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Editorial

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Abstract

Seeds show incredible variation in their attributes, such as dormancy, longevity and, hence, quality. It is of eminent importance to study this variation across and within species and higher taxa in order to ensure successful agricultural production and preservation of biodiversity, not least in times of a changing climate.

Editorial

Seeds are central not only to agriculture but also to the conservation of biodiversity. Both are, or will, be affected by the changing climate and this in turn will affect food security (Colville and Pritchard, 2019). Thus, it is of eminent importance to study seeds, their biology, physiology and ecology, in order to maintain their important role, especially in the context of a changing environment. It is of great importance to include diversity in such studies and not only resort to the obvious model plant species such as Arabidopsis and rice as there is a huge variation in seed traits. Studying more native species for (future) use as crops or medicinal resources is increasingly important. Many wild species are considerably more resilient than our major crops and likely more resistant to the projected increases in abiotic stresses, such as drought, flooding, heat and salt. In addition, these native crops may be used in more marginal areas for agriculture, thereby making up for losses in yield of conventional crops.

Seeds intended for both agriculture and species preservation present two major traits that are problematic to their intended use, namely longevity (storability) and dormancy. Therefore, it is no surprise that the majority of articles in this issue of *Seed Science and Technology* deal with these issues.

There are several types of dormancy (Baskin and Baskin, 2004) which each pose different problems in successful termination of the block(s) to germination. One of the most notorious dormancy types is morphological dormancy in which the embryo only completes its development or maturation after dispersal. That this may take a long time was demonstrated by Li *et al*. (2020b) for *Cardiocrinum giganteum* var. *yunnanense*, which is native to China. After dispersal, seeds of this plant require up to 500 days before seedling emergence, which is not uncommon among species with this type of dormancy (figure 1). However, applying a temperature regime of 25°C/15°C (60 days) followed by 15°C/5°C (60 days) and 5°C (60 days), shortened seedling emergence to 5-6 months. This also indicates that these seeds have morphophysiological dormancy, with a physiological block to germination in addition to the morphological impediment.

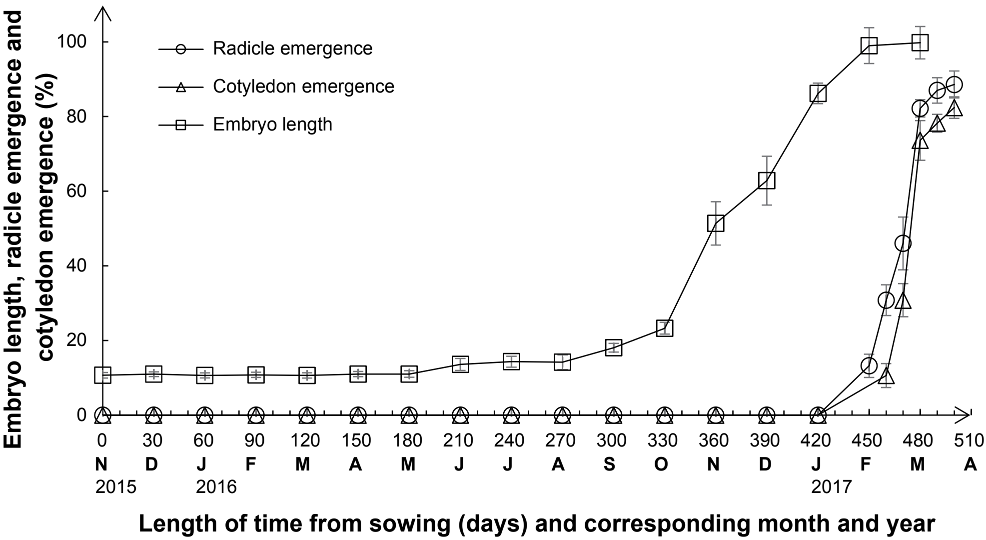

Figure 1. Embryo growth and radicle and cotyledon emergence in *Cardiocrinum giganteum* var. *yunnanense* outdoors in a shade shed (Li *et al*., 2020b). Figure published with permission of Li *et al*. (2020b).

The seeds of ginseng (*Panax ginseng* C.A. Meyer) and American ginseng (*P. quinquefolium* L.) also display morphophysiological dormancy. Seeds require 90-120 days of moist stratification at 18-25°C to break the morphological component and another 90-110 days of moist chilling for successful germination at room temperature. Li *et al*. (2020a) found that breaking of the physiological component could also be accomplished by removal of the endosperm. Embryo growth was promoted further by adding nutrients to the culture medium. Studies like this one provide valuable protocols to aid successful seedling production for native and medicinal plant species.

Another type of dormancy, physiological dormancy, can also be cumbersome for the production of seedlings within a reasonable time, as shown by Mursaliyeva *et al*. (2020). Their study species, *Allochrusa gypsophiloides* (Regel) Schischk, an endemic species from Central Asia and Kazakhstan, displays a moderately intense physiological dormancy which still requires up to 12 months of after-ripening to break dormancy. Quite remarkably, seeds developed some degree of secondary dormancy during dry storage, which poses an extra complication. A combination of cryopreservation and application of gibberellins reduced the after-ripening time and eliminated the induction of secondary dormancy. This Research Note again stresses the extreme variation in seed traits related to dormancy and, thus, the methods required to remove dormancy.

Another important dormancy problem particularly in grain crops is pre-harvest sprouting (PHS), which may cause huge losses in yield. This is likely a result of the disappearance of dormancy by persistent breeding for fast germinating progeny. Buckwheat is an important crop in many countries of the world. When buckwheat is sown in spring, harvesting may extend into the rainy season, presenting ideal conditions for PHS. In an attempt to select for PHS-resistant varieties, Suzuki *et al*. (2020) screened several varieties from three buckwheat species, including one wild one. Their hypothesis was that the depth of secondary dormancy correlated with primary dormancy. The wild species (*Fagopyrum homotropicum* Ohnishi) displayed considerable induction of secondary dormancy during dry storage and was proposed to be good candidate breeding material for better resistance to PHS.

While the induction of (secondary) dormancy in dry storage is uncommon, the breaking of dormancy under dry conditions (after-ripening) is observed across a wide variety of species, particularly those from arid or semi-arid regions. Bhatt *et al*. (2020) studied the effects of dry seed storage on dormancy and germination of seven desert legumes. Seeds from many legume species may possess a double dormancy, in that the embryo displays physiological dormancy but the seed coat adds a mechanical component, physical dormancy. Dry storage at room temperature for six months was effective in the partial breakage of both the physiological and physical components of dormancy but failed to do so in two species which remained impenetrable to water. In many physically dormant seeds, dormancy is broken by a combination of time, temperature and humidity. Under the right conditions the ‘water gap’ in the palisade layer of such seeds may be opened, allowing water to enter the seed.

Staying with the legumes, the breaking of the physical dormancy component often presents problems to efficient use of seeds, for example in forage legumes. Several methods for the breaking of legume hard-seededness have been developed, including mechanical and chemical scarification. In a study on the forage legumes *Aeschynomene abyssinica* (A. Rich.) and *A. americana* L., Sartie *et al*. (2020) compared different methods, of which scarification of seeds with a hot wire combined with optimal germination conditions proved to be cost-effective. Interestingly, in contrast with *A. abyssinica*, seeds of *A. americana* hardly responded to the scarification treatment. Moreover, there was considerable variation in the effectiveness of the methods across genebank accessions.

Physical constraints to germination by embryo-surrounding structures is also prevalent in corn rocket (*Bunias erucago* L.). It is an edible wild species native to the Mediterranean and slowly gaining importance as an alternative crop. Potential crops like corn rocket may gain importance as food in the (near) future when the demand for more resilient crops is increasing because of climate change. The dispersed propagules of this species are silicles, each containing four seeds and in which the pericarp forms the hindrance to germination (figure 2). Canella *et al.* (2020) tested four seed lots and, again, it can be noticed that there was variation in effectiveness of the four treatments to promote germination. While extracting the seeds from the silicles was most effective, mechanical scarification of silicles with sandpaper proved to be the most efficient at a larger scale.

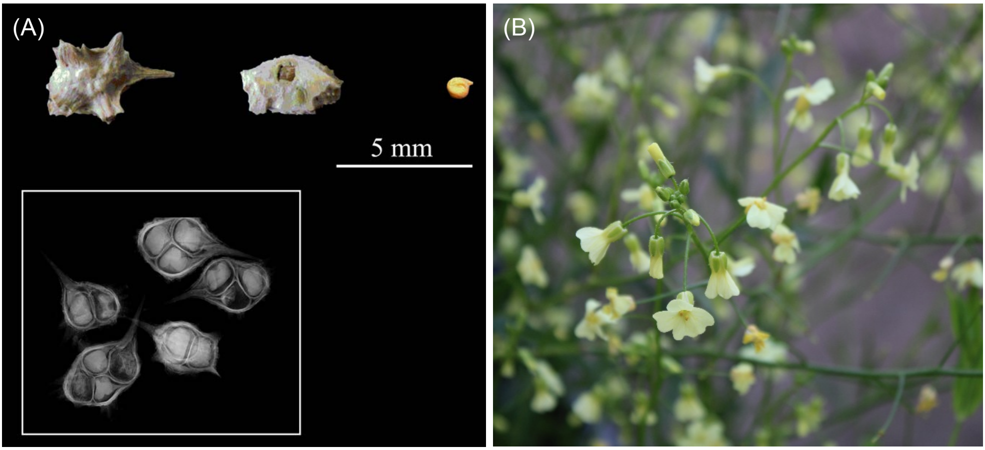

Figure 2. Silicles (**A**) of *Bunias erucago* (**B**). (A) Top, left to right = silicle, scarified silicle and extracted seed; bottom = X-ray scan of silicles. (A) Figure published with permission of Canella *et al.* (2020). (B) Image published with permission of M. Canella.

In a similar vein, Liyanage *et al.* (2020) attempted to break dormancy in three rainforest species from the *Acronychia* genus. Although these species do not contain a water-impermeable seed coat and, hence, are not strictly physically dormant, the seed coats do present a substantial mechanical restraint. Comparing different scarification methods, puncturing near the emergency point of the radicle proved to be most effective. As in *Bunias erucago* (Canella *et al.*, 2020), the application of gibberellins was not or only slightly effective. Further, as expected, the three species showed differing responses to the same treatments.

Like dormancy, there is an inherent variation in seed longevity, also depending on *inter alia* accession or variety, species, environment and maternal influence. Evidently, this poses problems to seed bank regeneration plans to maintain genetic diversity. This problem is most clearly emphasised in a *meta* study by Yamasaki and co-workers (2020). They analysed germination test results, collected over 30 years of storage in genebank conditions, of over 100,000 seed lots of 50 species with a shortest predicted longevity of 8.4 and a longest of 127.1 years (figure 3). This extensive study is of great value to seed bank managers as some conclusions may warrant re-evaluation of regeneration protocols, for example the initial seed viability does not always correlate with longevity, which is widely used as a rule of thumb to determine viability monitoring intervals. In addition, the shape of the survival curve may vary across species; thus, linear prediction of germination after storage is an unsafe practice in genebank management.

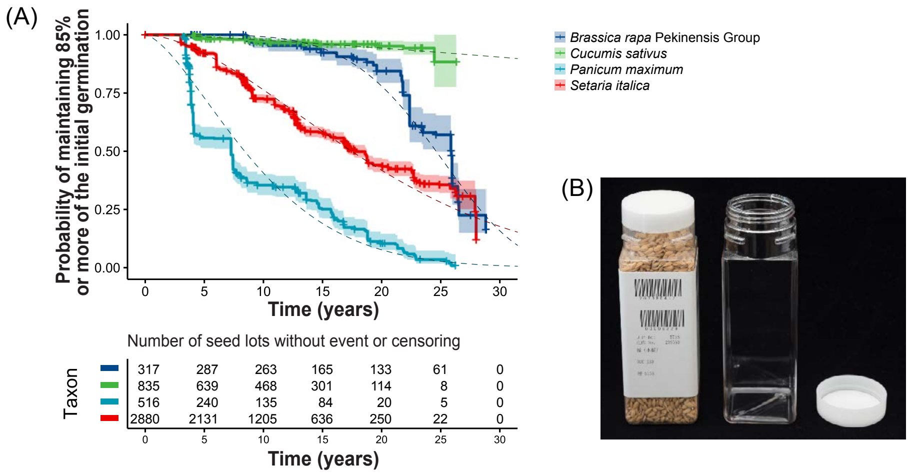

Figure 3. (**A**) Kaplan-Meier survival curves for seeds of four species stored in jars (**B**) in the genebank of the National Agriculture and Food Research Organisation, Japan. Event occurrence is defined as the moment when germination below 85% of initial germination is observed (solid line; the 95% confidence interval is indicated by a semi-transparent band) and approximate curves using the calculated Weibull parameters (dashed line). (A) Figure published with permission of Yamasaki *et al.* (2020). (B) Image published with permission of Fukuhiro Yamasaki.

A major problem in the preservation of biodiversity is the fact that a good number of species produce desiccation sensitive ('recalcitrant') seeds which cannot be dried. This means that storage of such germplasm can only be short-term, at high water content and temperature, or *in situ*. A wider category of problematic species in this respect produce so-called 'intermediate' seeds which display a lower critical moisture content than recalcitrant seeds and, thus, can be stored under semi-dry conditions. An example of this intermediate category of seeds is *Calamus palustris* var. cochinchinensi. Fan *et al.* (2020) tested various storage conditions and found that seeds of this species did not store well. Germination of seeds stored at 4°C dropped faster than seeds stored at 15°C, confirming the well-known sensitivity of recalcitrant and intermediate seeds to low temperature.

A well-known example of the intermediate category is *Coffea arabica* L. Coffee seeds also pose problems when they need to be (long-term) stored for seed banking purposes or breeding programmes. Guimarães *et al.* (2020) tested the hypothesis that total lipid and fatty acid profiles in the embryo and endosperm are related to the desiccation sensitivity of the seeds. The influence of drying rate is typical for intermediate-seeded species, as is a critical water content between 10 and 30% (figure 4). Comparison of lipid and fatty acid profiles of slow- and fast-dried seeds revealed that the rate of drying only influenced the lipid content of the embryos, in that fast-drying decreased lipid content by 15%. Since this could not be the cause of the difference in viability, the authors concluded that the higher levels of unsaturated fatty acids in the endosperm could be detrimental to the viability of the embryo, as these fatty acids are more prone to oxidation than saturated ones.

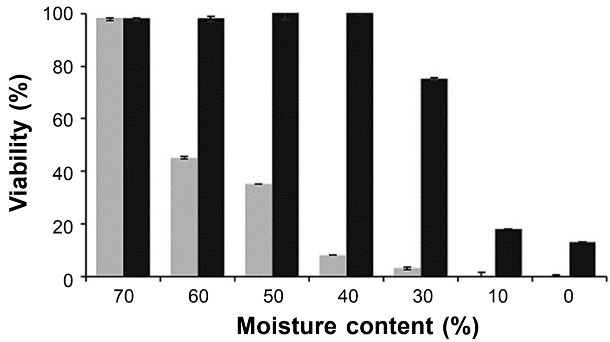

Figure 4. Viability in the tetrazolium test of coffee embryos separated from seeds and subjected to rapid drying in silica gel ( ) and slow drying in saline solutions ( ). Figure published with permission of Guimarães *et al*. (2020).

Staying with coffee, it is of eminent importance that coffee growers have access to high-quality seedlings, produced in nurseries from seed. Since the coffee seed shows very slow and asynchronous germination, combined with bad storability, the standard germination test is not the best suited for quality assessment. Instead the tetrazolium (TZ) test can be used, which is much quicker. Fantazzini *et al*. (2020) validated the TZ test by comparing historical data of results of the germination test with the TZ test in samples of coffee seeds (figure 5). They found good correlation between TZ test viability and germination testing at germination percentages above 70%, which is also the minimum requirement for commercial coffee seed sale in Brazil. For germination values below 70%, the TZ test was not valid.

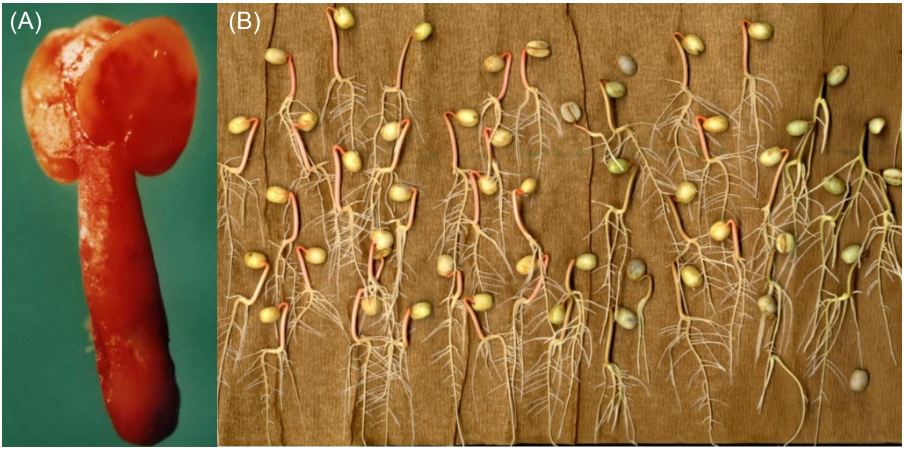

Figure 5. Tetrazolium was evaluated as an alternative to a germination test for evaluating the viability of coffee seeds by Fantazzini *et al*. (2020). (**A**) Viable coffee seed embryo stained with tetrazolium and (**B**) germinating coffee seeds Images published with permission of Fantazzini *et al*. (2020). Pictures published with permission of S.D.V.F. da Rosa.

Reliable seed testing is of great importance to the seed industry and genebanks alike. Seed testing is ideally reliable, accurate, fast and inexpensive. Seed imaging may be fast, simple and cost-effective. In addition, imaging is non-destructive, enabling the comparison of the physiology of single seeds with its (unique) image. It is therefore no surprise that there is currently considerable effort on the adoption of optical sensing technology in seed testing. Delayed luminescence (DL) is an imaging approach based on the non-heat related photon emission by substances, including living organisms. Luminescence may vary, depending on the material or source of initial excitation. Adeboye and Börner (2020) provide an overview of the exploration of DL as a possible tool for seed quality assessment over the last 40 years. They conclude that DL indeed has a potential for fast and non-destructive assessment of seed viability. However, more work is required before the method can be widely adopted, particularly so to clarify the sources and mechanisms of DL in seeds.

Seeds are the ultimate extremophytes which can withstand high levels of abiotic and biotic stress upon germination. Seeds from halophytes germinate in salt concentrations which severely inhibit non-halophyte seeds. Jiang *et al*. (2020) describe attempts to explore this phenomenon in the highly salt-tolerant halophyte *Salicornia europaea*. Halophytes are often tolerant to high metal concentrations, including strontium, which makes these plants good candidates for phytoremediation. This species produces dimorphic seeds of which the larger seeds proved to be more than two-fold more tolerant to the strontium concentrations used than the smaller ones. The authors conclude that direct seeding of this species might contribute to phytoremediation of soil contaminated by strontium.

While halophytes possess high tolerance to salt and metals, non-halophyte seeds are much less tolerant. Seed priming is often used to increase stress tolerance of seeds, based on the effect of so-called ‘cross tolerance’ in which one applied stress, i.e. osmotic stress by priming, may induce tolerance to other types of stress, e.g. salt or temperature. Muhie *et al.* (2020) applied this principle to increase the abiotic stress tolerance of onion seeds. They used a solid matrix priming method called vermicompost priming (VCP) and compared the effect with hydropriming or no priming. VCP proved to be superior to hydropriming and significantly increased both seed germination and seedling emergence under drought-, salt- and high-temperature-stress. An important finding as such treatments will be increasingly in demand in a changing climate when pressure from such abiotic stresses will only increase.

In the continuing quest for optimal seed and plant performance, treatments to attain this are sometimes co-interfering with an ultimate negative effect on plant growth. An example of this phenomenon is given by Pereira *et al.* (2020) who studied the interaction between coated maize seeds, containing pesticides, and the performance of the growth promoting *Azospirillum* bacteria. Indeed, the contact time between the bacteria and the pesticide-containing seed coat was inversely correlated with cell survival of the bacteria as compared to non-coated seeds. With the increasing interest in using growth promoting micro-organisms in agriculture such negative interactions may be expected, not only with pesticides but also biostimulants and fertilizers.

Seed vigour is an important seed quality attribute and is the sum total of factors contributing to field stress tolerance of the seeds. It has long been known that within a crop species, the larger seeds, containing more food reserves, perform better than the smaller, lighter seeds. Wang *et al.* (2020) explored this principle in hybrid rice seed production. There is asynchrony in growth and development of spikelets, resulting in superior and inferior spikelets containing heavier and lighter seeds, respectively, with the former 20% heavier than the latter. Interestingly, both total germination and the vigour index were always about 20% higher in the heavier seeds. It was suggested that this was caused by the somewhat higher total starch content of the superior seeds.

Coming to the end of this issue of *Seed Science and Technology*, it is clear from the 17 articles in it, that the major problem seed research and technology is dealing with is variation. Variation in dormancy, longevity, stress tolerance, seed quality, etc. poses problems for agricultural use and storage. While it is of the utmost importance to study fundamental processes in seeds, at the same time seed usage needs to be further optimised. The dazzling variation in seed attributes requires the study of many more species in many more taxa to get an idea of the extent of it across and within species. The further development of advanced imaging technology will be instrumental in handling such numbers of species. Finally, seeds are the basis of agriculture and this will be even more apparent in a changing climate. Ultimately, our current major crops may become useless in certain regions of the world. This also stresses the need for alternative crops, for example indigenous (orphan) crops which are often highly resilient and nutritious.

President of the International Society for Seed Science,
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