

Research Focus



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Curriculum Vitae

I am generally interested in questions addressing the phylogeny, evolution, biogeography, and radiation of the Brassicaceae in the light of recent progress in palaeoclimatic and genomic research. Furthermore, I am aiming for understanding the genetic basis of fruit and seed characters and regulation of character changes. I am also studying the influence of distinct fruit and seed traits on spatio-temporal diversification patterns within and among populations of selected weed species in Mediterranean habitats and S Africa, the role of abiotic and biotic stress factors on phenotypic plasticity of fruit and seed characters in a heterocarpic species, and the impact of distinct glucosinolate patterns in herbivory of diaspores. Finally, I am involved in studies how the origin of a single developmental control gene, *GORDITA* (*GOA*), by gene duplication and sequence divergence contributed to plant fitness and adaptation.

My projects are at the interface of phylogenetics, developmental biology, molecular genetics and evolutionary ecology (evo-devo and eco-evo), providing fundamentally novel, comprehensive and increasingly predictive insights into evolution and solutions that plant species have developed to match local environmental demands.

Fruit evolution and adaptation to Mediterranean habitats in *Raphanus* (Brassicaceae)

DFG Trilateral Project (Israel, Palestine, Germany; six groups), DFG MU 1137/16-1, lead PI

We are taking an interdisciplinary approach to investigate the adaptive value of the divergence in fruit and diaspore architecture in the genus *Raphanus* in respect to spatial dispersal patterns, germination synchronization, and patterns of genetic diversity within and among populations. *Raphanus* is a Mediterranean genus comprising two closely related allopatric wild annuals, *R. raphanistrum* and *R. pugioniformis* and the cultivated *R. sativus*. The first two are native to the East

Mediterranean and differ in fruit morphology and dispersal ability, suggesting that single-seeded units of *R. raphanistrum* and the heavy multi-seeded diaspores of *R. pugioniformis* are adaptive in their specific habitats. Accordingly, we hypothesize that in their native range, long-distance wind dispersal in *R. raphanistrum*, can explain its wide distribution along similar homogenous habitats, while short- distance dispersal in *R. pugioniformis* ensures remaining in safe sites for seedling establishment in heterogeneous mountainous environments. Thus, *Raphanus* provides an opportunity to investigate and develop a model of evolutionary processes in fruit architecture and dispersal mechanisms in a small genus. We suggest conducting a detailed population survey of each of the two wild species in Israel and the Palestinian Authority, e.g. spatial arrangements within populations, distribution patterns, and assessment of biotic, edaphic and climatic factors. Dispersal over long and short distances will be tested in confined sites. Furthermore, fruit and seed morphology, and fruit anatomy will be investigated, and short- and long- term germination trials, as well as longevity tests will be set on seeds enclosed in the pericarp vs. bare seeds. Population-based threshold models will be used to explain eco-physiological regulation of seed dormancy /germination by the environment. In this respect we hypothesize that germination of *R. raphanistrum* occurs upon long imbibition, while pericarp-mediated mechanical dormancy of *R. pugioniformis* is released only after decomposition of the pericarp by microbial activity or abrasion. With the use of microsatellites we aim also to understand how the differences in habitat and dispersal strategy affect genetic variation within and among populations of these species. The results of our project will provide insight into adaptive processes in annual Brassicaceae and we expect that this interdisciplinary study will stimulate Israeli and Palestinian students to join this research area.

SeedAdapt - Dimorphic fruits, seeds and seedlings as adaptation mechanisms to abiotic stress in unpredictable environments [https://www.seedadapt.eu/]

ERA-NET ERA-CAPS, 6 EU partner labs (G. Leubner, RHUL, lead PI), DFG MU 1137/12-1

Higher plant dispersal units - fruits and seeds - support the distribution and early life history of the progeny. The aim of the SeedAdapt project is to elucidate molecular mechanisms of fruit, seed and seedling traits that evolved in annual plant species as adaptations to changing and unpredictable environments. Although these traits are cornerstones for food quality and safety as well as for the fate of ecosystems, the molecular and developmental biodiversity of mechanisms underlying the adaptation to abiotic stresses including heat and drought are only poorly understood. To provide novel insight into this important adaptation mechanism, our interdisciplinary and integrative project utilizes the distinct 'dimorphic diaspores (DD)' that develop on the same plant of annual *Aethionema* species (Brassicaceae) as dormancy bet-hedging strategy. The 'Seed-Diaspore Syndrome (SDS)' resembles the 'default pathway' of weeds like *Arabidopsis*: dehiscent fruits disperse seeds with non-deep dormancy, these seeds form mucilage upon imbibition, and embryos emerge with radicles first during germination. The 'Fruit-Diaspore Syndrome (FDS)' constitutes a 'novel pathway': indehiscent fruits are dispersed that contain non-mucilaginous seeds with deep dormancy, and embryos emerge with cotyledons first during germination. We will compare SDS and FDS of two *Aethionema arabicum* accessions adapted to distinct climates, for their responses to abiotic stress during three sensitive

processes: (1) reproduction; (2) germination; and (3) seedling growth. For the dimorphic diaspore formation we will investigate the SDS/FDS-ratios depending on the parental environment, perform an evolutionary comparison of dispersal genes, and study syndrome- and stress related glucosinolate patterns (diaspore herbivory). The dimorphic diaspores' hormonomes, epigenomes, and transcriptomes provide 'syndrome x stress memories' which will be quantified in a comparative manner and integrated with stress physiology modelling, seed biomechanics, and growth imaging of dimorphic seedlings. The *Ae. arabicum* genome sequence and a RNA-Seq bioinformatics pipeline are available. The comparison of the 'syndrome x stress memory' data will provide differentially expressed genes and distinct epigenetic markers. Their targeted analyses will be extended across several *Aethionema* populations/species, as well as by phylogenomics (e.g. promoter elements) and cross-species reverse-genetics in crops and models. We will conduct forward and reverse genetics of SDS and FDS to separate individual traits, including EMS-mutant screens and QTL analyses using already existing RILs, and we will establish genetic transformation and resources.

We propose that investigating the regulatory basis of fruit, seed, and seedling trait diversity is ideal for integrating new technologies and complementary expertise in order to study a field with utmost importance in ecology, evolution, seed industry and crop breeding.

Evolutionary developmental genetics of fruit dehiscence in Brassicaceae

Joint DFG project with G. Theissen (Jena, DFG TH417/6-1), DFG MU 1137/8-1, MU 1137/8-2

The aim of the project is to better understand the developmental genetic basis and ecological implications of the recurrent transition from dehiscent to indehiscent fruits during evolution of Brassicaceae, using *Lepidium campestre* (dehiscent) and *L. appelianum* (indehiscent) as model systems. In the previous phase of the project we identified the *L. appelianum* *APETALA2* (*AP2*) ortholog as a likely repressor of dehiscence zone identity genes. To better understand its role in the evolution of indehiscence we will characterize the genomic sequences and expression patterns of the *AP2* genes in *A. thaliana*, *L. campestre* and *L. appelianum*. We will also determine whether overexpression of cDNA of any of the *AP2* orthologs is sufficient to transform dehiscent into indehiscent fruits. Moreover, we will transform the genomic loci of the *AP2* orthologs into both wild-type and *ap2* knock-out plants and will observe which transgenic plants develop dehiscent or indehiscent fruits. This will reveal whether the *AP2* locus contains the causative mutation of fruit indehiscence. In addition, we also will compare the transcriptomes of dehiscent and indehiscent fruits to get a more comprehensive picture of the gene regulatory differences between these fruit types. In yet another branch of the project we will analyze the consequences of fruit indehiscence for seed and fruit dispersal and germination timing mechanisms. We will determine if seeds of dehiscent and indehiscent fruits differ in dormancy and germination, and whether abrasion of the pericarp, fire, or fungal assistance are involved in pericarp-mediated dormancy release in indehiscent fruits. Finally, we will determine whether differences in glucosinolate patterns of dehiscent and indehiscent fruits represent different modes of defense associated with different dispersal strategies.

Seed coat and embryo pigmentation variants of *Lepidium sativum*

Joint project with S. Hassen and E. Molla (Debre Berhan University, Ethiopia) and G. Leubner (RHUL)

This project concentrates on germination biology of Ethiopian endemic seed colour variants of the salad cress (*Lepidium sativum*), a crop plant suggested to have originated in Ethiopia. Field experiments at the experimental garden of Debre Berhan University (3000m asl) are designed to study whether these colour variants represent an adaptation to higher levels of UV-radiation and / or temperature as a consequence of climate change.

Species which have adapted to high altitudes tolerate enhanced UV. High UV radiation affects the morphology and physiology of plants and the effect of radiation is high in plants from low altitudes not adapted to high altitudes. Low altitude plants when exposed to higher UV radiation showed specific morphological and physiological characteristics such as small and thick leaves, shorter petioles, shorter stems, increased axillary branching and altered root: shoot ratios, reduced shoot and root growth, reduced chlorophyll a and b content, suppressed germination percentage, increased anthocyanins and flavones contents. Based on the above facts, germination biology and life history traits of Eurasian and Ethiopian *L. sativum* seed colour variants will be studied in field experiments in Debre Birhan (2840 masl and Osnabrueck, 64 masl). Average annual temperature in Ethiopia and Germany is 22.8° C and 8.39° C, respectively and the average precipitation for the two countries is 848mm/year and 700 mm/year, respectively. Average daily ultraviolet radiation in Ethiopia and Germany differ between 5914 J/m² and 1812 J/m², respectively (WHO, 2011). Seed colour variants from *Lepidium sativum* will be compared in germination characteristics, life history and physiological traits by growing plants in Debre Birhan and Osnabrueck. Studies of several plant taxa demonstrated that environmental effects can persist beyond two generations and traits of seeds, seedlings, and adult plants can be influenced by environments (temperature and drought stress) experienced by the grandparental generation. To our best knowledge this comparative study (effects of altitude and corresponding climatic factors on germination, life history and physiological traits of seed colour variants) was not done before.

Impacts of Climate Change on Plant Recruitment

Joint project with S. Naidoo and S. Ramdhani (lead PIs, University of KwaZulu-Natal, South Africa; Thuthuka program) plus other scientists from South Africa

South Africa has rich floristic diversity and endemism, being the 3rd most diverse country in the world. Biodiversity loss in South Africa has been attributed to, apart from other factors, climate change. Currently there is a global call to monitor climate change driven shifts in biodiversity at the landscape level, to achieve more wide-ranging conservation strategies. The impacts of climate change on plant recruitment, the process by which new individuals found a population or are added to an existing population, has important implications for ecosystem functioning and forms the focus of the proposed project. Recruitment may occur through clonal offspring but is most

often achieved by means of seedlings. There is a general paucity of information on the ecophysiological responses of indigenous South African flora, particularly their propagules (e.g. seeds) and seedlings, to various climate change scenarios. Altered climatic conditions, together with other environmental changes that influence ecological cues can affect recruitment of plants and subsequently, population dynamics. The proposed project will investigate whether different climate change scenarios are likely to impact on plant recruitment by altering germination phenology, seed and seedling vigor and/or seed bank dynamics (amongst other things). To achieve this the project will, (1) compare plant recruitment patterns along environmental gradients within specific vegetation types (e.g. forest, grassland and wetland); (2) investigate the responses of seeds and seedlings of wild species to various climate change scenarios (e.g. elevated CO₂ and temperature, reduced water availability, and increased salinity); and (3) investigate the species composition and health of natural seeds banks and the responses of the seeds they harbour to different climate change scenarios. Studies within the project will include indigenous and alien species occurring within selected vegetation types in KwaZulu-Natal.

BrassiBase: Tools and biological resources to study characters and traits in the Brassicaceae

DFG priority programme 1529 “Adaptomics”: Evolutionary plant solutions to ecological challenges,

<http://www.ruhr-uni-bochum.de/dfg-spp1529/Seiten/index.html>

Joint project with M. Koch (Heidelberg) and I. Al-Shehbaz (Missouri Botanical Garden), KO 2302/13-1

We aim to develop a system of cross-referenced information and resources on Brassicaceae taxonomy, systematics, evolution, chromosome numbers, accurate enumeration of all species, traits and characters and germplasm resources. Biological, molecular and evolutionary knowledge is exponentially increasing in the mustard family (Brassicaceae, Cruciferae). However, because of the complex and overwhelming biological diversity in the family, it is difficult for non-specialists in this plant family to put any research result in a larger evolutionary framework. Many species are remarkable study objects but rarely available. Biological material and resources, either collected directly in the wild or held in germplasm collections, is often taxonomically misidentified; and very rarely the material is further characterized and documented. There is also no family-wide and comprehensive survey of character and trait distribution despite the fact that we approached a reliable phylogenetic framework quite recently. In order to close these various gaps and provide the full potential of research focusing on the adaptive characters and character-trait evolution in the Brassicaceae, we will provide a comprehensive documentation of the taxonomy and systematics of the entire family. This will include a database with all the relevant taxonomic, systematic and phylogenetic literature; a comprehensive data collection of characters and traits including all potentially adaptive traits scientists participating in SSP 1529 are interested in; a DNA-based identification tool for genera and species; electronic interactive keys for the identification of genera and species, and a setup of a carefully selected and documented germplasm collection representing the entire family. Basic research will be conducted to provide first and comparative insights into the evolution of characters and traits over the whole family utilizing also the data collected during the project. The results and framework provided herein will be the basis and starting point for

other projects focusing in more details on individual characters and traits – inside and outside SSP 1529 “Adaptomics”

Adaptomics of neofunctionalization: analysis of *GORDITA*-like genes in Brassicaceae

DFG priority programme 1529 “Adaptomics”: Evolutionary plant solutions to ecological challenges

<http://www.ruhr-uni-bochum.de/dfg-spp1529/Seiten/index.html>

Joint project with A. Becker (Bremen, lead PI) and G. Theissen (Jena, lead PI), MU 1137/9-1

The project investigates how the origin of a single developmental control gene, *GORDITA* (*GOA*), by gene duplication and sequence divergence contributed to plant fitness and adaptation in the Brassicaceae. While the ancestral B_{sister} genes (*ABS*-type genes) are involved in ovule development, the derived *GOA*-type genes acquired a new expression domain and function in fruit development. By comprehensive comparative analyses involving *GOA*-type and *ABS*-type genes from diverse Brassicales species we will investigate when the lineage that led to extant *GOA*-type genes originated, and by which molecular mechanisms these genes acquired their unique expression patterns, domain structures, and function during fruit development. To better understand how the ancestors of *GOA* escaped ‘Ohno’s dilemma’ we will analyze the molecular evolution in the different branches of B_{sister} genes during the phylogeny of Brassicales employing *in silico* methods. Using protein-protein interaction studies we will investigate how changes in the protein structure changed the protein interaction network of *GOA* in comparison of *ABS*. To assess how the origin of *GOA*-type genes contributed to the adaptation of Brassicaceae species we will determine proxies of plant fitness under greenhouse conditions using transgenic knock-out plants, and will do preparative work for future determination of plant fitness under natural growth conditions using non-transgenic mutants.

Phylogeny and systematics of Brassicaceae

Joint project with A. Franzke, DFG MU 1137/7-1 & MU 1137/7-2

In addition to the commercial potential of several cruciferous plants (i.e. cabbage), the mustard family (Brassicaceae) is also of great academic interest, as this family contains the most important model organism of modern plant biology, i.e., *Arabidopsis thaliana*. Notwithstanding this impact, the phylogenetic history of this plant family is only partly understood and a robust real family-wide phylogenetic concept is still missing. The present study deepens our understanding of the Brassicaceae phylogeny with two approaches being new to broad-scale phylogenetic research of the Crucifers: We (i) used a molecular marker from the mitochondrial genome and a (ii) contemporary relaxed molecular dating method to infer key dates in the Brassicaceae evolution. The results obtained from sequencing mitochondrial DNA generally confirms a recent tribal alignment of the Brassicaceae primarily based on chloroplast DNA analyses. Additionally, our data are also compared with a recent family-wide Brassicaceae phylogeny based on nuclear DNA. Combining the results from phylogenetic reconstructions and molecular dating, it is possible for the first time, to present a biogeographical scenario for the broad scale Brassicaceae evolution.