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RESEARCH ARTICLE

A review of factors that influence the production of quality seed for long-term conservation in genebanks

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Abstract Seed quality is a critical aspect in agriculture as well as in the long-term conservation of plant genetic resources in genebanks. Since potential seed longevity depends on initial quality, genebank curators need to be aware of the best management practices that contribute to the production of high quality seed during routine germplasm regeneration/multiplication. Among the factors influencing initial seed quality, those related to crop management, including plant nutrient and water supply during crop growth, climatic conditions during seed development and maturation, as well as the harvest and drying practices are of considerable significance. Seeds of high quality can be obtained by planting in suitable areas/fields and at appropriate times, applying good crop management practices, adoption of proper harvesting and drying techniques, careful handling and processing to minimize mechanical injuries and unwanted seed mixing with other accessions, and ensuring minimum deterioration before reaching the designated storage. However, seed production and post-harvest handling highly depend on the biology and agronomy of the species. As germplasm collections contain a wide range of diversity for morphological and agronomic characters and that there might well be critical gaps in knowledge among genebank staff or about the species in question, genebanks may also need to embark on research to gain crop specific knowledge on optimal seed production procedures to improve seed quality.

Keywords Genebanks · Germplasm regeneration · Seed quality

Introduction

Seed storage is the most important and widely used method for conserving plant genetic resources, particularly for species with orthodox seeds which could be dried to low moisture content and stored at freezing temperatures without damage to increase longevity. Worldwide, over seven million germplasm accessions are being conserved in the form of seeds in some 1750 genebanks (FAO 2010). The long-term maintenance of seed viability, combined with minimum loss of genetic integrity of the sample in question, is of crucial importance for effective conservation and use of plant genetic resources. Although orthodox seeds can be stored for very long periods (Roberts 1973), in practice this is rarely the case and many accessions held in genebanks are in need of frequent regeneration to maintain optimal seed viability, replenish the seed stock for distribution, and due to sub-optimal handling

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and storing of the seed samples. Regeneration of seed accessions is a crucial event in germplasm collection management. In addition to being expensive, regeneration involves the risk of losing the genetic integrity of an accession due to genetic shift owing to outcrossing and genetic drift due to inadequate sample sizes, handling errors, selection pressure, etc., which are compounded with each cycle of regeneration. Effective management of germplasm collections therefore entails minimizing the frequency of regeneration, which can be largely achieved by maximizing seed longevity. The potential longevity of a seed depends on its initial quality and the extent to which that potential longevity is maximized depends on storage conditions (Roberts 1992).

Seed quality, in general, refers to the performance of a seed lot under a wide range of environmental conditions. It is a relative term, expressing the status in comparison with an acceptable standard. In the context of germplasm management, Sackville Hamilton and Chorlton (1997) defined seed quality in terms of effective viability, measured as percentage of seeds that germinate in an appropriate controlled environment. However, other attributes of seed quality such as genetic purity, physical purity, health, vigour, moisture content and germination, defined for seed industry are equally important to the genebanks. Adequate conservation of germplasm in the form of seeds also requires that the genetic integrity of individual accessions be maintained to the highest standards over prolonged periods of time (Dulloo and Engels 2003). The new 2013 international genebank standards set by the Food and Agriculture Organization of the United Nations (FAO) (FAO 2013), contain a number of standards that aim at ensuring maximum seed quality. For example, seed collecting should be made as close as possible to the time of crop/species maturation and prior to natural seed dispersal, the period between seed collecting and transfer to a controlled drying environment should be within 3–5 days or as short as possible, the seeds should be as clean as possible, free from weed seeds, pests and diseases; they should be capable of rapid and as uniform as possible emergence under a wide range of field conditions; the seed moisture content should range between 3 and 7 %, depending on the species; and initial germination values should exceed 85 % for most species or a lower percentage for species which do not normally reach high levels of germination (FAO 2013). It is obvious that the full benefits of a good storage system will be realized only when the seeds prepared for storage have high initial vigour and viability and are free of pest and diseases and adequately represent the genetic information of the accession that is intended to be conserved for the long-term.

The updated second Global Plan of Action (GPA II) that was originally adopted at the International Technical Conference on Plant Genetic Resources, held at Leipzig in 1996 and updated through a consultation process by FAO in 2007 (FAO 2012), underscores the urgent need for devising methods to sustain ex situ conservations through, inter alia, the regeneration of seed accessions which are at risk of losing viability. The FAO second State of the World Report on Plant Genetic Resources for Food and Agriculture also reported great concerns regarding the lack of regeneration of aging stocks of accessions. In the past decade, significant advances have been made in regenerating collections at risk, in part due to efforts made by the Global Crop Diversity Trust (GCDT) in supporting regeneration programmes of globally important genebank collections for 22 priority crops for which crop specific regeneration guidelines have been produced (Dulloo et al. 2008, 2010).

However, any plans to sustain the conservation of germplasm (seed) collections will be ineffective unless the curators have the pertinent scientific and technical knowledge and information to produce seeds of high initial quality and maintain the genetic integrity during regeneration. There is literature providing standards for conservation of germplasm (e.g. Rao et al. 2006; FAO 2013) and dealing with broader issues of genebank management (Engels and Visser 2003) and regeneration in particular (Sackville Hamilton and Chorlton 1997). However, specific aspects of seed quality have not received due attention in these publications. Several factors, including agronomic and environmental, together with seed handling procedures affect the initial quality of seeds. It is important for genebank curators to be aware of these factors so as to make informed decisions under the operating conditions and obtain seeds of high quality from germplasm regeneration grow-outs. Best practices for seed handling have been developed for some major crops (see the SGRP-CGIAR Crop Genebank Knowledge Base, http://cropgenebank.sgrp.cgiar.org/) but there is still a lack of information for other crops.

In this paper, we have reviewed the effects of factors that can influence initial quality and storage life of orthodox seed accessions during the process of regeneration. Genetic integrity issues will not be addressed here and could be consulted in Sackville Hamilton and Chorlton (1997). The aforementioned factors are conveniently divided into four main headings, namely: crop management practices, climatic factors, stage of seed development and postharvest processing. We have not attempted to offer specific solutions to the problems that generally affect seed quality as this cannot be done without adequate knowledge of the prevailing field and climatic conditions in the regeneration areas. Often the procedures are species-specific, requiring prior knowledge of the optimal requirements for crop growth, flowering and seed quality development, harvest and post-harvest seed handling. In this sense, this review is mainly aimed at creating awareness and where necessary, stimulate germplasm collection managers to first search for applicable information in the literature and to undertake problem-solving research under the prevailing conditions of the genebank operations to produce high-quality seeds for long-term conservation. Although most studies reviewed here are related to initial vigour, viability and crop performance, they are of significance because initial seed quality affects storage life, as described earlier.

Factors affecting initial seed quality

Crop management practices

To produce good quality seeds, it is essential that the crop is grown under optimal field conditions. Thus, the selection of suitable areas and fields in terms of soil texture, pH and fertility status are important considerations for regeneration of a particular crop. Crop specific guidelines on suitable soil characteristics for seed production are available in seed production manuals (e.g. McDonald and Copeland 1997; Kelly and George 1998; Copeland and McDonald 2001) which can be followed for germplasm regeneration. In general, soils should be uniform, well drained and deep with good water-holding capacity. Fields with a history of disease problems or that possess other negative characteristics such high salinity, water logging etc. should be avoided. Planting areas alongside trees can be exposed to shade and restricted wind movement, thereby affecting temperature and moisture, the two environmental factors that can have a big effect on seed quality development as discussed in later sections. Low-lying areas which are cool and moist with water drainage problems should be avoided as they favour disease incidence and possibly poor crop development. Tillage methods are also an important consideration. For example, no till and minimum tillage practices reduce water loss and soil erosion, but may favour the survival of many plant pathogens in plant debris which provide sources of inoculum for diseases. Planting the same crop in the same field year after year can allow build-up in that field of insects, nematodes, and other diseases and crop rotation can help reduce this problem. Soil fumigation and solarization (heating soil by covering the irrigated regeneration plots with polyethylene sheets during hot summer) also help in the control of soil-borne diseases, pests and weeds. The succession of a germplasm multiplication or regeneration on a commercial field with the same or related crop during the previous year should be avoided to lower the risk of undesirable cross pollination between the germplasm and the commercial plants or of harvesting from such plants that survived the winter or off-season. The most common approach is to rotate crops by families or alternate grain crops with vegetable and forage crops. However, like the guidelines on suitable soils, there are crop specific recommendations on rotation for seed production programs which also can be adopted for germplasm regeneration.

It is obvious that fertile soils provide the best environment for plant development. Soils low in fertility or those suffering from mineral deficiencies would produce less vigorous plants and should be avoided. Under certain circumstances, soils with high fertility also may not be recommended because they produce excessive vegetative growth, which can induce lodging. Lodging, especially before flowering, can affect pollination and seed set and also the quality of the seeds if they touch the soil. Deficiencies of microelements like calcium, boron, manganese and zinc are known to produce characteristic damage, lowering seed quality (e.g. Adams and Hartzog 1991; Crittenden and Svec 1974; Ramamoorthy and Sudarsan 1992). Prior to regeneration, it is advisable to determine the nutrient status of the soils by chemical analysis to determine the most optimum fertilizer application.

For germplasm seed production, the water management strategy should consider rainfall probability and seasonal distribution from long-term records to avoid stress at flowering and pod filling stage and to supply additional water by irrigation, if necessary. Water stress during seed development is known to interrupt seed development, leading to the production of low quality seeds (Cox et al. 1976; Vanangamudi et al. 1990; Zehtab-Salmasi et al. 2006; Alqudah et al. 2011; El Balla et al. 2013; Chibarabada and Mabhaudhi 2015). However, Vieira et al. (1992) found that drought stress had little effect on seed quality unless it was severe enough to produce shriveled, shrunken, and miss- shaped seed, while a few studies also show that water stress during later stages of plant growth actually increases storability of the seeds (Ramamoorthy and Basu 1996; Sinniah et al. 1998; Shock et al. 2006). Obviously, the evapo-transpiration rates and microclimate play an important role in relation to water stress experienced by plants and the seed quality development. For example, in humid and temperate regions, the plants may not actually suffer the stress although irrigation was withheld as evapo-transpiration rates are expected to be low. In these areas, stoppage of irrigation may even result in a more favourable microclimate, reducing pest and disease incidence, thus leading to improved seed quality.

Dense planting results in stress on individual plants, resulting from competition for water and nutrients. Stress during reproductive growth can limit the ability of seed to develop properly (Dornbos 1995). Dense plant canopies also reduce air movement and promote many foliar and stem diseases, ultimately affecting seed development. Woodruff et al. (1967) reported that high rates of nitrogen fertilizer, irrigation, narrow row spacing and other practices which contributed to dense canopy and high humidity within the canopy increased the degree of deterioration of cotton (*Gossypium hirsutum* L.) seed. Spacing requirements and optimum plant density for germplasm regeneration are usually the same as that required for conventional seed production. The details for individual crop species can be found in seed production manuals. Germplasm curators should consider the germination potential of the individual seed accessions to arrive at an optimum seed rate for sowing. Field establishment is often lower than that predicted from the standard laboratory germination test. Under field conditions, seedling emergence is influenced by several interacting factors, including genetic constitution, seed dormancy, seed vigor, soil condition, depth of planting, temperature at planting time and water supply (Forcella et al. 2000; Samarah and Al-Kofahi, 2008). Consequently, although many seeds germinate satisfactorily under ideal laboratory conditions, they may fail to emerge successfully in the field (Kolasinska et al. 2000; Wang et al. 2004). In general, 90 % emergence is a good rule of thumb. However, if seedling survival rates are expected to be low because of poor conditions for germination, higher seeding rates will be required to achieve optimum plant stands. In case of heterogeneous accessions, either populations of outcrossing species or mixtures of largely pure lines in the case of inbreeding species, possibly an even higher standard should be applied in order to avoid possible selection of ‘weaker’ genotypes from the mixed accession. Studies also show that weed competition can influence subsequent vigour of seeds. For example, Saayman and van de Venter (1996) observed that germination and vigour of corn (*Zea mays* L.) seeds decreased with increase in weed density. Perennial weeds also serve as alternate hosts and reservoirs for many plant pathogens, particularly plant viruses. Removing the alternate hosts can help reduce not only the amount of the pathogen present each year, but also the resident insect population that is capable of transmitting the disease. Therefore, complete control of the weeds throughout the regeneration cycle is essential.

During regeneration, special care is required to ensure the maintenance of genetic integrity. Among the various factors that can influence genetic integrity (e.g. sample size, pollination, diseases, etc.), the management of pollination is probably the most critical one that has direct impact on seed quality (Engels and Rao 1998). Techniques such as caging, bagging and other such pollination control methods are used to reduce cross pollination and contamination in germplasm accessions. It is often not realised that such techniques can modify the microenvironment around the developing seeds, thereby affecting their overall quality. For example, in pearl millet (*Pennisetum glaucum* (L.) R. Br.), seeds regenerated by cluster bagging (where panicles from 3–4 adjacent plants are enclosed in a single paper bag before anther dehiscence) deteriorated faster than open pollinated or selfed seed lots (Rao et al. 2002a). In cluster bagging, the microclimate within the bags—characterized by high humidity and temperature—promoted the growth of seedborne pathogens (especially fungi), hence affecting seed quality. It was surmised that seeds with maximum potential longevity could be harvested when regenerated by spatial isolation, avoiding the use of any artificial barriers to prevent out-crossing. However, isolation by space becomes difficult when a large number of germplasm accessions have to be regenerated at one time, as is common in most genebanks. Further, the isolation distance required varies for different species taking into account the method of pollination. For example, greater distances are required for species pollinated by wind than for those pollinated by insects. If artificial barriers such as cages and bags are to be used to control pollination, genebank curators should be aware of the possible changes to microclimate and adopt measures to minimise the effect on seed quality. The plant densities within cages could for instance be reduced to increase air movement around plants, making it unfavourable for disease development. The paper bags used to prevent open-pollination should be thin so that they dry quickly after dew or rains and also allow moisture to escape freely from the covered plant parts without facilitating mould growth. Further, the bags or any artificial barriers used to control pollination should be kept on the plant only as long as necessary and removed once pollination is achieved. Such measure may help to improve seed quality.

Microorganisms, especially fungi, invade the seeds during or after ripening and during harvesting operations (Christensen 1972). The problems can be minimised by taking appropriate plant protection measures, including chemical control. Thus, the use of pre-harvest fungicide sprays to control internally seedborne fungi has been reported in a number of crops (Agarwal and Sinclair 1996). Seed sowing and processing procedures offer many opportunities where microorganisms such as fungi and bacteria may infest the seeds. Not only may seeds be brought into contact with contaminated equipment but also clean seeds may come in close physical contact with contaminated seeds. Sanitation should be integral part of every step in seed handling process and only clean equipment and containers be used to avoid possible cross contamination (Thomsen and Schmidt 1999).

Besides chemical control, modification of environment also helps in managing diseases and improving crop health. For example, availability of free moisture influences the development of many diseases, especially the mildews. Although rainfall and dew which contribute to free moisture cannot be controlled, irrigation methods, schedules and rates can be managed to regulate plant diseases. Crop spacing, both between and within rows influences the availability of free moisture. Growing plants in rows increases the air exchange in the canopy and reduces air humidity with a positive side effect on disease regulation.

Like diseases, insects are part of the total environmental pattern affecting seed quality. Insects, besides providing openings for subsequent invasion of pathogens and moisture that cause deterioration, also transmit diseases directly. In pigeonpea (*Cajanus cajan* (L.) Millsp.), infestation by pod-borer (*Helicoverpa armigera* Hübn.) (pod-borer) and pod-fly (*Melanagromyza obtusa* Mall.) during pod formation affects seed quality and results in higher percentage of abnormal seedlings (Kashyap and Punia 1995). Seck (1991) reported that the level of damage caused by grain moth (*Sitotroga cerealella* Oliv.) in Senegal was 10 times more on pearl millet ears harvested from fields close to dwellings—probable source of infestation, than those away from dwelling houses. Although pests can be controlled through application of pesticides, good sanitation, cultural modifications such as growing trap crops, also help to minimize the problem.

The time from harvest to storage is another critical period where insects can infect seeds and reduce quality. Fumigation of seeds after harvest and prior to processing to keep insects from infecting seeds may be considered when there is a real need (but should be avoided when not really necessary). High doses of fumigant coupled with temperatures above 30 °C and seed moisture content greater than 12 % can negatively impact seed germination and care is necessary in the choice of fumigant in combination with the storage environment when fumigating the seeds meant for germplasm conservation (Singh et al. 2003). Phosphine and methyl bromide are the two common fumigants used for stored-product protection world over, but the use of plant products as alternative fumigants has increased in recent years as a result of environmental concerns and insect populations becoming resistant to conventional chemicals (Rajendran and Sriranjini 2007; Ayvaz et al. 2010).

Seed predation by granivores—especially rodents and birds that feed on the seeds of plants as a main or exclusive food source, in many cases leaving the seeds damaged and not viable. Domestic cattle, and wild herbivores can also cause considerable damage to the seed crops. Depending on the severity, a range of protective measures such as manual guarding (bird chasing during the ripening period might be necessary on a daily basis during the critical hours), various types of nets, fences, trenches and other devices may need to be applied to protect the regeneration fields.

Climatic conditions

Climatic conditions during seed formation significantly affect the initial quality of seeds. Low precipitation and low relative humidity during seed maturation favour the production of high quality seeds as pest and disease incidence will be low under these conditions (Delouche 1980). Frequent rainfall and high relative humidity, temperature extremes such as hot weather and frost occurring during maturation can adversely affect the seed quality. Caldwell (1972) made a detailed study of field deterioration in cotton seeds and established a relationship between viability and vigour and the period of exposure to adverse field environment. The seeds from bottom bolls which open first and are exposed to the field environment longest before harvest were consistently lower in quality than those from bolls produced in the upper half of the plant. In crops with indeterminate flowering, where the seeds mature over long periods, sequential and regular harvesting minimises the exposure of the mature seeds to adverse weather conditions and preserves the high seed quality.

The concentration of seed production programmes in specific areas in several countries bears testimony to the influence of climatic factors on seed development and quality. For example, in the USA, a major portion of the seed of temperate forage and lawn/turf grasses is produced in the Pacific Northwest, especially in Oregon where the mild winters and ample rainfall facilitate good growth and dry summers enable harvesting with little risk of rain and wind. Similarly, the arid irrigated areas in California, Idaho and Arizona, characterized by low humidity, minimal rainfall and favourable temperatures are important producers of vegetable, flower and forage legume seeds (Delouche 1980).

Germplasm collections generally contain cultivars originating from a wide range of environments and the seed production environment at the site of regeneration may not be optimal for all accessions. For example, the rice (*Oryza sativa* L.) germplasm collection conserved at the International Rice Research Institute (IRRI), Los Banõs, Philippines, contains several japonica rice accessions originating from temperate regions and studies showed that potential longevity of these cultivars will be less when produced in the warmer climatic conditions of Los Banõs (Ellis et al. 1993; Rao and Jackson 1996a). Similarly, in the common bean (*Phaseolus vulgaris* L.), seed quality determined by survival in air-dry storage was greater in cooler seed production regime (Sanhewe and Ellis 1996). Ideally, such germplasm accessions should be regenerated in near-optimum locations that meet the specific requirements of accessions, not only to minimise genetic drift but also to maximise seed quality. In countries with sufficiently diverse climates, establishment of seed production in near-optimum areas may not be a problem. However, for countries with more or less uniform climate, altering planting dates to allow critical stages of seed maturation to coincide with the favourable segments of field environment can improve seed quality. For example, in regions of West Africa, with bimodal rainfall, soybean (*Glycine soja* Sieb. et Zucc.) seed quality was found to be better when planted in the minor season (September–November) compared to those planted in the major season (April–August) (Mercer-Quarshie and Nsowah 1975; Nangju 1977). This aspect is also considered in a regional context to look for optimal conditions. In the major season, seed ripens during rains, thus the quality suffers greatly due to weathering. In Taiwan, soybean seed lots produced during autumn (corresponding to seed ripening in the dry season) will have better quality than those produced in summer (corresponding to seed ripening in the wet season) (AVRDC 1990). The European Cooperative Programme for Plant Genetic Resources (ECPGR) aims at the regeneration of the accessions of it dispersed European Collection in areas that are as close as possible to the conditions of the collection site. For the temperate japonica rices conserved at IRRI genebank, Rao and Jackson (1997) showed that seeds of highest quality and longevity can be obtained when planted in October in Los Banõs, Philippines, as seed ripening coincided with the coolest and driest time of the year. Thus, it is worthwhile for germplasm curators to consult long-term meteorological data for probable temperature, rainfall and relative humidity conditions and adopt appropriate planting strategies to produce high quality seeds.

Strong winds may also affect seed production. It is common to install temporary or permanent windbreaks to prevent lodging of plant and seed bearing organs. However, it should be noted that permanent windbreaks, especially of perennial plants, may harbour pests and pathogens and provide the source of contamination of the seed crops leading to loss in quality of seeds. Greenhouse and plastic tunnels provide protected environment for both crops and pollinating insects to obtain good yields of high quality seeds, when seed production in open field is very difficult because of unfavourable environmental conditions such as frost, photoperiod or others. For instance, plastic tents within a greenhouse are routinely used as the primary regeneration method for germplasm that is poorly adapted to local field conditions at the North Central Regional Plant Introduction Station, Iowa, USA (Brenner and Widrlechner 1998). Greenhouses also help in production of virus-free seed stocks especially of crops which are prone to insect transmitted viruses. Besides, they have the advantage of allowing for some outcrossing among plants of the same accession, which is desirable for maintaining inherent levels of heterozygosity or in the initial multiplication of rare seeds limited in quantity. As the optimal growing conditions for many of the crop wild relatives (CWRs) are unknown it makes good sense to use protected conditions such as green- or screen-houses for their regeneration, thus also facilitating close(r) observation and allowing for possible timely remedial action.

Locations close to the seas or oceans can reduce the risks of diseases and viruses and may thus support disease-free seed production as long as the strong winds, sea spray and high humidity do not become the limiting factors. For instance, a very low pressure of aphids was observed in the coastal region compared to a higher pressure in the inland sites (Böhm and Fittje 2002)—hence the reason for using coastal areas for potato (*Solanum tuberosum* L.) seed production in Germany and the Netherlands. The oceanic effect in coastal areas also prevents over-drying of unthreshed material in the field and can assist in reducing loss from shattering prior to harvesting (George 2009). However, windbreaks will be needed to reduce any impact of strong winds and wind-borne salts originating from sea spray.

Stage of seed development

Ideally, seed should be harvested when the quality is highest. In general, immature seeds are known to deteriorate rapidly during storage, and delayed harvesting beyond optimum maturity leads to weathering and loss in quality. Harrington (1972) suggested that seeds under development attain maximum viability and vigour at physiological maturity (defined as the stage when seeds reach maximum dry weight during development) and they begin to age with viability and vigour declining thereafter. There is now considerable evidence from a wide range of crops [e.g., barley (*Hordeum vulgare* L.), rapeseed (*Brassica napus* L.), marrow (*Cucurbita pepo* L.), pearl millet, pepper (*Capsicum annuum* L.), rice, soybean, tomato (*Solanum lycopersicum* L.) and wheat (*Triticum aestivum* L. em. Thell.)] that seed quality continues to improve even after physiological maturity and seeds attain maximum potential longevity some 1–3 weeks (depending on crop and environment) after the end of the grain-filling period (Pieta Filho and Ellis 1991; Rao et al. 1991; Demir and Ellis 1992, 1993; Zanakis et al. 1994; Rao and Jackson, 1996b; Nkang and Umoh 1997; Mendez-Natera et al. 1998; Demir and Samit 2001; Elias and Copeland 2001; Demir et al. 2002, 2004; Dias et al. 2006; Ozcoban and Demir 2006; Probert et al. 2007). However, seed quality improvement may not be the same in all crops as seed maturity is genetically controlled and a complex of environmental conditions frequently override the expression. Therefore, it is advisable for genebanks to conduct pilot studies for a given crop species (especially the CWRs) to determine the optimal stage of maturity for harvest to ensure maximum potential longevity, as undertaken for the japonica rice accessions conserved in the International Rice Genebank.

In order to obtain maximum quantities of high quality seeds, it is also necessary that the bulk of seeds is harvested at the correct stage of maturity. Time of harvest will still be a difficult management decision, especially in crop species with indeterminate flowering habit and sequential maturity and/or in the case of mixtures of genotypes in the same accessions. A number of visual indicators for harvest have been proposed but these are somewhat subjective. For example, seed quality in pepper is higher in seeds harvested from red fruits compared to those harvested from immature green fruits on the same plant. In tomato, maximum seed germination is reportedly attained when the fruits are at a mature green stage compared to those that are at red or fully-ripe stages. Germplasm collections are highly variable for individual traits and the general applicability of these visual indicators is therefore questionable. The decision to harvest should also take into consideration the prevailing weather conditions as well as the harvesting method used. Time of the day can be important and crops prone to shattering can be best harvested with dew in the morning to minimise seed losses. Furthermore, it might well be advantageous to harvest whenever possible and meaningful in several steps and to harvest at any given moment only those fruits that have reached their best maturity stage with respect to seed quality.

Post-harvest processing

A variety of factors, including the method of harvest, drying and seed handling affect seed quality and subsequent longevity. Usually, orthodox seeds attain the ability to withstand desiccation during development close to mass maturity or the end of grain filling-period (Ellis et al. 1987; Ellis and Pieta Filho 1992). At mass maturity, the seed moisture content will remain too high—usually in the range of 32–35 % in cereals and 50–55 % in legumes—to harvest and thresh without mechanical injuries. For example, Andersen and Andersen (1972) found extensive threshing damage in wheat grain harvested at an early stage of maturity. Therefore, seeds are generally allowed to dry on the plant until they reach harvest maturity, i.e., the moisture content at which they can be safely harvested and threshed mechanically (Ellis et al. 1987). Critical damage was reported to be the least when harvested at 16–18 % moisture in many crops including, corn, soybean, and groundnut (*Arachis hypogaea* L.). In semi-arid and arid climates, where the ambient relative humidity is low, maturation drying can reduce the seed moisture content to very low levels (8–10 %), which can also cause problems like cracking and rupture of testa during threshing and handling, as happens in many legumes. The moisture content of individual seeds at the time of harvest also causes wide differences in the extent and seriousness of injuries. Mechanical impacts can be destructive to cell membranes under drying stress. For instance, Bunch (1960) reported that corn shelled at 14 % kernel moisture encountered less damage than shelling at 10 % moisture content. At 4–5 % kernel moisture content, the damage was nearly 100 %. In pinto beans (*Phaseolus vulgaris* L. Pinto), impact velocity, moisture content and seed orientation significantly influenced the physical damages during harvesting (Shahbazi et al. 2012). The percentage of damaged beans decreased significantly from 41.2 to 4.3 % with increase the moisture content from 9.3 to 17.5 % and increasing the impact velocity from 5.5 to 15 m/s caused an increase in the mean values of damage from 0.4 to 37.3 %. It is therefore obvious that seeds must be harvested and threshed before their moisture content becomes too low, in particular when good drying facilities are available.

In tropical and sub-tropical environments where ambient relative humidity is high, some post-harvest drying becomes necessary. Sun or shade drying and/or systems based on forced ventilation with moderately heated air or using desiccants are generally used to reduce moisture content. Whatever method is used for drying, there is likely to be some effect on overall seed quality—especially high temperatures which affect drying, can also contribute to (fast) seed deterioration. It is therefore important that the choice of suitable drying systems should involve minimum seed deterioration. Probert and Hay (2000) mention overheating and erratic drying as two major drawbacks to sun drying. Direct drying under the sun and on surfaces that would heat up much, such as tin or other metal sheets, should be avoided especially if the seed temperatures can exceed 40 °C. Seeds should be spread in thin layers on a canvas or other water-proof base to avoid transfer of moisture from the ground into the seeds and they should be turned over frequently to promote uniform drying. Unfortunately, sun drying will be ineffective in humid environments.

It should also be noted that drying with apparently no effect on seed germination if tested immediately after drying, might still significantly affect longevity during subsequent storage. Most studies on seed drying report the effect on initial viability and vigour but not on their survival in storage. In this context, the reportedly safe temperatures (Witcombe 1984; Nautiyal and Zala 1991) or studies showing no effects of drying even at high temperatures like 50–60 °C (e.g. Singh and Latchanna 1985; ShuChun et al. 2009) can be misleading. Further, what are considered as safe temperatures for drying vary with seed moisture content. For long-term conservation, as required for germplasm material, it is recommended that seeds be dried in an environment of 10–15 °C with 10–15 % relative humidity (RH) (Chromarty et al. 1982). However, Vertucci and Roos (1993), Walters (2003) and Walters et al. (2005) reported that the optimum moisture content and the optimal drying protocols for storage vary with storage temperature and that drying seeds at a relative humidity lower than 15 % could be counter-productive to seed longevity for most species. As a compromise, FAO (2013) recommended drying seeds at 10–25 % relative humidity and 5–20 °C to maximise the benefit of desiccation to subsequent longevity. All the same, preliminary results of a global seed experiment are showing that there is a critical water content below which drying does not increase seed longevity and a significant benefit or damage by drying below the critical water content is not detected (Walters, personal communication).

Rapid drying to very low moisture contents can cause problems like case hardening or seed coat splitting (cleavage damage) in crops like soybean, groundnut and chickpea (*Cicer arietinum* L.) (Chromarty et al. 1982; Rao et al. 1990) or reduce germination as observed in green panic (*Panicum maximum* Jacq.) seeds (Okada 1986). A two stage drying can avoid such problems—in the first stage, the seeds can be dried slowly at 40–45 % RH, followed by the second stage drying at the very low relative humidities.

Mechanical injuries during harvesting and threshing predispose the seeds to microbial attack, which can accelerate their deterioration when stored under poor conditions. Seeds of different species vary widely in both the extent and intensity of damage. Seeds that are spherical are better protected against mechanical injuries than seeds that are elongated or irregularly shaped (Moore 1972). Large-seeded legumes, because of greater surface area are particularly susceptible to injuries that reduce viability. In sorghum (*Sorghum bicolor* (L.) Moench) and corn, the lower portion of the germ extends beyond the general outline of the endosperm and as a result the radicles are often damaged. The natural protrusion of the tip of radicle in seeds like groundnut and chickpea promotes root injuries, which lead to accelerated deterioration and loss of viability. Usually seeds with hairline cracks and other such microscopic damage escape separation during cleaning and processing and affect the overall quality of seed lots.

In several crops, mechanically threshed seeds were found to deteriorate faster than hand-threshed seeds (e.g. Kantor and Webster 1967; Vanjari and Kulkarni 1977). Preferably, germplasm accessions should be hand harvested and manually threshed because of the wide range of variation within and between accessions in seed characteristics and maturity, in addition to the usually small size of the samples handled. Manual harvesting is particularly convenient in species with indeterminate flowering, especially horticultural crops with fruits maturing and ripening over a long period. When using machines for harvesting and threshing, it is essential that they are cleaned to be free of seeds and other debris before processing each seed lot to avoid contamination. With mechanical threshing, the cylinder speed and clearance between the beater bars and the cylinder drum should be regulated depending on the moisture level and seed size to minimise damage. Use of blenders, fermentation treatments and chemical treatments (such as hydrochloric acid, sodium carbonate, etc.) should be avoided to extract seeds from fruits.

Covering structures like glumes and shells protect the seeds from mechanical injuries and inhibit or offer protection to moulds and storage fungi. Kalashnik and Naumenko (1979) reported that unhulled sorghum seeds store better than hulled seeds, which implies the protective role of hull or chaff. In shattercane (*Sorghum bicolor* (L.) Moench subsp. *drummondii* (Nees ex Steud.) de Wet et Harlan), Fellows and Reoth (1992) reported that survival of seeds was positively correlated with glume tightness, caryopsis lignin and glume tannin which appear to act as barriers to microbial invasion. Baskin (1979) and Navarro et al. (1989) reported that shelled groundnut seed lose viability faster than unshelled seeds. More recently, Rao et al. (2002b) found that although in-shell seeds had marginally greater longevity than shelled seeds, the differences in time for regeneration under medium-term storage conditions (5–10 °C and relative humidity of 15 ± 3 %) were small. Considering the much lesser volume required for storage and the insignificant differences in regeneration interval, conservation of shelled seeds was suggested to be highly cost-effective under controlled environmental conditions as compared to in-shell seeds. The process of removing the covering structures before storage can sometimes damage the testa, lowering quality and predisposing the seeds to pest and disease attacks. Therefore, seeds are better conserved with covering structures as long as they do not require much additional storage space (e.g. forage grasses). However, for crops like groundnut, curators need to carefully evaluate the relative benefit to longevity vis-à-vis the cost of conservation with covering structures owing to the additional space required for their storage.

Special attention must be paid to seedborne pathogens because of the consequences of infection on longevity of seeds in storage. Appropriate preventive techniques should be applied, for example, known diseased seed lots should be isolated from non-diseased lots and individual heads should be scrutinized for infected seeds before threshing to avoid contamination of the equipment (see Sackville Hamilton and Chorlton 1997).

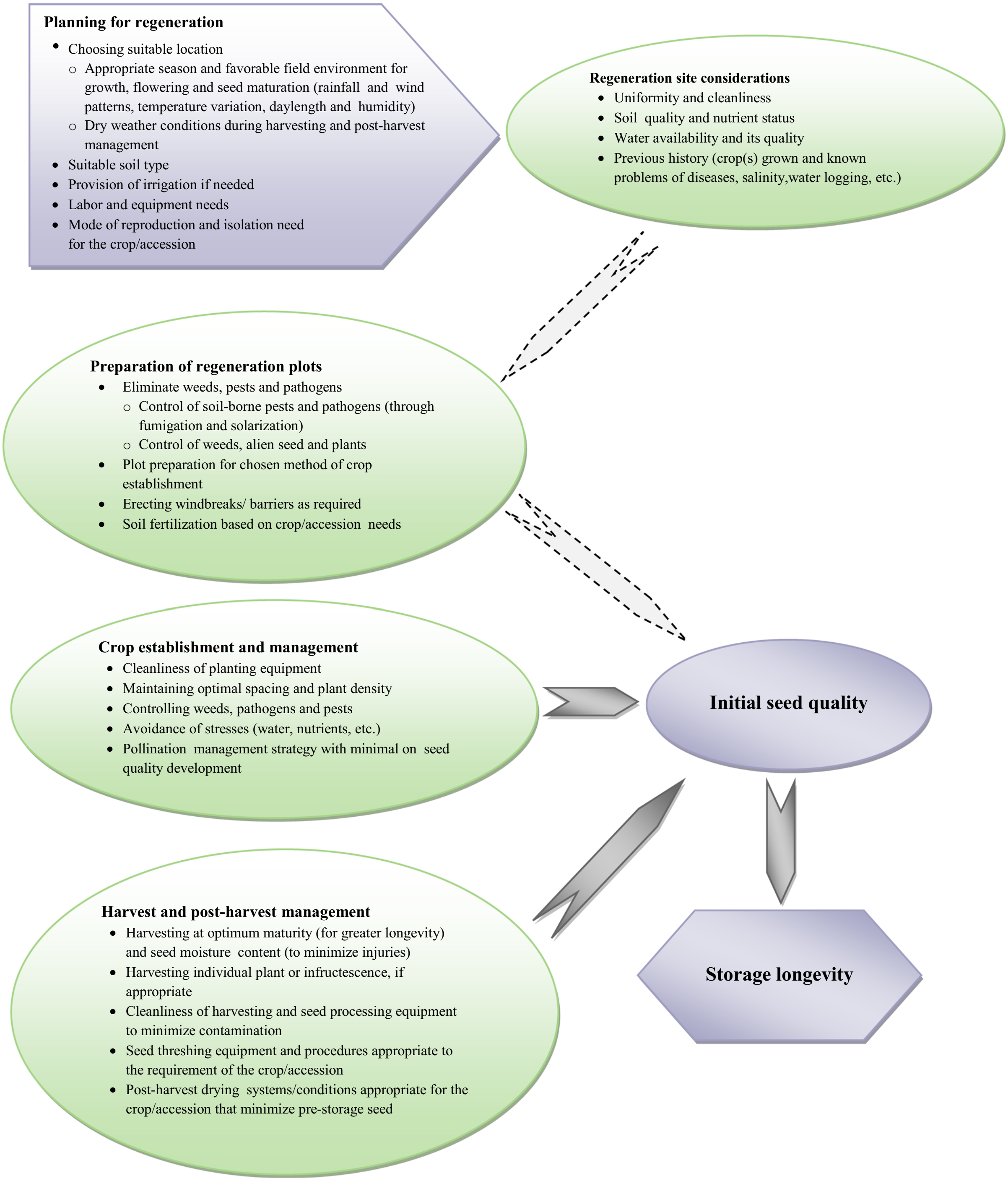
As discussed above, a wide range of factors, including agronomic practices, seed production environment, maturity, harvesting and drying practices will affect the initial seed quality and therefore subsequent storage longevity. For the benefit germplasm curators, Fig. 1 illustrates all the essential factors contributing to or influencing seed quality development. In summary, regenerating in suitable environments under optimal conditions, harvesting at appropriate stage of maturity and adopting proper harvesting techniques to avoid mechanical injuries and drying methods that do not adversely affect seed longevity are important considerations to ensure high initial seed quality.

Concluding remarks

Seeds prepared for conservation in the genebank should have high initial quality to ensure highest possible longevity during storage. Genebanks should aim at maximizing seed storage life to minimise the frequency of regeneration, both for maintenance of genetic integrity and minimizing the cost of operations and in this regard, genebank curators should be aware of the best management practices that contribute to production of high quality seed from their regeneration programmes. Optimum crop specifications for quality seed production, developed for commercial seed lots, have limited application in the context of germplasm regeneration, given the variation in morpho-agronomic characters within the species. This suggests the critical need for research to gain crop-specific knowledge necessary to optimise regeneration protocols to maximise seed quality in genebanks. It should be noted that much of the available literature relates seed quality to germinability, seedling vigour and crop yield and there is meagre information in relation to storage and germplasm conservation in genebanks. Further, seed production practices highly depend on the biology and agronomy of the species and sometimes even on the genotypes.

While production of high quality seeds is crucial to efficient management of germplasm collections, the time and storage conditions from harvest to storage is equally critical and seeds should be processed for storage as quickly as possible and until that time they should be held under controlled conditions such as an air-conditioned room that minimises pre-storage deterioration. As emphasised, good storage conditions can only delay seed deterioration, but cannot stop the process altogether. The extra cost and time spent by genebanks to ensure high initial seed quality through improved practices of regeneration and seed handling will repay handsomely in the longer run through increased shelf-life of the seeds.

Finally, it should be recognized that the optimal protocols for production of high quality seeds during germplasm regeneration depend on a number of factors as discussed in this review and often a compromise is required between theoretical consideration and practical constraints such as the size of collection, the type of material (i.e. genetically uniform or heterogeneous accessions), availability of space, labour and funds for germplasm regeneration. The most critical factor in decision making is well-informed and open-minded curators who are able to adopt protocols based on whatever knowledge is available and apply new research findings in practice to maximise the seed quality.



Planning for regeneration

- Choosing suitable location
  - Appropriate season and favorable field environment for growth, flowering and seed maturation (rainfall and wind patterns, temperature variation, daylength and humidity)
  - Dry weather conditions during harvesting and post-harvest management
- Suitable soil type
- Provision of irrigation if needed
- Labor and equipment needs
- Mode of reproduction and isolation need for the crop/accession

Regeneration site considerations

- Uniformity and cleanliness
- Soil quality and nutrient status
- Water availability and its quality
- Previous history (crop(s) grown and known problems of diseases, salinity,water logging, etc.)

Preparation of regeneration plots

- Eliminate weeds, pests and pathogens
  - Control of soil-borne pests and pathogens (through fumigation and solarization)
  - Control of weeds, alien seed and plants
- Plot preparation for chosen method of crop establishment
- Erecting windbreaks/ barriers as required
- Soil fertilization based on crop/accession needs

Crop establishment and management

- Cleanliness of planting equipment
- Maintaining optimal spacing and plant density
- Controlling weeds, pathogens and pests
- Avoidance of stresses (water, nutrients, etc.)
- Pollination management strategy with minimal on seed quality development

Initial seed quality

Harvest and post-harvest management

- Harvesting at optimum maturity (for greater longevity) and seed moisture content (to minimize injuries)
- Harvesting individual plant or infructescence, if appropriate
- Cleanliness of harvesting and seed processing equipment to minimize contamination
- Seed threshing equipment and procedures appropriate to the requirement of the crop/accession
- Post-harvest drying systems/conditions appropriate for the crop/accession that minimize pre-storage seed

Storage longevity

Fig. 1 Relationship of different factors that influence seed quality during regeneration

Compliance with ethical standards

The authors declare that this manuscript has been prepared according to the ethical standards formulated by Genetic Resources and Crop Evolution. It does not contain any studies with human or animal subjects.

Conflict of interest The authors declare that they have no conflict of interest.

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