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Seed germination

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Published in:
 Plant Biology

DOI:
[10.1111/plb.12522](https://doi.org/10.1111/plb.12522)

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Document Version
 Publisher's PDF, also known as Version of record

Publication date:
 2017

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Elzenga, J. T. M., & Bekker, R. M. (2017). Seed germination: Ecological aspects - special issue editorial. *Plant Biology*, 19(1), 3-5. <https://doi.org/10.1111/plb.12522>

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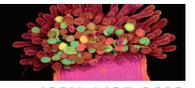
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EDITORIAL

Seed germination: ecological aspects – special issue editorial

doi: 10.1111/plb.12522

Seeds have been studied in detail in the past decades and several extensive reviews on different aspects of seed biology have produced a fairly complete picture of what is known about a number of model plant species (Simpson 2007; Koornneef *et al.* 2002; Karssen & Laçka 1985). Of seed dormancy and seed germination the molecular details have been elucidated, and on aspects related to vigour and persistence in the seed bank, advanced studies are available (Thompson *et al.* 1997; Leck *et al.* 1989).

When considering the evolutionary success of vascular plants on land, seeds must receive special attention. The role of seeds as the main unit of dispersal is one of the main causes of the present-day domination of spermatophytes. The survival of humans and the historical development of culture were incident on the adaptation of seeds as an important source of food. The realisation that the harvesting and sowing of seeds enables control over the production of food resources must have instilled in mankind a great appreciation for the small grains.

In the reproductive cycle, seeds have several contrasting functions: they represent the next generation of plants when they germinate and develop into a seedling; they are also the insurance policy or lottery ticket to ensure that a period of hardship can be survived. As seeds develop after gamete fusion, they enable testing of the suitability to deal with abiotic conditions, pathogen attack and competition of new genotypes (Fenner & Thompson 2005; Baskin & Baskin 2001; Grime *et al.* 1988).

The combination of these functions is illustrated through two large areas of seed research: dormancy and persistence, on the one hand, and vigour and germination, on the other. Dormancy has to be maintained in order to survive periods of unfavourable conditions (*i.e.* in temperate regions the winter season and in (semi-)deserts periods of drought). The timing of dormancy breaking and germination is often critical since the process cannot be reversed and 'getting it wrong' is lethal. As 'getting it right' is essential, germination is under control of many environmental parameters (light quality and quantity, low temperature, temperature increase, water availability, *etc.*) that can signal unsuitable or suitable conditions for germination. The redundancy in some of the sensory systems (*i.e.* the light perception by phytochromes and cryptochrome in *Arabidopsis*) indicates the importance of perceiving and processing the available information correctly. Apart from these indispensable functions, seeds carry special features to facilitate long-distance dispersal, resist pathogen infestation and excessive water loss.

The study of seed developmental processes has been motivated by economic incentives, nature conservation objectives, concerns about genetic erosion of the necessary diversity needed to secure future food security and scientific curiosity. This has resulted in a wealth of information on cellular processes before and during dormancy breaking and germination.

It seems timely to try to put these findings into an ecological context.

For the selection of papers for this special issue of *Plant Biology* we opted for a different approach. We wanted to bring together papers that are mostly not performed on model species, but rather with species that have to deal with the challenges that their specific ecological niche brings. These species might be taken as examples of how the generalised understanding that we have of the few well-studied model species can (or sometimes cannot) be applied in an ecological setting.

SEED VIABILITY

Seeds have been reported to remain vital for generations when stored under dry and cold conditions. Paradoxically, the so-called recalcitrant seeds are desiccation-sensitive and lose vitality when the tissue moisture content drops below a critical value. In evergreen forests up to 40% of the species produce seeds that are desiccation-sensitive and therefore at most can delay germination for about 4 months when not kept moist. For *Eugenia stipitata*, an Amazon rain forest tree, Calvi *et al.* (2017) demonstrated that desiccation is accompanied by a shift from reduced to oxidised glutathione, a process that might indicate oxidative stress and that potentially can be used as a marker for seed vitality.

The timing of the dehiscence of the pericarp of fruits of Brassicaceae differs between species. The dehiscence of the pericarp can occur immediately after maturation of the seeds and subsequently as the seeds are being spread, or the pericarp can become hard and corky and the seeds remain inside the fruit, which is dispersed as a whole. Still other species exhibit some intermediate association between fruit and seeds. In some species the fruits do not dehisce, but after some months the pericarp softens sufficiently for the seeds to germinate. Lu *et al.* (2017) found that in *Leptaleum filifolium* and *Neotorularia korolkovii*, two cold desert species that are indehiscent at maturity, the presence of the pericarp influences seed dormancy, germination phenology and retention of viability. When the seeds lost the pericarp under wet conditions in the lab, the survival of the seeds was strongly diminished.

GERMINATION STIMULATED OR REDUCED BY ENVIRONMENTAL FACTORS**Water**

Mediterranean shrublands are characterised by winter and spring rains and a long dry spell during the summer. Plants are subjected to water scarcity and summer fires. An adaptation of seeds of typical shrubland plants is the fire cue (heat shock and smoke), which induces germination even under water stress

conditions. Since most fires occur during the dry summer months, the germination success is very variable and correlated to local rainfall. The study of Luna *et al.* (2017) showed a large variation in water stress sensitivity between species, but germination in hard-seeded species was reduced by water stress, an effect that was increased when the seeds were exposed to fire cues.

Temperature

Plants in mountainous environments have resistance to a short growing season, frost damage and cold drought. Short grasses and cushion plants that can create their own, less harsh microclimate, by growing in low and dense patches dominate the alpine plant communities. Using seeds from 22 alpine and subalpine grassland species Fernandez-Pascual *et al.* (2017) determined species-specific optimum temperature for germination and the effect of cold and warm stratification on dormancy breaking. Most subalpine species germinated in snow-like conditions, indicative of germination under snow cover, thereby avoiding drought stress, whereas most alpine species needed warmer germination niches, thus avoiding frost damage in the seedling stage.

Light and temperature

Seeds use both light cues and temperature fluctuations over a 24-h period as proxies for burial depth in the ground. Small-seeded species can thus prevent germination when on the surface under desert conditions or when buried so deep that the resources of the seedling will not allow it to reach the soil surface. Whether plants can substitute the light cue for the alternating temperature cue and how constant temperature and alternating temperature regimes affect the thermal time necessary for 50% germination is the topic of the study of Galindez *et al.* (2017) on four *Lippia* species. Their results indicate that when the seeds are exposed to a more ecologically relevant alternating temperature regime, the cool temperature and darkness limit the permissible temperature range. Seed germination requires certain niche-specific conditions that are species-dependent.

DORMANCY INDUCTION AND BREAKING

The phenomenon of dormancy induction in seeds, as a means to delay germination until a period of more suitable

conditions, is widespread in many plant species and is present in many ecosystems (Baskin & Baskin 2001). It might even be a key factor to predict the possible response of plant species to climate change. On top of the primary status of dormancy, some species display secondary dormancy, with even more specific requirements to overcome this phase. These species may still show rather high fecundity. Copete Carreño *et al.* (2017) present a study elucidating the complex interplay between environmental drivers such as temperature, frost and water stress, which both induce and lift the intraspecific variability in morpho-physiological dormancy they found in a set of (sub-)alpine species.

Many species produce seeds that are released from the mother plant with a built-in physical barrier to instant germination (Grime *et al.* 1988). The mechanisms to break down this type of barrier differ between species and type of physical dormancy. The physical dormancy that occurs in seeds of three subfamilies of the Fabaceae determines the germination ecology of these species by water content. These seeds have a water gap structure that works as a fine-tuned inlet of water for the seeds to imbibe. It is hard to manipulate *in vitro*. Jaganathan *et al.* (2017) show in detailed measurements *in vitro* combined with a burial experiment *in situ* that high summer temperatures open this 'gate' and make these seeds temporarily water permeable, resulting in timely germination of a proportion of the seeds *in situ*, such that the ecological risk of fatal germination is effectively spread.

Even deeper down in the cellular regulation of seed ripening and subsequent germination, a certain set of genes is involved in raising protein levels for seed priming after imbibition, thus mobilising seed reserves for the seedling to grow until it becomes autotrophic (Bewley *et al.* 2013). Wang *et al.* (2017) used a 2D-gel electrophoresis system to investigate the protein changes during seed priming in rice. By comparing the data of protein and mRNA levels, three potential biomarkers for seed priming were found. These results could be used in seed quality improvements in rice and other crops.

GERMINATION AND ESTABLISHMENT

Once seeds have developed and are ready for dispersal, many successful dispersal mechanisms have evolved, as well as many symbiotic relationships between seeds and dispersing agents such as ants (Levey & Byrne 1993). Bromeliad seed containing



Fig. 1. Fruit (left) and seed (right) of *Lavatera trimestris*. Photos by F. Bottema. In: Cappers R.T.J., Neef R., Bekker R.M. (2000) *Digital Atlas of Economic Plants*. Barkhuis, Eelde, The Netherlands. 2000 pp.

ant-rewarding substances ‘in return’ for transport to favourable germination sites is the focus of a study from Leroy *et al.* (2017). They asked whether the seed origin in relation to the ant species and position of its nests influences the plant habitat preference, proof of the effect of ants on the plant’s traits and performance. Understanding the finesse of this plant–ant dependency is a further step in understanding the ecological impact of plant–animal interactions in the early phases of germination and establishment and of the subsequent performance of the adult plants.

Previous research mainly focused on optimisation of germination success both in time and space. But another successful strategy might be to produce compounds that prevent possible competitors from germinating successfully nearby, also known as allelopathy. One of these compounds (trans-caryophyllene, TC) was studied by Araniti *et al.* (2017). This terpenoid was found to inhibit seed germination and root growth of four weed species. This chemical inhibition is an external effect, possibly useful as a weed control mechanism, which might determine the fate of seeds after dispersal onto a site next to a plant species producing this terpenoid.

Overall we can conclude that the germination and establishment phase of plants in natural environments is hazardous.

Even if seeds ‘got it right’, they still might have to cope with external effects that cannot be anticipated and might cause a loss from the potential seed supply from recent dispersal or from the soil seed bank archive.

SEED IMAGE ANALYSIS

In this special issue on seeds we also include the introduction of a computer vision-based system to classify seeds on the basis of their shape, size and textural traits. The technique was applied to taxa of the genera *Lavatera* and *Malva*. With this technique Lo Bianco *et al.* (2017) established that seed morphometrics supported not only the classical differentiation in *Lavatera* or *Malva*, but could also differentiate between sections of the genus *Lavatera*, demonstrating that computer vision-based analysis can be used for systematic studies. For a picture of the sample seeds, see Fig. 1.

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