental cues, such as temperature, and the control and rate of plant growth. In this context the groups at Jülich Research Center (Dr. Schneider and Dr. Walter) provide the groups at HHU and MSU with access to a state-of-the-art non-invasive plant phenotyping platform that permits detailed non-invasive investigations of plant performance. One aspect of balanced plant growth is the requirement for the coordination of complex developmental, metabolic and transport processes in distant tissues and organs. As a particular prerequisite of a highly coordinated action via long-distance pathways, the different tissue types and organs of a given plant must be tightly hydraulically coupled. On the other hand, individual tissues and organs must act like isolated systems, given that they have to be selectively supplied with different amounts of water, nutrients and metabolites depending on local environmental conditions and developmental stage. Therefore, in the group of Dr. Schneider (Jülich Research Center) plants are investigated under controlled conditions to test the hypothesis that (colloid)-osmotically active metabolites such as sugars and (glyco)proteins and their local dynamics of conversion and/or translocation provide dynamic driving forces for coordinated water and solute movement in higher plants. Another aspect that influences plant growth is that plants are exposed to an ever-changing temperature cycle, which differs in phasing and amplitude between above- and belowground environments. The project of Dr. Walter's group (Jülich Research Center) aims at gaining a mechanistic understanding of the interaction of growth and temperature, which will provide fundamental

information that is relevant to studies of heat and cold tolerance (where deviations from average temperatures are problematic) with potential for crop breeding. In addition to the plant shoot also the root system can sense changes in the availability of nutrients, water supply, minerals and also temperature, and respond by adjusting growth direction and growth rate, and by initiation of lateral roots. In *Arabidopsis* and several other plant species, peptides of the CLE family have been shown to affect shoot and root meristem development. Therefore in Prof. Simon's group at the HHUD the role of one of these peptides, CLE40 in signaling during root and shoot growth of *Arabidopsis* will be elucidated.

C4 photosynthesis as an adaptation to abiotic and biotic stress

Among the land plants, angiosperms are unrivalled in their photosynthetic capacity and, hence, in their growth. The evolutionary success of angiosperms indicates that adaptive innovations give their leaves superior photosynthetic capacity. This culminates with the evolution of C4 photosynthesis, the most efficient mode of photosynthesis. C4 plants contribute about 25 percent of total terrestrial photosynthesis, although they account for only 3 percent of all vascular plants. The high efficiency of C4 photosynthesis is attributed to its effective containment of photorespiratory carbon losses, which is accompanied by increased water- and nitrogen-use efficiencies. C4 photosynthesis is a complex, multigenic trait associated with distinct anatomical, physiological, and biochemical leaf characteristics. C4 plants have evolved from C3 ancestors at least 45 times independently within the angiosperms, indicating that the evolutionary trajectory towards C4 photosynthesis must be relatively simple and that C3 angiosperms are predisposed to evolving C4 photosynthesis. The C4 photosynthetic pathway is an adaptation to the oxygenase activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and the resulting photorespiratory CO₂ losses. Through the establishment of a CO₂ pump that concentrates CO₂ at the site of Rubisco, the C4 pathway effectively compensates for photorespiration, and consequently C4 plants dominate the floras of hot and dry environments. In C4 plants phosphoenolpyruvate carboxylase (PEPC) isoenzymes play an important role in the initial step in CO₂ fixation where they operate as the primary carboxylase. PEPC catalyses the irreversible carboxylation of phosphoenolpyruvate (PEP) to form oxalacetate (OAA) and phosphate. The C4 photosynthetic pathway evolved polyphyletically, implying that the genes encoding the C4 PEPC originated from non-photosynthetic PEPC progenitor genes that were already present in the ancestral C3 species. The group of Prof. Groth elucidates the structural evolution that occurred when the C3 isoform of PEPC shifted towards the C4 isoform by crystallization of C3 and C4 PEPC isozymes and determination of their X ray structures.

The C4 syndrome might not only be associated with higher water use efficiency and heat tolerance, but also with more general adaptations to abiotic stress, due to the selective pressure exerted by abiotic environments that favor the evolution of C4 metabolism. Prof. Weber's group is using a system biology approach that includes detailed physiological, biochemical, metabolic, genetic, and genomic characterization of a range of C3, C3 to C4 intermediate, and C4 species of the genus *Flaveria* and *Cleome*. This includes the generation of experimental data at the levels of the transcriptome,

metabolome, and enzymatic activities. In close collaboration with Prof. Lercher the generated data will be used to provide a solid database for associating plant performance under various conditions with specific molecular traits that are part of the C4 syndrome. Moreover, also biotic stress can influence the use of C4 and C3 metabolism in plants. Therefore, Prof. Feldbrügge's group is using the maize/*Ustilago maydis* pathosystem to study the dynamic response of plants during biotic stress.

Study program

In the iGRAD-Plant program a study – and qualification concept was developed that consists of mandatory formal classes and seminars that will be taken at HHUD and MSU, a mentoring program that is tailored to each student's needs by his/her guidance committee, and, at the heart of the program, of an independent scientific dissertation research project. Biology is a highly integrative discipline that is based on chemistry, physics, mathematics, and statistics. Generating new biological knowledge heavily relies on probabilistic and quantitative models, thus requiring solid understanding of mathematics and statistics. A particular strength of the formal training program is that all students will be trained in both experimental biology and in quantitative biology, including biostatistics, bioinformatics, and computational biology. This ambitious goal is only possible through the collaboration with quantitative and computational biologists at our international partner MSU who complement and extend the expertise available at HHUD. The iGRAD-Plant program consists of two different studying periods, the qualification and the research period (Fig. 2). The basic philosophy of our qualification program is that all incoming students with a bachelor's degree will be initially trained in a structured one-year program. During this qualification period, each student will be assigned to a temporary faculty supervisor and a senior student mentor, who will guide and consult the student in the first year. The qualification period will consist of three 6 week rotation periods in three different laboratories and a structured program of lecture and seminar courses. After successfully passing the qualification period, the students will have up to six months to start their dissertation project and to develop a research proposal, that they will submit to their guidance committee in writing and that they will defend in an open session. After defending the proposal, the students will move on to

Qualification period		Research period					
1 st Semester	2 nd Semester	3 rd Semester	4 th Semester	5 th Semester	6 th Semester	7 th Semester	8 th Semester
Three 6 week lab rotations		Developing + defending research proposal	PhD research project + 6 to 9 month research stay at MSU				Project + dissertation completion
Two B module courses (out of the master program)		One class in "Quantitative Biology"		Two workshops in "Advanced methods in Plant Biology"			
External and internal lecturer program							
Regular practice in scientific writing, communication and presentation skills							
One workshop in transferable skills		One workshop in transferable skills			One workshop in transferable skills		

Fig. 2: Overview of the structured PhD training program

the research part of their PhD, which is accompanied by mandatory and optional seminars and workshops, and by regular meetings with their guidance committee. Guidance means supporting the students in independently developing short-term and long-term research plans, testable hypotheses, and writing-up and presenting their results. It further means broad training that goes beyond the individual's thesis research and that includes cross-disciplinary training. Therefore the study program of the iGRAD-*Plant* is divided into five different parts, the Research Project, Scientific Training Courses, Lecture Series, Presentation and Communication Skills, and Transferable Skills (Fig. 2).

Research Project

Being the basis of the PhD study the research project spans throughout the whole period of the students stay in the program. The research project aims at qualifying the student for independent and professional scientific work. All students will complete a six to nine months research stay at the Michigan State University, thus promoting their early integration into the international research community. The students will have to select a graduate guidance committee, consisting of at least three faculty members, with one faculty member serving as the major professor. The guidance committee will have at least one member of the faculty of the Michigan State University. Throughout the PhD research project the student will deliver annual reports to the committee members, followed by annual committee meetings. A written report will be issued after the presentation of the research proposal and each committee meeting. The written reports will become part of the student's file, which together with the PhD thesis will provide the foundation for evaluation of performance at the end of the program.

Scientific training courses

The core research groups of the iGRAD-*Plant* offer practical workshops in all methods and topics of advanced plant biology. During their study the students will be trained in these areas qualifying them to select, apply, and adapt them to solve their scientific questions. Generating new biological knowledge heavily relies on probabilistic and quantitative models, thus requiring solid understanding of mathematics and statistics. A particular strength of the iGRAD-*Plant* program is its strong emphasis on the quantitative aspects of biology, including bioinformatics and computational biology, and biostatistics. Therefore several classes in this area are mandatory for all students in the program. Part of the study program will be taken at HHUD, whereas other parts are integrated in the research stay at MSU. The guidance committee will assist the student with selecting the class work.

Lecture series

In order to deepen and broaden the theoretical background in plant biology all students need to attend several lecture series every year throughout the study program. The iGRAD-*Plant* students will be organizing at least once per semester a lecture unit with a student-invited speaker. This will allow the students to practice active scientific networking, including selection and invitation of a guest speaker.

Regular Practice in Presentation and Communication Skills

All student members of the iGRAD-Plant program will actively participate in a weekly seminar series throughout their association with the program to foster the interaction and team spirit within the group and to enforce a regular scientific exchange between all group members. This program will be complemented by regular (annual) joint retreats of faculty members, from HHUD and MSU and students to further strengthen the corps spirit of the training group and to integrate new members. In addition, students are expected to present their findings at national and international research conferences, such as the annual meetings of the American Society of Plant Biologists (ASPB). Because it is of outmost importance that students will take responsibility for writing up their research findings in the form of publications to be submitted to peer-reviewed journals, the students will be systematically guided towards independent writing of research papers throughout the program.

Transferable Skills

The iGRAD-Plant program considers a broad range of national and international demands and suggestions regarding an up to date and forward looking training of PhD students. Since the iGRAD-Plant program is a member of the Interdisciplinary Düsseldorf Graduate School in Science (iGRAD), all students will benefit from the excellent didactic program offered therein. During one- to two-day workshops the students will be trained by professional experts in the fundamentals of a broad range of transferable skills. These include scientific writing and speaking (in German and English), project management, good scientific practice, preparation of a curriculum vitae, preparation for job interviews, and personnel management. The workshops will be selected from the yearly iGRAD program, on basis of individual learning aims with consulting support by the responsible graduate guidance committee.

The Transferable Skills Program in combination with daily practice in the course of the research projects and other areas of the iGRAD-Plant Teaching Program enables the students to build up an individual and sustainable profile of diverse key competences next to an exceptional scientific expertise and professionalism.