

Steven P.C. Groot (2022).  
*Seed Science and Technology*, **50**, 1, **Suppl.**, 141-151.  
<https://doi.org/10.15258/sst.2022.50.1.s.08>



## Invited Review

# Seed maturation and its practical implications

**Steven P.C. Groot**

Wageningen University & Research, Wageningen Seed Science Centre, P.O. Box 16, 6700AA Wageningen, The Netherlands (E-mail: [steven.groot@wur.nl](mailto:steven.groot@wur.nl))

*(Submitted August 2022; Accepted October 2022; Published online October 2022)*

### Abstract

The use of high vigour seeds for crop production is increasing in importance. Seed vigour develops during the late maturation phase, after deposition of reserves and attainment of maximum dry weight. During this phase, various protective mechanisms are imposed in the seeds that will aid survival after release from the mother plant. These mechanisms include the production of protective metabolites such as antioxidants and pigments, specific proteins and degradation of chlorophyll. All are essential for maximum quality of seeds used as propagation material, since they aid in providing increased tolerance to diverse biotic and abiotic stresses. Physical sanitation treatments, ageing during storage and threat by pathogens are some of the stresses that the seeds can experience during production, processing and germination. However, harvesting seeds at the fully mature stage and with maximum vigour is a big challenge in seed production. For most seeds, analysis of chlorophyll levels can be used as a measure of relative maturity. This is a rather sensitive technique as it uses the fluorescence properties of chlorophyll, and can also be used for upgrading seed lots containing relatively large fractions of less mature seeds. Sorted seed fractions are also useful to study processes during late seed maturation and the different seed vigour aspects gained during late seed maturation.

**Keywords:** chlorophyll fluorescence, longevity, maturity, seed development, seed sorting, stress tolerance, vigour.

### Introduction

Seed vigour is critical for seedling establishment and early crop growth, and seed maturity is an important aspect of seed vigour. But what is a ‘mature’ seed? Agronomists use the term ‘physiological maturity’ to define the moment in which a seed has acquired its maximum dry weight and, thus, maximum agronomic yield (Shaw and Loomis, 1950); even though the harvest may be delayed beyond this point, to reduce the seed moisture level. At this developmental stage the nutrient uptake from the mother plant stops (Harrington, 1972).

---

© 2022 Steven P.C. Groot. This is an open access article distributed in accordance with the Creative Commons Attribution Non Commercial (CC BY-NC 4.0) license, which permits others to distribute, remix, adapt, build upon this work non-commercially, and license their derivative works on different terms, provided the original work is properly cited and the use is non-commercial. See: <https://creativecommons.org/licenses/by-nc/4.0>

However, this definition does not take into account the physiological and morphological processes happening in seeds after reaching maximum dry weight and that are essential for gaining maximum seed vigour and reach full maturity (TeKrony *et al.*, 1979). To avoid semantic discussions and reduce confusion, seed biologists often accept the definition and call the subsequent period of seed development the ‘late maturation stage’. The relative length of this late maturation stage differs largely among species (Leprince *et al.*, 2017). For attaining full seed vigour, seeds should be harvested at ‘harvest maturity’ defined as “the end of the seed maturation phase, by which point, seed moisture content has declined to values approaching equilibrium with the ambient environment” (Ellis, 2019). In natural conditions, completion of the late maturation stage coincides with shedding of the seeds or mature fruits.

Most seed production studies show that fully mature seeds have better seed germination quality compared to seeds at physiological maturity (Finch-Savage and Bassel, 2016), especially when exposed to stressful conditions. Fully mature seeds also have a better longevity (the capacity to remain viable for a long period of dry storage) (Verdier *et al.*, 2013). This increase in seed quality during the late maturation stage has been reported for a large number of species. These include a considerable number of publications in the 50 volumes of this journal, *Seed Science and Technology*, on species such as carrot (Steckel *et al.*, 1989), sorghum (Shephard *et al.*, 1996), tomato (Demir and Samit, 2001), wild barley (*Hordeum brevisubulatum* (Trin.)) (Wang *et al.*, 2006), chickpea (Samarah and Abu-Yahya, 2008), moringa (Kundu, 2009) and *Melia dubia* Cav. (a tropical tree with fruits taking more than a year for maturation; Mohamed Faisal and Umarani, 2016). Two studies on seed maturity published in *Seed Science and Technology*, using wheat and physic nut (*Jatropha curcas* L.) seeds, mentioned that maximum germination quality was already acquired at physiological maturity (Rasyad *et al.*, 1990; Silva *et al.*, 2011). Although for most crops maximum seed longevity is obtained at harvest maturity, there are exceptions and it can also be influenced by seed production conditions, as reviewed by Ellis (2019). This review discusses the practical implications of seed maturation for harvesting and seed quality, and is restricted to desiccation tolerant (orthodox) seeds. For details on the molecular events characterising the late seed maturation phase and its genetic regulation, reviews by Sano *et al.* (2015) and Leprince *et al.* (2017) are recommended.

### Late maturation processes

After fertilisation, seed development starts with organogenesis, which is followed by the seed filling phase. During seed filling, orthodox seeds also acquire desiccation tolerance, while the transcription and translation machinery is mainly dedicated to the production of storage reserves in the form of oil, proteins and starch or other carbohydrates. With the deposition of this storage material, the relative moisture level of the seeds decreases. At physiological maturity, the synthesis of reserves ceases and the seed enters into the late maturation phase with the building of protection mechanisms accompanied by a further drying until they reach a quiescent stage (Sano *et al.*, 2015 Leprince *et al.*, 2017). These protection mechanisms play an important role in maximising seed vigour and include

the production of Late Embryogenesis Abundant (LEA) and heat shock proteins, and the accumulation of raffinose family oligosaccharides and various types of antioxidants. In many species, seed dormancy also develops during late maturation, to protect the seed from germinating under environmental conditions unfavourable for seedling establishment and reproduction.

Cell protection is essential to limit deterioration of the seed after shedding and for survival under low moisture levels. The relatively dry detached seed is prone to ageing by oxidation of lipids (including membranes), proteins, DNA and RNA. Antioxidant enzyme activity requires a minimal amount of moisture, as does enzymatic repair of oxidative damage. Thus, in the dry state, scavenging of reactive oxygen species (ROS) relies completely on molecular antioxidants. Tocopherol levels increase during seed maturation and are the main lipophilic anti-oxidant protecting the cell and mitochondrial membranes against ROS (Zhou *et al.*, 2018). Seeds from mutants deficient in the synthesis of these antioxidants have a very short shelf-life (Sattler *et al.*, 2004). Chlorophyll degradation and synthesis of carotenoids or phenolic compounds during (late) maturation also offer protection against light-induced ROS accumulation. Arabidopsis mutants hampered in chlorophyll degradation show loss of germination capacity upon prolonged light exposure during seed maturation and drying (Clerkx *et al.*, 2003; Li *et al.*, 2017). While phenolic compounds can have antioxidant, antimicrobial or anti-feedant activity (Sano *et al.*, 2015). Reducing monosaccharides such as glucose and fructose are also degraded during maturation, as they can react with amino acids, in the so-called Maillard reaction, resulting in the formation of toxic compounds. The accumulation of non-reducing sugars such as sucrose and raffinose family oligosaccharides plays an important role in forming a cytoplasmic glassy state with a very low molecular mobility upon seed drying (Ballesteros and Walters, 2011). During the late maturation phase, nuclear DNA condenses (van Zanten *et al.*, 2012), which reduces the risks of ROS-induced double strand breaks (Falk *et al.*, 2010).

### Markers for seed maturity

Many species have an extended period of flowering and, consequently, fully mature seeds can be shed while other parts of the plant are still flowering. When this concerns seed crops, for example of carrot, parsley or kale, the presence of less mature seeds in a once-over harvest is often inevitable. Seeds that have not reached physiological maturity can be sorted out by size or density, but since the late maturation phase hardly adds extra dry weight, other markers are needed. As mentioned above, in most species, chlorophyll is degraded during late seed maturation and due to its fluorescent properties, can be quantified at very low levels (figure 1). Using this knowledge, a method was developed to sort a seed lot into different maturity fractions based on the analysis of chlorophyll fluorescence (CF) signal of individual seeds (Jalink *et al.*, 1998). The technique is relatively simple and suitable for fast sample analysis and seed sorting. Jalink *et al.* (1998) used this method to separate a commercial cabbage seed lot with too low quality. After sorting the seed lot into six fractions, the authors observed a negative correlation between the seed CF signals

and their performance in a germination test. Removal of seeds with high CF signals could upgrade the seed lot to commercial level (Jalink *et al.*, 1998). This clearly demonstrated the importance of the late maturation phase in the acquisition of seed quality. CF analysis is also a valuable technique to study the role of late seed maturation processes in seed vigour. With such subsamples from a single seed harvest, experiments requiring thousands of seeds for treatments and subsequent germination testing can be performed on for instance seed storage and sensitivity to physical seed sanitation. The positive correlation between low CF levels, seed maturity and seed vigour has been demonstrated for a diverse set of crops, including barley (Konstantinova *et al.*, 2002), carrot (Groot *et al.*, 2006), chicory (Ooms and Destain, 2011), melon (Wilson *et al.*, 2014), parsley (Dericquebourg *et al.*, 2022), pepper (Kenanoglu *et al.*, 2013), rice (Costa *et al.*, 2014) and soya bean (Cicero *et al.*, 2009). The sorting technique was also used to study gene expression during the late maturation phase (Soeda *et al.*, 2005). Several types of equipment have been produced to analyse or sort seed lots based on chlorophyll fluorescence. An example of analysis of individual *Brassica oleracea* L. seeds is presented in figure 1.

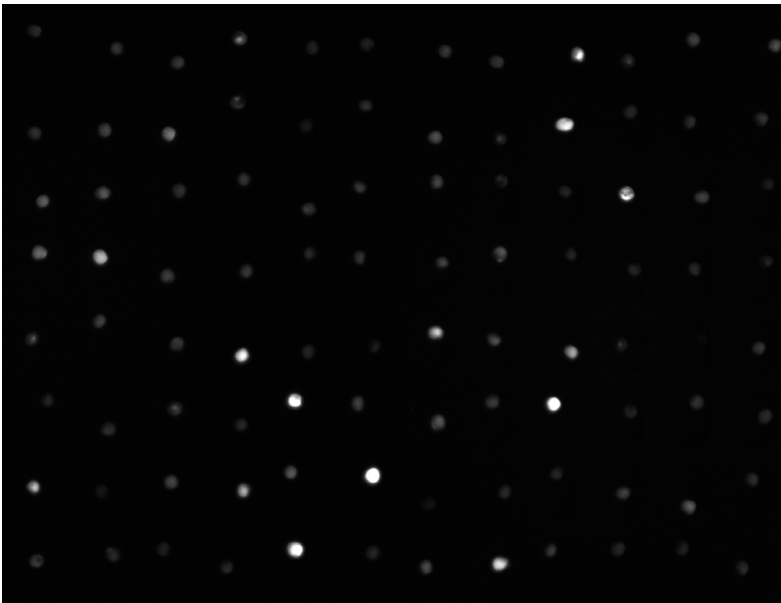


Figure 1. Variation in chlorophyll fluorescence among individual seeds in a *Brassica oleracea* seed lot. Seeds showing a brighter signal have a higher level of chlorophyll fluorescence (less mature).

The relationship between CF levels and seed quality is demonstrated for a commercial rice paddy seed lot with data from Costa *et al.* (2014). Half of the rice seeds in the lot had a low level of CF and a, for rice, high frequency of germination and normal seedlings (table 1). With increasing CF levels, the frequency of total germination and normal seedlings dropped and the time to 50% of total germination increased.

Table 1. Germination, normal seedlings and time to 50% total germination (T50) for an example commercial paddy rice seeds divided into five fractions based on their chlorophyll fluorescence levels. Data previously published by Costa *et al.* (2014).

Chlorophyll fluorescence levels (units mm <sup>-2</sup> )	Proportion of seeds in the fraction (%)	Germination (%)	Normal seedlings (%)	T50 (hours)
<i>Non-sorted</i>		97 a*	64 a	53.2 a
0-60	50	96 a	77 a	50.7 a
60.1-105	35	95 a	66 a	52.3 a
105.1-130	5	95 a	68 a	60.7 b
130.1-175	5	90 b	55 b	60.4 b
> 175	5	91 b	48 b	61.5 b
<b>Coefficient of variance (%)</b>		<b>3.6</b>	<b>9.6</b>	<b>6.3</b>

\*Within a column, different letters mean significant differences (5%) found by Scott-Knott test.

Although chlorophyll levels show a clear negative correlation with seed vigour within seed batches, there is no one-to-one correlation when comparing different seed batches (Powell, 2022). The reason is that seed production, harvesting, rate of drying and genetic variation have an influence on the rate of chlorophyll degradation. CF analyses has been explored for optimising the time of harvest for rice seeds to maximise longevity in genebank storage (Hay *et al.*, 2015). The authors harvested seeds from 20 diverse rice accessions on four occasions after peak flowering and analysed the distribution of CF levels with individual seeds. For some accessions they observed a strong relationship between CF and longevity, but for other accessions, such a relation was absent (Hay *et al.*, 2015). Despite these limitations, the CF analyses and sorting technique is increasingly used by seed companies to optimise harvesting and for upgrading seed lots.

Unfortunately, the CF technique cannot be used for all crop species because not all seeds contain chlorophyll during development, and some seeds retain their chlorophyll at the end of maturation, such as with green peas. Also, in seeds with a very dark seed coat, for example, the black seeds of onion, the CF signal cannot be detected in a reliable way. Thus, other markers of seed maturity are needed for those seeds. With many species, the seed coat or the fruit changes in colour during seed maturation, through the accumulation of flavonoids, phenols or other compounds in the seed coat layer. Darkening upon maturation is well known with beans (Zhao *et al.*, 2022) and cruciferous species (Lepiniec *et al.*, 2006). With sugar beet seeds, quantitative changes in pericarp colour are significantly correlated with seed germination traits (Mirzaei and Rajabi, 2021). These compounds offer protection to the seeds after shedding, having a negative effects on digestion by herbivores, or acting as antioxidants or as germination inhibitors to tune seedling emergence. In some crops, plant breeders have selected for absence of these pigments, for instance in oil seed rape meal to improve oil yield and feed quality (Chao *et al.*, 2022). Plants evolved a synchronisation between fruit ripening and seed maturation, favouring the attraction of natural dispersers. In Solanaceae fruits, chlorophyll is degraded

during ripening and red-coloured metabolites accumulate, normally coinciding with seed maturation. However, breeding for early fruit ripening may have resulted in loss of the linkage with seed maturity, and for new cultivars, seed companies have to determine the optimal seed harvest time independent of fruit maturity.

### Other maturity effects

As mentioned above, many studies have shown the importance of the late maturation phase for seed longevity in nature or under commercial storage conditions. Late maturation events can also have effects on other vigour aspects. For example, carrots flower in sequential umbels and seeds from more mature umbels are more responsive to priming treatments (Nascimento *et al.*, 2013). Another aspect influenced by the seed maturity level and seed vigour is sensitivity to seed sanitation. Physical sanitation treatments with hot water, steam or an electron beam are getting more popular as alternatives to chemical disinfection. Less mature subsamples of cabbage or carrot seed lots, separated using the CF sorting technique, are more sensitive to the hot water or steam treatments (Groot *et al.*, 2006). Sensitivity to the electron seed treatment is not influenced by seed maturity, likely because this treatment touches only the seed coat.

With kale crops, seedlings can suffer from blindness, a phenomenon where shoot apical meristem activity may terminate after sowing at low temperatures (de Jonge *et al.*, 2016). The sensitivity of the seeds has both a genetic and seed production influence. It was shown that less mature *Brassica oleracea* seeds appear to be more susceptible for producing these so-called blind seedlings under cold stress (Bello and Bradford, 2021). A study with peanut seeds found that the use of fully mature compared with less mature seeds can even have an effect on subsequent plant generations as a ‘seed maturity memory’ (Song *et al.*, 2021). The mechanism behind this transgenerational effect remains to be elucidated; epigenetics or seed-transmitted microbiota may play a role, but it is worth studying this phenomenon with more crops and production conditions. Germinating mature cabbage seeds are less colonised by the pathogenic fungus *Alternaria brassicicola* (Schw.) compared with germinating less mature seeds (Knox-Davies, 1979), showing an effect of seed maturity on biotic stress tolerance.

Plants are holobionts, with a large number of associated microorganisms. Their microbiota (often referred to as microbiome as their presence is analysed by DNA sequencing), play an important role in plant health and vigour (Vandenkoornhuys *et al.*, 2015). Part of these microbiota is transferred through the seeds to the next generation (Verma and White, 2019). In the past, seed technologists almost only paid attention to pathogenic organisms in relation to seed health, while nowadays the importance of other organisms in the seed microbiome is acknowledged (Berg and Raaijmakers, 2018). It has become clear that during plant evolution, beneficial relations have also developed, where part of these microbiota can support the seedling in biotic or abiotic stress tolerance (Bergna *et al.*, 2018). For instance, rice endophytic bacteria that are transmitted from the mother plant through the seeds can provide the seedlings with resistance against damping-off disease (Matsumoto *et al.*, 2021). Another example of beneficial seed microbiota is

with perennial ryegrass where the endophytic fungus *Epichloë festucae* is transmitted from the mother plant with the seeds, to provide the next generation plants with tolerance against biotic and abiotic stress (Bastias *et al.*, 2017; He *et al.*, 2017). This protection method has found its application in commercial grass seed production. It was observed that the transfer of *Epichloë festucae* to the seedlings is better maintained through harvesting mature seeds (Hill *et al.*, 2005). The latter indicates that also seed microbiota may have a kind of ‘maturation’ process for which the timing is in concert with that of the seed itself.

### Seed production challenges

Producing high quality seeds is both a challenge and a skill, especially for crops that flower over an extended period, and shed fully mature seeds, and with large production fields showing heterogeneities in crop development. For economic reasons, with most crops, a single harvest time has to be used and that optimal time has to be decided, also in relation to weather forecasts. Sampling at different spots in the field and analysing the maturity by colour or CF can be used. A promising new tool is a combination of multispectral scanning of the entire field with an unmanned aerial vehicle (drone) and computational deep learning methods, as demonstrated for parsley seed harvesting (Dericquebourg *et al.*, 2022).

For some crops, it can be useful to dry the seeds slowly after harvest, depending on harvesting method. Soya bean seeds harvested before full maturity retain germination quality better when dried inside intact pods compared to depodded seeds (Samarah *et al.*, 2009). With for instance bean and kale crops, the mother plants, with pods containing seeds at different maturity stage, can be cut and slowly dried as a swath. Seeds that have passed physiological maturity can finish their late maturation process during slow drying, as long as they are still moist enough. During slow drying, seeds that are not at physiological maturity may be directed into late maturation and still gain quality, but they will have a smaller seed size. With tomato, a short period of post-harvest fruit storage can improve seed quality if the fruits are harvested at the green-mature stage and stored until the pericarp is completely red (Dias *et al.*, 2006). A similarly result was obtained with sweet pepper, where seed quality from fruits harvested at 50 days after anthesis was improved by 12 days post-harvest storage, although the best seed quality was obtained with fruits left on the plants until 60 days after anthesis (Vidigal *et al.*, 2009).

Although waiting to harvest seeds until they are fully mature is the best strategy for optimal seed vigour, there are also risks when waiting too long. While in nature fully mature seeds are often shed, in the domestication and breeding of many crops, there has been a selection for genotypes that do not shed their seeds. Similarly, genotypes with no or low levels of seed dormancy have often been selected. During humid weather conditions or in moist fruits, this creates the risk of preharvest sprouting, whereby the seeds lose their desiccation tolerance. But even when germination processes do not progress beyond radicle protrusion (sprouting), seed longevity may decline, comparable with the decline seen in primed seeds (Ellis, 2019). Tomato seeds for instance, should not be harvested too late as this results in reduced seed quality (Demir and Samit, 2001).



Other risks of late harvest are pests or pathogen infection, which can occur during later phases of seed production. With organic wheat and barley seed production in Sweden, it was observed, that infection by the fungal pathogen *Bipolaris sorokiniana* increased during the last three weeks before harvest; early harvest was advised (Olvång, 2004).

## Conclusions

The use of high vigour seeds to provide maximum germination and more resilient seedlings is increasing in importance. At physiological maturity, defined as reaching the maximum dry weight, seeds have not yet acquired their maximum quality as starting material for a new crop. The late seed maturation phase, following after the point of maximum dry weight, is important for development into fully mature seeds and the acquisition of maximum seed vigour. Fully mature seeds are more tolerant to biotic and abiotic stresses and have a better storability. The higher seed vigour is related to various natural protection mechanisms imposed during this last phase of seed development, with an important role for production of anti-oxidants. Optimising the harvest moment with crops that show an extended period of flowering, to obtain maximum yield with high vigour seeds, is a challenge and a skill. The challenge is enlarged by selection and breeding against some natural processes and their timing during seed and fruit maturation. Although with many crops the colour of the fruit or seed coat can be used as an indicator for seed maturity, CF is often a more sensitive marker to optimise the harvesting moment or to remove less mature seeds for upgrading of seed lots. The CF sorting technique also offers an opportunity to create subsamples from a single seed lot to study the processes happening in seeds that are important for the acquisition of seed vigour.

## Acknowledgements

Mariana Silva Artur from Wageningen University & Research is acknowledged for discussions on the draft manuscript.

## References

- Ballesteros, D. and Walters, C. (2011). Detailed characterization of mechanical properties and molecular mobility within dry seed glasses: relevance to the physiology of dry biological systems. *The Plant Journal*, **68**, 607-619. <<https://doi.org/10.1111/j.1365-313X.2011.04711.x>>
- Bastias, D.A., Ueno, A.C., Machado Assef, C.R., Alvarez, A.E., Young, C.A. and Gundel, P.E. (2017). Metabolism or behavior: explaining the performance of aphids on alkaloid-producing fungal endophytes in annual ryegrass (*Lolium multiflorum*). *Oecologia*, **185**, 245-256. <<https://doi.org/10.1007/s00442-017-3940-2>>
- Bello, P. and Bradford, K.J. (2021). Relationships of *Brassica* seed physical characteristics with germination performance and plant blindness. *Agriculture*, **11**, 220. <<http://doi.org/10.3390/agriculture11030220>>
- Berg, G. and Raaijmakers, J.M. (2018). Saving seed microbiomes. *The ISME Journal*, **12**, 1167-1170. <<https://doi.org/10.1038/s41396-017-0028-2>>
- Bergna, A., Cernava, T., Rändler, M., Grosch, R., Zachow, C. and Berg, G. (2018). Tomato seeds preferably transmit plant beneficial endophytes. *Phytobiomes Journal*, **2**, 183-193. <<https://doi.org/10.1094/PBIOMES-06-18-0029-R>>



- Chao, H., Guo, L., Zhao, W., Li, H. and Li, M. (2022). A major yellow-seed QTL on chromosome A09 significantly increases the oil content and reduces the fiber content of seed in *Brassica napus*. *Theoretical and Applied Genetics*, **135**, 1293-1305. <<https://doi.org/10.1007/s00122-022-04031-0>>
- Cicero, S.M., van der Schoor, R. and Jalink, H. (2009). Use of chlorophyll fluorescence sorting to improve soybean seed quality. *Revista Brasileira de Sementes*, **31**, 145-151.
- Clerkx, E.J., Vries, H.B., Ruys, G.J., Groot, S.P.C. and Koornneef, M. (2003). Characterization of green seed, an enhancer of *abi3-1* in Arabidopsis that affects seed longevity. *Plant Physiology*, **132**, 1077-1084. <<https://doi.org/10.1104/pp.103.022715>>
- Costa, D.S., Kodde, J. and Groot, S.P.C. (2014). Chlorophyll fluorescence and X-ray analyses to characterise and improve paddy rice seed quality. *Seed Science and Technology*, **42**, 449-453. <<https://doi.org/10.15258/sst.2014.42.3.11>>
- de Jonge, J., Kodde, J., Severing, E.I., Bonnema, G., Angenent, G.C., Immink, R.G.H. and Groot, S.P.C. (2016). Low temperature affects stem cell maintenance in *Brassica oleracea* seedlings. *Frontiers in Plant Science*, **7**, 800. <<https://doi.org/10.3389/fpls.2016.00800>>
- Demir, I. and Samit, Y. (2001). Seed quality in relation to fruit maturation and seed dry weight during development in tomato. *Seed Science and Technology*, **29**, 453-462.
- Dericquebourg, E., Hafiane, A. and Canals, R. (2022). Generative models-based data labeling for deep networks regression: application to seed maturity estimation from UAV multispectral images. *arXiv*. <<https://doi.org/10.48550/ARXIV.2208.04611>>
- Dias, D., Ribeiro, F.P., Dias, L.A.S., Silva, D.J.H. and Vidigal, D.S. (2006). Tomato seed quality in relation to fruit maturation and post-harvest storage. *Seed Science and Technology*, **34**, 691-699. <<https://doi.org/10.15258/sst.2006.34.3.15>>
- Ellis, R.H. (2019). Temporal patterns of seed quality development, decline, and timing of maximum quality during seed development and maturation. *Seed Science Research*, **29**, 135-142. <https://doi.org/10.1017/S0960258519000102>.
- Falk, M., Lukasova, E. and Kozubek, S. (2010). Higher-order chromatin structure in DSB induction, repair and misrepair. *Mutation Research/Reviews in Mutation Research*, **704**, 88-100. <<https://doi.org/10.1016/j.mrrev.2010.01.013>>
- Finch-Savage, W.E. and Bassel, G.W. (2016). Seed vigour and crop establishment: extending performance beyond adaptation. *Journal of Experimental Botany*, **67**, 567-591. <<https://doi.org/10.1093/jxb/erv490>>
- Groot, S.P.C., Birnbaum, Y., Rop, N., Jalink, H., Forsberg, G., Kromphardt, C., Werner, S. and Koch, E. (2006). Effect of seed maturity on sensitivity of seeds towards physical sanitation treatments. *Seed Science and Technology*, **34**, 403-413. <<https://doi.org/10.15258/sst.2006.34.2.16>>
- Harrington, J.F. (1972). Seed storage and longevity *Seed biology*, pp 145-245, Academic Press, New York.
- Hay, F.R., Timple, S. and van Duijn, B. (2015). Can chlorophyll fluorescence be used to determine the optimal time to harvest rice seeds for long-term genebank storage? *Seed Science Research*, **25**, 321-334. <<https://doi.org/10.1017/S0960258515000082>>
- He, L., Hatier, J.H.B. and Matthew, C. (2017). Drought tolerance of two perennial ryegrass cultivars with and without AR37 endophyte. *New Zealand Journal of Agricultural Research*, **60**, 173-188. <<https://doi.org/10.1080/00288233.2017.1294083>>
- Hill, N., Bouton, J., Hiatt, E. and Kittle, B. (2005). Seed maturity, germination, and endophyte relationships in tall fescue. *Crop Science*, **45**, 859-863. <<https://doi.org/10.2135/cropsci2004.0057>>
- Jalink, H., van der Schoor, R., Frandas, A., van Pijlen, J.G. and Bino, R.J. (1998). Chlorophyll fluorescence of *Brassica oleracea* seeds as a non-destructive marker for seed maturity and seed performance. *Seed Science Research*, **8**, 437-443. <<https://doi.org/10.1017/S0960258500004402>>
- Kenanoglu, B.B., Demir, I. and Jalink, H. (2013). Chlorophyll fluorescence sorting method to improve quality of capsicum pepper seed lots produced from different maturity fruits. *HortScience*, **48**, 965-968.
- Knox-Davies, P.S. (1979). Relationships between *Alternaria brassicicola* and *Brassica* seeds. *Transactions of the British Mycological Society*, **73**, 235-248. <[https://doi.org/10.1016/S0007-1536\(79\)80107-2](https://doi.org/10.1016/S0007-1536(79)80107-2)>
- Konstantinova, P., Van Der Schoor, R., Van Den Bulk, R. and Jalink, H. (2002). Chlorophyll fluorescence sorting as a method for improvement of barley (*Hordeum vulgare* L.) seed health and germination. *Seed Science and Technology*, **30**, 411-421.
- Kundu, M. (2009). Effect of seed maturity on germination and desiccation tolerance of *Moringa oleifera* seed. *Seed Science and Technology*, **37**, 589-596. <<https://doi.org/10.15258/sst.2009.37.3.08>>

- Lepiniec, L., Debeaujon, I., Routaboul, J.M., Baudry, A., Pourcel, L., Nesi, N. and Caboche, M. (2006). Genetics and biochemistry of seed flavonoids. *Annual Review of Plant Biology*, **57**, 405-430. <<https://doi.org/10.1146/annurev.arplant.57.032905.105252>>
- Leprince, O., Pellizzaro, A., Berriri, S. and Buitink, J. (2017). Late seed maturation: drying without dying. *Journal of Experimental Botany*, **68**, 827-841. <<https://doi.org/10.1093/jxb/erw363>>
- Li, Z., Wu, S., Chen, J., Wang, X., Gao, J., Ren, G. and Kuai, B. (2017). NYEs/SGRs-mediated chlorophyll degradation is critical for detoxification during seed maturation in *Arabidopsis*. *The Plant Journal*, **92**, 650-661. <<https://doi.org/10.1111/tpj.13710>>
- Matsumoto, H., Fan, X., Wang, Y., Kusstatscher, P., Duan, J., Wu, S., Chen, S., Qiao, K., Wang, Y., Ma, B., Zhu, G., Hashidoko, Y., Berg, G., Cernava, T. and Wang, M. (2021). Bacterial seed endophyte shapes disease resistance in rice. *Nature Plants*, **7**, 60-72. <<https://doi.org/10.1038/s41477-020-00826-5>>
- Mirzaei, M.R. and Rajabi, A. (2021). Relationship of seed pericarp color with seed quality in sugar beet (*Beta vulgaris* L. var. altissima Döhl). *Genetic Resources and Crop Evolution*. <<https://doi.org/10.1007/s10722-021-01120-9>>
- Mohamed Faisal, M. and Umarani, R. (2016). Study on fruit and seed maturation in *Melia dubia*. *Seed Science and Technology*, **44**, 422-427. <<https://doi.org/10.15258/sst.2016.44.2.13>>
- Nascimento, W., Huber, D. and Cantliffe, D. (2013). Carrot seed germination and respiration at high temperature in response to seed maturity and priming. *Seed Science and Technology*, **41**, 164-169. <<https://doi.org/10.15258/sst.2013.41.1.19>>
- Olvång, H. (2004). Early harvest - a possible method for production of healthy seed for organic farming. *Seed Testing International*, **127**, 22-265.
- Ooms, D. and Destain, M.F. (2011). Evaluation of chicory seeds maturity by chlorophyll fluorescence imaging. *Biosystems Engineering*, **110**, 168-177. <<https://doi.org/10.1016/j.biosystemseng.2011.07.012>>
- Powell, A.A. (2022). Seed vigour in the 21st century. *Seed Science and Technology*, **50**, 45-73. <<https://doi.org/10.15258/sst.2022.50.1.s.04>>
- Rasyad, A., Sanford, D.A.v. and TeKrony, D.M. (1990). Changes in seed viability and vigour during wheat seed maturation. *Seed Science and Technology*, **18**, 259-267.
- Samarah, N.H. and Abu-Yahya, A. (2008). Effect of maturity stages of winter- and spring-sown chickpea (*Cicer arietinum* L.) on germination and vigour of the harvested seeds. *Seed Science and Technology*, **36**, 177-190. <<https://doi.org/10.15258/sst.2008.36.1.19>>
- Samarah, N.H., Mullen, R.E., Goggi, S. and Gaul, A. (2009). Effect of drying treatment and temperature on soybean seed quality during maturation. *Seed Science and Technology*, **37**, 469-473. <<https://doi.org/10.15258/sst.2009.37.2.20>>
- Sano, N., Rajjou, L., North, H.M., Debeaujon, I., Marion-Poll, A. and Seo, M. (2015). Staying alive: Molecular aspects of seed longevity. *Plant and Cell Physiology*, **57**, 660-674. <<https://doi.org/10.1093/pcp/pcv186>>
- Sattler, S.E., Gilliland, L.U., Magallanes-Lundback, M., Pollard, M. and DellaPenna, D. (2004). Vitamin E is essential for seed longevity and for preventing lipid peroxidation during germination. *Plant Cell*, **16**, 1419-1432. <<https://doi.org/10.1105/tpc.021360>>
- Shaw, R.H. and Loomis, W.E. (1950). Bases for the prediction of corn yields. *Plant Physiology*, **25**, 225-244. <<https://doi.org/10.1104/pp.25.2.225>>
- Shephard, H., Naylor, R. and Stuchbury, T. (1996). The influence of seed maturity at harvest and drying method on the embryo, alpha-amylase activity and seed vigour in sorghum (*Sorghum bicolor* (L.) Moench). *Seed Science and Technology*, **24**, 245-259.
- Silva, L.J., Dias, C.F.S., Dias, L.A.S. and Hilst, P.C. (2011). Physiological quality of *Jatropha curcas* L. seeds harvested at different development stages. *Seed Science and Technology*, **39**, 572-580. <<https://doi.org/10.15258/sst.2011.39.3.04>>
- Soeda, Y., Konings, M.C.J.M., Vorst, O., van Houwelingen, A.M.M.L., Stoopen, G.M., Maliepaard, C.A., Kodde, J., Bino, R.J., Groot, S.P.C. and van der Geest, A.H.M. (2005). Gene expression programs during *Brassica oleracea* seed maturation, osmopriming and germination are indicators of progression of the germination process and the stress tolerance level. *Plant Physiology*, **137**, 354-368. <<https://doi.org/10.1104/pp.104.051664>>
- Song, Y., Tseng, Y., Rowland, D., Tillman, B., Wilson, C., Sarnoski, P. and Zurweller, B. (2021). Multiple-generation seed maturity effects on seedling vigour in a production environment. *Journal of Agronomy and Crop Science*, **207**, 1024-1040. <<https://doi.org/10.1111/jac.12559>>

- Steckel, J.R.A., Gray, D. and Rowse, H.R. (1989). Relationships between indices of seed maturity and carrot seed quality. *Annals of Applied Biology*, **114**, 177-183. <<https://doi.org/10.1111/j.1744-7348.1989.tb06798.x>>
- TeKrony, D.M., Egli, D.B., Balles, J., Pfeiffer, T. and Fellows, R.J. (1979). Physiological maturity in soybean. *Agronomy Journal*, **71**, 771-775. <<https://doi.org/10.2134/agronj1979.00021962007100050016x>>
- van Zanten, M., Carles, A., Li, Y. and Soppe, W. (2012). Control and consequences of chromatin compaction during seed maturation in *Arabidopsis thaliana*. *Plant Signal Behaviour*, **7**, 1-4. <<https://doi.org/10.4161/psb.19281>>
- Vandenkoornhuysse, P., Quaiser, A., Duhamel, M., Le Van, A. and Dufresne, A. (2015). The importance of the microbiome of the plant holobiont. *New Phytologist*, **206**, 1196-1206. <<https://doi.org/10.1111/nph.13312>>
- Verdier, J., Lalanne, D., Pelletier, S., Torres-Jerez, I., Righetti, K., Bandyopadhyay, K., Leprince, O., Chatelain, E., Vu, B.L., Gouzy, J., Gamas, P., Udvardi, M.K. and Buitink, J. (2013). A regulatory network-based approach dissects late maturation processes related to the acquisition of desiccation tolerance and longevity of *Medicago truncatula* seeds. *Plant Physiology*, **163**, 757-774. <<https://doi.org/10.1104/pp.113.222380>>
- Verma, S.K. and White Jr., J.F. (2019). *Seed Endophytes*, Springer. <<https://doi.org/10.1007/978-3-030-10504-4>>
- Vidigal, D., Dias, D., Von Pinho, E. and Dias, L. (2009). Sweet pepper seed quality and lea-protein activity in relation to fruit maturation and post-harvest storage. *Seed Science and Technology*, **37**, 192-201. <<https://doi.org/10.15258/sst.2009.37.1.21>>
- Wang, P., Zhou, D. and Valentine, I. (2006). Seed maturity and harvest time effects seed quantity and quality of *Hordeum brevisubulatum*. *Seed Science and Technology*, **34**, 125-132. <<https://doi.org/10.15258/sst.2006.34.1.13>>
- Wilson, H.T., Khan, O. and Welbaum, G.E. (2014). Chlorophyll fluorescence in developing 'Top Mark' cantaloupe (*Cucumis melo*) seeds as an indicator of quality. *Seed Technology*, **36**, 103-113.
- Zhao, P., Chu, L., Wang, K., Zhao, B., Li, Y., Yang, K. and Wan, P. (2022). Analyses on the pigment composition of different seed coat colors in adzuki bean. *Food Science & Nutrition*, **10**, 2611-2619. <<https://doi.org/10.1002/fsn3.2866>>
- Zhou, W., Branch, W., Gilliam, L. and Marshall, J. (2018). Phytosterol composition of *Arachis hypogaea* seeds from different maturity classes. *Molecules*, **24**, 106. <<https://doi.org/10.3390/molecules24010106>>