

Chapter

Influence of Seed Development and Maturation on the Physiological and Biochemical Seed Quality

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Abstract

Seed quality is one of the widely discussed topics in seed system and seed biology; thus, many countries with functional and vibrant seed system have invested heavily in seed quality assurance and quality control. Good quality seed is crucial for any cropping system, for without it, there is poor field establishment and wastage of other production inputs. Good quality seed responds well to added inputs, ensures uniform crop establishment, and has higher yield advantage to poor quality seed under the same management practice. It is, however, important to note that seed quality is influenced greatly by seed development and maturation. Storage reserves are deposited in seed storage tissues during seed development and maturation, and these reserves are important in the early stages of germination and maintenance of seedling life when it has not yet developed good photosynthetic capacity. The development stage at which the seed is harvested has enormous influence on its performance either in the field or storage, in terms of germination behavior and vigor characteristics, and maintenance of viability. This chapter presents some of the current understandings and findings on seed development and maturation, with emphasis on the physiological and biochemical quality.

Keywords: seed development, seed maturation, physiological seed quality, biochemical seed quality, physiological maturity

1. Introduction

Seed quality, the standard of excellence in the seed characteristics is what determines its performance when sown or stored [1]. Seed quality has been recognized as a complex trait, and has therefore been described as the viability and vigor characteristics of the seed that allows emergence and establishment of seedlings in diverse environmental conditions [2]. The fundamental and most important input in agriculture is good quality seed [3]. The main objective of any seed system is to ensure that good quality seed is delivered to the end users who are farmers. Every country in the world has put in place regulatory measures which seed producers must adhere to, in order to reduce quality loss or adulteration of seed along the seed value chain. A case in point, Uganda through the Ministry of Agriculture, Animal Industry and Fisheries (MAAIF) enacted the national seed policy 2018 with the vision of a competitive,

profitable and sustainable seed sub-sector where farmers and all seed users have access to affordable quality seed”, and four strategic policy objectives of (i) strengthening research and development for the seed sector, (ii) strengthening capacity of the key players along the seed value chain to achieve an effective and efficient seed sector, (iii) strengthening the seed quality control system along the entire value chain and (iv) enhancing knowledge and information management for the seed sector [4]. Seed testing, certification, variety release and registration, phytosanitary measures and protection of plant breeders’ rights are some of key activities governed by a seed law, and the management of these activities either at a country, regional or continental level affects the outcome of seed production, availability, accessibility, and hence the design of agricultural system [5].

Four seed quality attributes commonly talked about are; physical quality, pathological quality, physiological quality and genetic quality [6, 7]. Biochemical seed quality is often put together with the physiological quality although the two are different. To attain maximum seed quality, it has been argued that seed should be harvested at physiological maturity (PM). However, controversies exist in the concept of physiological maturity as explained by [8]. Some crop species maintain high seed moisture content at PM that makes harvesting difficult due to mechanical damages to the seed, hence harvesting should be delayed for some days after PM. Harvesting of seeds which are produced in fleshy fruits can be done just before PM and fruits given a period of after ripening to complete seed maturation [9]. Three common concepts of PM have been presented [10] (i) stage of maximum seed dry matter accumulation, (ii) growth stage beyond which there is no significant increase in seed dry weight and (iii) growth stage when seed attains maximum dry weight, germination and vigor. Given the existing controversies in the use of PM concept, seed development should be traced during seed development and maturation. This should involve tagging flowers at anthesis, harvesting seed or fruit at different development stages and evaluating morphological, physiological and biochemical changes in the seed, as well as correlation between these attributes in order to give a concrete judgment on when maximum seed quality is attained during seed development. This book chapter therefore looks at studies that have been done in different crop species to evaluate physiological and biochemical seed quality during seed development and maturation.

2. Seed development and maturation

Seed development is the changes in structural and physiological events in the seed right from the time of fertilization until the seed reaches maturation. A viable pollen comes in contact with the stigma, followed by its germination to form pollen tube carrying two male nuclei. The pollen tube penetrates the embryo sac containing egg nucleus and polar nuclei. The first male nucleus fuses with the egg cell to form a diploid zygote and the second one fuses with the polar nuclei to form a triploid endosperm; this is referred to as double fertilization and it marks the process of successful seed development in angiosperms [11]. Seed development is characterized in three stages; Histodifferentiation and cell expansion (stage I), Reserve deposition, cell expansion and maturation (stage II), and Maturation drying (stage III) [12, 13]. Stage I is characterized by the formation of embryonic tissues and those encompassing it, stage II is characterized by an increase in seed dry weight as a result of the accumulation of storage reserves, and physiological maturity is reached at the end

of this stage. Stage III exhibits a decrease in seed dry matter as the seed reaches its mature form [12, 13]. The very prominent attribute of stage III is the acquisition of desiccation tolerance, arrest of growth, and entry into dormancy [14]. In orthodox seeds, the seed loses about 10–15% of its moisture content to develop a desiccation tolerance and remain quiescent [12]. Embryogenesis in dicot and monocot occurs with similar pattern of events but the embryos formed are structurally different [13]. Seeds develop desiccation tolerance even before attaining a physiological maturity status. Physiological maturity is the development stage of the seed when the seed attains maximum dry weight [10]. Deposition and aggregation of storage compounds such as heat shock proteins, late embryonic abundants (LEAs) proteins and antioxidants of lower molecular weights in the seed embryo during seed development and maturation are associated with the desiccation tolerance in seed [15]. Seed development is regulated by several hormones. Indole-3-acetic acid (IAA), is crucial in determination of embryo size and structure during embryogenesis [16, 17]. Absciscic acid (ABA) induces dormancy which prevents unwanted seed germination and also promotes deposition of storage reserves during seed development, and formation of late embryonic abundants (LEAs) proteins which protect the seed from desiccation [18]. There is variation in ABA peaks during seed development, for example wheat has two peaks while rice has one peak during seed development [19, 20]. Cytokinins promotes cell division and differentiation and counteracts the negative effects of ABA during seed development [21]. Gibberellic acid is another hormone which is very critical during seed development as it antagonizes the inhibitory effects of Absciscic acid, but complex relationship exist between the two hormones in different crop species during seed development. Other than hormones, several transcriptional factors form a complex network to regulate seed development and maturation events [22]. Such events are storage reserve accumulation, chlorophyll degradation, and the acquisition of primary dormancy, desiccation tolerance, and longevity [23, 24]. During seed development and maturation, physiological and biochemical changes related to seed germination, vigor, seed storage proteins, lipids, antioxidant enzymes, sugars occur in the seed, with marked variations among crop species and varieties of the same crop. When seed attains maximum dry weight, deposition of storage reserves ceases as the seed enters the late maturation phase during which seed vigor is developed and the seed builds a defensive mechanism to aid survival after dispersal from the mother plant [25–27]. Seed harvest maturity stage greatly impacts seed germination, vigor, viability, storability and longevity hence production of good quality seed is very dependent on this factor [28–30]. In an informal seed system where farmers exchange seed among themselves, no much attention is paid to the seed age at harvest because of limited knowledge on how this aspect affect seed quality. An example is the vegetable farmers who keep harvesting the fruits and extract seeds from last harvest or from those left from fruits sold in the market. This practice has resulted in marked variability in the seed quality in the informal system. Farmer training to help them understand seed development is very crucial in addressing seed quality issues that they encounter.

3. Seed development and maturation effects on physiological seed quality

Seed harvest maturity stage is one of the factors that affect physiological seed quality. Physiological maturity, often defined as a maturity stage at which the seed accumulates maximum dry matter, sometimes coincides with maximum seed germination, example in *Solanum aethiopicum* [31] and Okra [32] but in the case of species such

as tomato [33], soybean [34] and pepper [35], this scenario is not applicable. Botey et al. [36] studied seed development of two African eggplant cultivars; *Oforiwa* and *Kpando* at different seed development stages of 20, 34, 48, 62, 76 and 82 days after anthesis (DAA) and reported that maximum seed dry weight was attained at 48 and 76 DAA in *Oforiwa* and *Kpando* respectively under a characteristic tropical climate, and 62 and 76 DAA respectively under a characteristic temperate oceanic climate, but maximum germination percentage only coincided with physiological maturity in cultivar *Kpando*. Another study in six eggplant cultivars; *Dwomo* and *Kpando* belonging to *Solanum gilo* group, GH 3870 and GH 3887 belonging to *Solanum melongena* group, GH 107 and GH 4918 belonging to *Solanum macrocarpon* group showed that seed germination and vigor improved when seed were harvested from 4 weeks to 8 weeks after full maturity of the fruits [31]. This study tends to suggest that maturation of seeds in fleshy fruits may not coincide with that of the fruit itself as maturation of the seeds continue even after the fruit reaches full maturity. Kwankaew et al. [37] studied the seed quality of Upland Rice cultivar *Dawk Pa-yawm* at eight different maturity stages of 8, 12, 16, 20, 24, 28, 32, and 36 days after flowering (DAF) and observed that seed physiological characteristics in terms of germination and vigor were all maximum at physiological maturity but all decreased after this stage. Accordingly, the authors reported maximum seed dry weight of 21.89 mg/seed, germination capacity (97%), soil emergence (96.5%), and maximum seedling dry weight (7.51 mg/seedling), root length (13.3 cm) and shoot length (7.92 cm), and lowest electrical conductivity of 8.05 $\mu\text{S}/\text{cm}/\text{g}$ at 28 DAF. Low electrical conductivity, high seedling dry weight, high root and shoot lengths are indicators of high seed vigor. In Okra cultivar *Asontem*, [32] studied five seed development stages of 10, 20, 30, 40 and 50 DAA and reported no seed germination up to 20 DAA, and maximum seed germination of 77% at 50 DAA. Santos et al. [38] studied seed development in Okra cultivar Santa Cruz 47 by tagging flowers and harvesting fruits from 5 DAA to 65DAA and extracted seeds immediately or stored for 7 days, and reported maximum seed germination, seedling emergence and germination first count at 50DAA both for seeds extracted immediately after harvest and those extracted 7 days after harvest. They observed no germination and seedling emergence up to 25 DAA for seeds extracted immediately after harvest while those extracted after 7 days of storage started germinating at 20 DAA. Their result in an indication that seeds borne in fruits continue to develop during post-harvest period when detached from the mother plant, provided they are stored in suitable conditions. Evaluation of free space percentage and aspect ratio of Okra seed during seed development using X-ray imaging analysis showed that both free space and aspect ratio decreased during seed development, stabilizing around 50DAA and were strongly linked to good germination and vigor of the seed [38]. By harvesting three soybean varieties *Nangbaar*, *Anidaso*, *Jenguma* at physiological maturity (PM), one week after PM and two weeks after PM, [39] observed 85.25%, 85.25% and 66.75% in *Nangbaar*, *Anidaso*, *Jenguma* respectively at PM while the germination decreased to 67.33%, 60.92% and 58.83% in *Nangbaar*, *Anidaso*, *Jenguma* respectively when they were harvested two weeks after PM. The same study reported high seed vigor when seed was harvested at PM and low seed vigor at one week and two weeks after physiological maturity, as indicated by low electrical conductivity (EC) of seed at PM and high EC of seed one week and two weeks after PM. In cucumber seeds, [40] reported a maximum germination capacity of 80.84% when fruits grown under open field conditions were harvested at 40 days after flowering followed by 30 days postharvest ripening. Seed vigor characteristics such as seedling dry weight, seedling vigor index I and II were also maximum at the same fruit harvest stage under the same environment. In Bell pepper (*Capsicum annuum*), [35] studied the effect of harvesting

time on seed quality of two cultivars *Fyuko INTA* and *Lungo INTA* by tagging flowers and harvesting at 4, 5, 6, 7, 8 and 9 weeks after anthesis (WAA). Their study reported very poor germination and low seed vigor in both cultivars for seeds harvested from 4 to 7 WAA both in fresh seeds and those stored for one year, while maximal seed quality in terms of seed germination and vigor was only attained in the two cultivars when seeds were harvested at 9 WAA. In sweet pepper cultivar *Amarela comprida*, [41] tagged flowers and harvested fruits from 20 DAA to 75 DAA, and reported no seed germination up to 40DAA, with maximum seed germination and seed vigor coinciding with maximum dry matter at 75DAA. In a related study in Habanero pepper (*Capsicum chinenses* Jacq), [42] harvested the green, yellow and orange fruits corresponding to 30, 38, and 42DAA and stored for 7 and 14 days and observed highest seed germination and vigor in seeds harvested from orange fruits followed by yellow while those extracted from green fruits had the least germination and vigor both under storage period of 0, 7 and 14 days. In another study, [43] evaluated the physiological seed quality of *Physalis angulata* L. seeds under different harvesting periods of 15, 22, 29, 36 and 43 DAA, and observed 100% seed germination, and maximum field emergence of 70.5%, at 29DAA, while the seed attained maximum seed dry weight of 28 mg at 36DAA indicating that maximal seed quality was attained before physiological maturity. Tetteh et al. [44] studied seed development in two tomato cultivars GH 9207 and GH 9305 and classified the fruits as initially ripe, half ripe, fully ripe and rotten depending on the development stages, and observed good seed vigor and germination in fully ripe fruits but were not statistically different from germination of those harvested from half ripe and rotten fruits. Seed should be harvested at the maturity stage when germination and vigor are maximum [45, 46]. A study evaluated seed development in pumpkin by harvesting the seed at 30, 40, 50 and 60 DAA and observed less than 20% germination for seeds harvested at 30 and 40DAA, and more than 80% for seeds harvested at 60DAA in both round type and oval type pumpkin fruits in all the three locations [30]. It was asserted that seeds of most crops attain maximum germination and vigor at PM and declines after [47], but this concept of PM has been debated by many authors including [8, 10]. Crop species differ in their seed and fruit maturation characteristics, hence the maturity stage at which seed attain maximum germination and vigor varies. This phenomenon has been demonstrated, for example maximum germination and vigor in tomato seeds were attained 15 days after PM [48] while [49] reported 20 days after PM in the same crop, and [50] reported 10 days after PM in pepper. Changes in fruit color, fruit weight, fruit diameter and length, seed dry weight and seed moisture content during seed development can be used as indicators for seed maturation and harvesting to attain good seed quality [36, 42, 44]. Seed vigor during seed development can be measured indirectly using electrical conductivity, with lower EC values indicating high seed vigor and vice versa. Seed vigor is low at initial stages of seed development, as indicated by very high electrical conductivity but increases as the seed matures due to strengthening of seed membrane integrity that reduces the leakages of electrolytes from the seed. This has been verified during seed development in *Capsicum baccatum* [51], onion [52], *C. annum* [41] and faba bean [53]. No seedling emergence was observed in *C. baccatum* seeds until 30 DAA, but emergence increased from 39.5% at 40 DAA to 73.5% at 50 DAA and remained statistically unchanged until last harvest at 80 DAA [51]. Several studies on seed development and maturation have revealed that seeds of some species attain germination potential very early just few days after anthesis but some requires sometime in order to attain the ability to germinate. This variation exists even within the same species as observed in two species of *S. aethiopicum*, *Oforiwa* and *Kpando* [36]. However, as discussed previously, it is also possible to harvest seeds one or two weeks

before physiological maturity and give them a period of after ripening to attain full maturity and hence good germination and vigor, particularly for those borne in fleshy fruits [54]. Seed development and maturation, and hence attaining of maximum seed quality is also influenced by environment and genotype, thus recommendations for seed production should capture genetic variations as well as conditions in the production environment. In addition to that, morphological changes in the fruit and seed should be related to the seed quality in terms of seed germination and vigor so that seed producers can know the best time for harvesting seed with the highest quality.

4. Changes in biochemical seed quality during seed development and maturation

A number of biochemical changes related to structural proteins, carbohydrates, lipids, antioxidant enzymes, phytic acid and tannins occur during seed development and maturation. Changes in some of these compounds are related to acquisition of desiccation tolerance in the seeds and maintenance of cell membrane integrity which improves seed vigor and longevity [55, 56]. Maximum accumulation of seed proteins, and activity of alpha-amylase and dehydrogenase enzyme at 28DAA was observed in Proso millet (*Panicum miliaceum* L) [57]. Antioxidant enzyme activity of sweet pepper (*C. annuum* L) cultivar Florinis NS 700 increased during seed development from 410 µg/g FW at 10 DAA reaching a maximum of 1550 µg/g FW at 80 DAA, with total seed phenolics following the same trend [58]. Similar results were obtained by earlier study that reported higher antioxidant activity in sweet pepper seeds extracted from mature fruits in comparison to those extracted from immature fruits [59]. However, this seems to be affected by genotype as [60, 61] obtained contrasting results in antioxidant enzyme activity trends in the same crop. High antioxidant enzyme activity during early seed development has been reported in African eggplant [62] and *Hevea brasiliensis* L [63]. Both authors reported a decline after an early increase, and increase at the end of the seed maturation phase. Antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD), peroxidase (POX) and ascorbate peroxidase (APX) protect the seed cells from oxidative damage caused by reactive oxygen species [64]. Accumulation of structural proteins such as late embryonic abundants (LEAs) has been reported to be high at 60 DAA in sweet pepper [41]. A study in *S. melongena* revealed that the levels of CAT, SOD and POX antioxidant enzymes were high in seeds harvested at 40 DAA with a progressive decrease up to 60DAA (maturation stage) and an increase after this period [65]. A similar observation in the activity of CAT and SOD was made in sweet pepper, with a decrease in their activity until maturation and an increase thereafter [66]. High respiration in younger fruits results in the production of oxidative reactive oxygen species which triggers the antioxidant enzyme system to protect the cells, hence high levels and activity of the enzymes [67, 68]. Changes in tannins content during seed development has been reported as an indicator for attaining good quality seed, as [62] observed highest tannins content in seeds of *solanum aethiopicum* cultivar *Oforiwa* harvested at physiological maturity (62DAA) and was strongly correlated with germination percentage, germination index and mean daily germination. Tannins is an antioxidant and thus improves cell wall integrity and protects it from degradation. Condensed tannins, a group of flavonoids were observed to increase throughout seed development in common bean and decreased after seed maturation [69]. A study in *Magnolia zenii* Cheng revealed a significant increase in soluble

sugar, protein and lipid content of seed between 30 to 165 DAF [70]. In *capsicum baccatum*, [51] observed that soluble protein content increased by 66% from 10 to 40 DAA and remained unchanged until last harvest at 80DAA while neutral lipids content increased 14-fold between 10 and 30 DAA, reduced from 30 to 60 DAA and later increased until 80 DAA. The same authors reported that starch content was very high at the beginning of seed development, but decreased until 30DAA, and later increased until 60DAA, and remained unchanged thereafter until last harvest at 80 DAA. Starch serves as a temporary carbon storage during early seed development and constitutes to seed reserve biosynthesis [71, 72]. Non reducing sugars were observed to increase throughout seed development until 60 DAA with a slight decline until 80 DAA in *capsicum baccatum* seeds while total soluble sugars and total free amine acids showed opposite trend, but were very high at the beginning of seed development [51]. As seed undergoes desiccation during late maturation, a considerable amount of water is lost which has a potential to cause damage of cell membrane and thus affecting its stability. However, nonreducing sugars binds to the hydrophilic heads of the membrane lipids to replace the lost water and hence stabilize the cell membrane of the seed [73]. Biochemical changes during seed development have been used as markers for determination of physiological maturity and seed harvest maturity stage [51, 52, 74]. Antioxidant enzyme activity, electrical conductivity, accumulation of tannins, total sugars, total proteins and lipids have been widely used to characterize seed development and maturation in a number of crops. Using metabolites accumulation, storage reserve and seed dry weight, and moisture loss during seed development of *capsicum baccatum*, [51] were able to recognize the three seed development stages of histodifferentiation, reserve deposition and maturation drying. A study evaluated three *S. melongena* L. varieties ie Serbian variety, Italian variety and Chinese variety, through seed ripening phases of commercial ripeness, semi ripeness and full ripeness [75]. The authors reported increase in seed proteins during seed development with the highest protein accumulation at the full ripeness stage corresponding to 75, 90 and 110 DAA in Serbian, Italian and Chinese variety respectively. The same seed development stage also had highest seed germination for the three varieties. Phytic acid, the seed storage reserve of phosphorus [76] is another important compound for early seedling growth. Phytic acid binds with metallic cations to form phytate which is hydrolyzed by phytase enzymes during germination to release inorganic phosphorus and other mineral elements [77–79]. About 30–80% of seed phosphorus reserve is stored in the form of phytate [80]. High seed phosphorus content is reported to have a strong positive and significant correlation with the seed vigor [81]. A slight decrease of inorganic phosphate (Pi) throughout seed development up to 30 DAA was observed in rice both in the endosperm and aleurone layers while phytic acid content showed an increasing trend particularly in the aleurone layers peaking at 30 DAA [76], suggesting assimilation of Pi into phytic acid during seed development and maturation. In Bambara groundnut, [82] observed a gradual increase in seed phosphorus concentration from 14 DAA to 42 DAA and a sharp increase up to 62 DAA in all the four landraces evaluated. The authors also reported a strong correlation between seed phosphorus content and phytic acid. Similarly, a strong correlation between seed phosphorus concentration and phytic acid was reported in chickpea [83] and soybean [84]. Other studies have also shown that phytic acid accumulate in the seed during maturation phase in cowpea [85], chick pea [86] and mungbean [87]. Up to date, fewer studies have related biochemical markers to physiological seed quality. Accumulation of seed metabolites and storage reserves that constitute seed quality have not been well correlated with physiological state of the seed. Relating

biochemical markers with morphological and physiological markers is important to give a strong justification on the seed harvest maturity period when maximal seed quality can be attained. The seed storage reserves (phytochemicals) play very important roles during seed germination when the seedling is not receiving any external input and has low photosynthetic capacity. These reserves are hydrolyzed upon reactivation of metabolic enzymes and are channeled to the growing regions of the seed during germination, thus constituting to seed vigor and establishment of strong and healthy seedlings.

5. Conclusion

Understanding of seed development and maturation is very important in producing good quality seeds in a seed system. Harvesting of seed before physiological maturity results in poor quality seeds due to immature embryo while very late harvesting results in seed aging and deterioration which lowers seed quality. However, controversies exist among several authors on the concept of physiological maturity. Some authors argued that seed harvesting at PM is not practical and economical in some species which maintain high seed moisture content at PM, thus they suggest that seed harvesting should be delayed for some time after PM to reduce seed damage especially for mechanical harvesting. For seeds borne in fleshy fruits, seed maturation can continue during postharvest ripening which improves seed quality. Several markers of physiological maturity including maximum dry matter accumulation, fruit color, leaf color and seed moisture content have been identified. To effectively study seed development, flowers should be tagged at anthesis and fruit or seed should be harvested at different times to trace seed germination and vigor characteristics, and accumulation of seed storage compounds and phytochemicals during seed development stages. However, several other factors other than seed development and maturation affect seed quality. This includes after ripening, production environment and nutrition of the mother plant, post-harvest management related to storage, and drying. During seed production, good management is required to reduce stress on the mother plant especially during seed filling, as most metabolites and phytochemicals that contribute to seed quality are accumulated in the seed during this stage. After seed filling, no more accumulation of dry matter occurs in the seed, thus irrigation and fertilizer application are not necessary. Seed development and maturation is a complex process involving many phytohormones, genes as well as transcriptional factors that play various roles at every development stage right after pollination, to development of embryo and other essential seed structures, accumulation of storage reserves and attaining physiological maturity, maturation and development of desiccation tolerance.

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