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Editorial to the special issue on Seed Innovation Systems for the 21st Century

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Editorial

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This Special Issue on Seed Innovation Systems for the 21st Century follows on from the International Society for Seed Science virtual conference in August 2021. The conference was organized by the Seed and Stress Biology group of the Royal Botanic Gardens, Kew in the United Kingdom. The conference programme comprised 5 plenary, 10 keynote, 60 oral and 40 poster presentations across five themes and attracted a global audience of 350 participants from 47 countries.

***Seed Memory* (Theme 1)** explored how the maternal environment during development influences seed quality traits such as germination, vigour and longevity, and the biochemical and molecular signalling networks that control seed responses. Keynote speaker, Ruthie Angelovici (University of Missouri, USA), explored 'The metabolic and genetic mechanisms controlling seed amino acid composition and how they may relate to stress response'. Using multi-omics approaches, an understanding is emerging of the precise mechanisms controlling seed storage protein amino acid composition following severe drought stress, for example in Arabidopsis and maize (Yobi et al., 2020; Shrestha et al., 2022). Any abiotic stress has the potential to have oxygen as a modulating factor, as it plays a key role in molecular networks, particularly the hormone signalling pathways that regulate germination and dormancy. Françoise Corbineau (Sorbonne Université, France), who delivered one of the plenary award lectures, The J. Derek Bewley Career Lecture, reviewed how the major advancements in 'Oxygen, a key signalling factor in the control of seed germination and dormancy' have influenced her exceptional career (pp. 126–136). The regulation of dormancy also formed the topic of The Michael Black Founders Lecture by Guillaume Née (University of Münster, Germany). His work on 'A watch DOG to prevent shut down of ABA responses during early seed imbibition' has shown that the interaction of the DOG1 protein with the type 2 C Protein Phosphatases (PP2C), ABA-HYPERSENSITIVE GERMINATION 1 (AHG1) and 3 (AHG3), controls dormancy, and is the mechanistic basis for crosstalk between the abscisic acid (ABA) and the DOG1 pathways in seed dormancy (Née et al., 2017). Beyond the triggering of relatively rapid signalling responses, seeds have a memory (Fernandez-Pascual et al., 2019). In her keynote talk on 'Ghosts of the past: parental environmental history regulates seed traits', Gabriela Auge (FCEN-UBA. Buenos Aires, Argentina) explored the effect of environmental changes experienced by previous generations and how transgenerational plasticity influences early development traits and the expression of adaptive responses to fluctuating climates (Vayda et al., 2018).

***Seed Lifespan* (Theme 2)** examined the science of maximizing seed survival which is a complex trait that varies between and within species due to genetic, phenotypic and structural factors. Keynote speaker, Daniel Ballesteros (Royal Botanic Gardens Kew, UK and University of Valencia, Spain) presented on 'Dry and frozen architecture: from tissues and cells to the submolecular' and showed how techniques including cryo-microscopy, micro-computer tomography, thermal and mechanical analysis, and neutron scattering in combination with traditional seed biology can reveal the mechanisms of seed survival and deterioration and inform the design of preservation strategies (Ballesteros et al., 2020). One way to reveal inter- and intra-species variation in seed longevity is the use of time for viability to fall to 50% (p50). In a Research Opinion on 'More on seed longevity phenotyping', Fiona Hay (Aarhus University, Denmark) et al. critiques the use of Kew's Millennium Seed Bank comparative longevity protocol to generate p50s, and its adaptation for hermetic storage conditions (pp. 144–149). The authors recommend adoption of consistent protocols for seed storage experiments and highlight the usefulness of p50 as a measure of longevity, but caution that consistent definition of p50 is important. Agreed standards for measuring and reporting longevity are vital for such, and other, data to be included in seed traits databases, which formed a topic of discussion at the conference workshop on a 'Global Seed Information Facility (GSIF)'. Beyond structural and mathematical determinations of the longevity trait, significant progress has also been made in its molecular and biochemical basis. As Eduardo Bueso (Universitat Politècnica de València-Consejo Superior de Investigaciones Científicas, Valencia, Spain) explained in his keynote lecture on 'The legacy of the mother, key for seed survival', the molecular mechanisms responsible for the establishment of apoplastic barriers in the maternally derived seed coat play an important role in seed longevity (Renard et al., 2021). Moreover, as Moritz Stegner (University of Innsbruck, Austria) et al. note in 'Antioxidant depletion during seed storage under ambient conditions' (pp. 150–156), seeds of all seven species stored under ambient conditions sustained oxidative damage to lipids. More specifically, germination level is positively correlated with tocochromanol content and negatively correlated with the half-cell reduction potential of low molecular weight thiol/disulphide couples.

Seed Innovation Systems **(Theme 3)** covered the future of seed science and the technological innovations which will define the rate of advances in seed science in the 21st century, from small scale innovations on seed quality to 'omics' technologies at the single cell level, high-throughput germination phenotyping, bioimaging, etc. In his keynote on 'Seed systems supporting legume crop development' across Africa, Chris Ojiewo (ICRAF, Kenya) stressed the need to establish a system that increases the availability of varietal performance data and early-generation seed (EGS). To do this, it will be necessary to strengthen public EGS systems and provide a path from variety development through to commercialization so that the adoption of improved legume varieties can be accelerated (see Ojiewo et al., 2020). The important connection between science and practice was further elaborated by Richard Ellis (University of Reading, UK), in his J. Derek Bewley Career Lecture on 'Seeds-plants-crops-biodiversity-environment-people: illustrating understanding and ideas'. Reflecting on his career, he emphasized the importance of mentoring and teamwork, and the role of illustration in clear communication of results. His advice to early-career seed researchers is to cross the synthetic divide between pure and applied science as much as possible. Concluding that seed science research can make a vital contribution to addressing the complex global challenges of food security, loss in biological diversity and climate change, 'but only if that research can be – and then is – applied' (pp. 118–125). An aspect of seed innovation research that is attracting considerable interest is the germination phenotype. Keynote speaker Ji Zhou (University of Cambridge & NIAB, Cambridge, UK) explored this topic in his talk on 'SeedGerm 2.0: from crops to wild species', detailing the development of the SeedGerm 2.0 platform. His research uses hyperspectral imaging and AI-based algorithms to analyse dynamic seed phenotypes, which clearly has huge potential in agriculture and is likely to be of increasing value when defining fit-for-purpose seedlots under changing climate conditions. Another innovation fuelling the development of seed science is increasing access to plant transcriptome data across the phylogeny of plants, and providing a framework for examining the evolution of green plants (One thousand Plant Transcriptomes Initiative, 2019). In his opening plenary lecture on 'Seed traits and phylogenomics: prospects for the 21st century', Hiro Nonogaki (Oregon State University, USA) highlighted the potential of phylogenomics – the integration of genomics and evolutionary biology – for understanding the molecular evolution of seed genes, such as *DELAY OF GERMINATION1* (*DOG1*) gene family. *DOG1-like* (*DOGL*) genes can be traced back to the algae Zygnematophyceae. The origins of dormancy mechanisms and seed maturation programmes may extend even further back than this to ancient algal lineages. As Nonogaki et al. write (pp. 137–143) 'plants and seeds have performed a myriad of experiments over the course of evolution' and 'many of the experimental records of plants have probably been written in their genomes'. Expressing ancient genes in *Arabidopsis* and introducing modern seed genes to basal angiosperms could lead to future technology development by recovering ancient seed traits of value in agriculture and other applications.

Seed Form and Function **(Theme 4)** considered the physical and functional traits of seeds and how evolution has shaped their contribution to the success of a species. Gerhard Leubner (Royal Holloway University of London, UK) delivered The Alfred Mayer Plenary Lecture on 'The germination of diaspores: origin, diversity and destiny of the seed habit'. He examined the diversity in seed traits and responses to the environment, and the importance of understanding and exploiting this diversity in addressing global challenges including climate change, food security and planetary health. Focussing in on seed dormancy, keynote speaker Filip Vandelook (Meise Botanic Garden, Belgium) examined 'The ecological significance and evolutionary history of seed traits'. Two case studies were presented: water impermeable seed coats (physical dormancy) and morphophysiological dormancy. Climate drying has been proposed to be the selective force for evolution of physical dormancy, but protection (against predation, herbivore ingestion and pathogens) has also been proposed as a driver for hard, impermeable seed coats. Having an impermeable seed coat is often associated with the seeds being quite large, desiccation tolerant, and having nutrients stored in the embryo rather than the endosperm. In contrast, morphological and morphophysiological dormancy tend to occur in seeds with small embryos and copious endosperm and are considered the most ancient dormancy mechanisms. Storage of nutrients outside of the embryo may provide protection against partial predation. Furthermore, seeds with small embryos are more prevalent in shaded, forest environments and the endosperm may provide a source of nutrients post-germination. There are many pieces of the puzzle still to be completed, and it is important to recognize that seed functions are linked, and their interactions should be studied rather than focussing on a single function, such as germination. As keynote speaker Tina Steinbrecher (Royal Holloway University of London, UK) noted in her talk on 'Functional morphology of seeds: a biomechanics view', the mechanical properties of cells, tissues and organs govern the plant life cycle from fertilization, seed dispersal, germination, seedling establishment and beyond, and determine the plants' structure and function. Understanding the relationships between structure and function form the basis of functional morphology and provides insight into evolutionary history of morphological features. One group of plants where seed form and function are inextricably connected is the orchids. Miniaturization of orchid seeds, and the loss of endosperm, hugely increases the seed yield per plant and represents a trade-off between plant competition and colonization. These small, light seeds have greater potential for longer-distance dispersal and are reputed to have morphological or morphophysiological dormancy. Prasongsom et al. (Mahidol University, Thailand) in 'Seed dormancy concepts in orchids: *Dendrobium cruentum* as a model species' (pp. 175–186) explored the germination potential of orchid seeds in the absence of potentially dormancy-breaking treatments, that is, disinfection with hypochlorite and growth on medium containing nitrate. Combined with an assessment of the effects of light *versus* dark, fresh *versus* stored seeds and constant *versus* alternating temperature, the authors found that rather than conforming to the DUST class of dormancy, *Dendrobium cruentum* seeds were able to germinate under a range of conditions immediately after dispersal and concluded that orchid seeds can be non-dormant.

Seed Germination and Stress **(Theme 5)** expounded how environmental thresholds for germination and the germination niche relates to species' resilience. The germination niche may appear to be more difficult to describe in tropical regions, such as the biologically diverse Campo Rupestre, where there are no major seasonal variations in temperature. Rather, local climate influences the environmental signals required for germination and dormancy cycling. Keynote speaker Queila Garcia (Universidade Federal de Minas Gerais, Brazil) in a talk on 'Germination and dormancy in tropical species: an overview from Campo Rupestre' revealed that interactions between soil humidity and temperature modulate seed hormonal balance and dormancy cycling. This is further elucidated by Santos et al. (pp. 157–165) for dormancy-breaking and germination in two palm species, *Mauritia flexuosa* and *Attalea speciosa*, which vary in their seed desiccation tolerance, and show distinct germination responses to a range of temperatures. ABA and ROS signalling play a role during dormancy break and germination and the haustorium is proposed to be source of ROS for signalling pathways for germination. Overall, germination niche is narrowed by interactions between environmental conditions, for example, temperature × moisture, as detailed by keynote speaker Lydia Guja (Australian National Botanic Gardens, Canberra, Australia). In her talk on 'Seed ecology of Australian native seeds – germination thresholds and stress tolerance', examples were presented from the Australian alpine regions where the future climate is predicted to be warmer and drier, and coastal regions where warmer and drier conditions will combine with salt stress due to an increased frequency of extreme sea-level events. The grasslands of south-eastern Australia are dominated by kangaroo grass (*Themeda triandra*), which has different ploidy races. Diploid seeds had a broader germination niche, while tetraploid seeds had a narrower niche but more likely to survive (Stevens et al., 2020). The research raises some important questions about whether having a broad germination niche is advantageous for regeneration in future climates, or is potentially maladaptive leading to low establishment or persistence in the long-term? Future research needs to address germination niche in the context of global patterns across phylogeny and ecoregions. One ecoregion in which germination is precarious is hot desert. In this habitat, not just extreme temperature and sporadic rainfall are limiting factors for germination but also light quality and quantity, as explained by Xiangyun Yang (Kunming Institute of Botany, China). Light promotion of germination is a common feature of small seeds of a number of plant families, including Cactaceae. Investigating the light mediated responses of the cactus, *Cereus repandus*, the authors found that the seeds were highly sensitive to RED light, which enabled rapid germination in high quality microsites. The effect of RED light was reversed by FR, which supports the formation of a soil seed bank (Yang and Pritchard, pp. 166–174).

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