Doi: HTTPS://DOI.ORG/10.23910/2/2023.0504

Physiological Maturity of Tropical Forest Seeds: A Boon to Improved Harvest and Storage Practice of Recalcitrant Seeds?

Vidya P. R.[1,2] and Jose P. A.[1*]

[1] Dept. of Tree Physiology, Kerala Forest Research Institute, Peechi, Thrissur (680 653), India
[2]University of Calicut, Thenhipalam, Kerala (673 635), India

Corresponding Author

Jose P. A.
e-mail: pajosekfri@gmail.com

Article History

Article ID: IJEP0504
Received on 23rd November, 2022
Received in revised form on 27th April, 2023
Accepted in final form on 20th May, 2023

Abstract

The fruit harvest at physiological maturity of seeds is a globally accepted practice. This method has been traditionally practiced in horticultural crops where quality seeds and vigorous seedlings are ensured for cultivation of the species. The assessment of seed physiological maturity in the harvest of forest fruits and seeds are seldom practiced as seed physiological and biochemical studies in tropical seeds is little attempted. Since recalcitrant seed behavior among forest species is increasing, maintenance of seed viability and longevity *ex situ* becoming a challenging task in the forestry sector. Further, seed loss through fruit predation and pest infestation are other handicaps to these species. An improved technology for harvesting, storage and longevity of recalcitrant seeds will be a breakthrough for the germplasm conservation, management and utilization of forest genetic resources. Identification of biochemical factors at physiological maturity of seeds in conjunction with fruit morphological characters considered as optimum harvest practice for recalcitrant forest fruits and seeds. The practice could extend shelf life of recalcitrant seeds and bypass seed loss prior to the conventional harvest practices. This review outlines the research works carried out in seed physiological maturity of crops and its broad scope among recalcitrant forest seeds for long term germplasm storage.

Keywords: Biochemical factors, physiological maturity, recalcitrant forest seeds

1. Introduction

The physiological classification regarding seed desiccation tolerance and storage behavior is indispensable for *ex situ* conservation since the knowledge of the moisture content and environmental temperature of storage are essential for seed viability maintenance (Hong and Ellis, 1996). According to the ability to survive different moisture contents and storage temperature, seeds are classified into recalcitrant, orthodox (Roberts, 1973) and intermediate (Ellis et al., 1990) categories. Recalcitrant seeds are not able to tolerate water removal, losing its viability when reaching 12–31% of water content (Barbedo and Marcosfilho, 1998), and thus they have short lifespan and cannot be stored long term (Clavi et al., 2017). These seeds show intense metabolism during its developing and post harvesting stages (Farnsworth, 2000). Further, have large fruits and seeds that prevent them from drying through desiccation (Pritchard et al., 2004; Sivasubramaniam et al., 2012). Most of the tropical forest trees are classified under recalcitrant species. Statistics shows that 15% of world's flora is producing recalcitrant seeds and it is approximately 17,500 species (Figliolia and Kegeyama, 1994). Seed desiccation sensitivity is potentially a high-risk regeneration strategy for plants. A prolonged dry spell occurs at the time of shedding causes annihilation of the entire annual seed lot and if this mechanism continues, majority forest species will be passed over to untimely endangerment. Nature itself has an efficient mechanism to conserve these species, even though they are most affected by the erratic climate changes and global warming. Increase in temperature and reduction in rainfall in tropical region due to climate change has become an important threat to recalcitrant species. Along with this, predation and pest attacks in developmental stages make a catastrophic effect on these species. Hence, reinventing the methodologies for the harvesting and storage practices of recalcitrant forest species is high time.

In terms of *ex situ* conservation, the most efficient method to preserve recalcitrant seeds is the cryopreservation of embryonic axes, which is highly expensive (Sershen et al., 2012; Hamilton et al., 2013; Walters et al., 2013). Seed physiological maturity is the point at which the seeds possess its maximum dry weight and is the most metabolically active stage of a seed (Tura, 2018). Storage studies must start from its physiological maturity that assures the best quality seeds. Studies on many horticultural crops resulted successful attempt for fixing physiological maturity and harvesting good quality and quantity of seeds (Hasina et al., 2013; Sreedevi and Manomani, 2019; Ramya et al., 2016). Seed bank can be considered as a potential seed source for conservation and restoration of several plant communities (Fiona and Robin, 2013). For seed banking, there must be a profound understanding about the seed type and seed physiology. Seed physiological maturity is a dynamic stage which determines the quality of a particular seed for its harvest with higher germinative capacity, energy and subsequent long term storage (Mehta et al., 1993; Robert, 2020). Determining the optimum time for harvest of a particular fruit / seed is highly challenging as the physiological maturity based on visual methods is found to be subjective and the results may have affected by its environmental conditions (Yesica et al., 2021; Zia and Zhu, 2021).

Major studies on seed physiological maturity have been focused on crop plants where quality seeds with high germinability, enhancement in seedlings and subsequent productivity are ensured. This communication unravels the knowledge gaps in harvest and storage of recalcitrant forest seeds where quick loss in viability is becoming a limiting factor for long term storage.

2. Physiological Maturity- Overview

Seed development is the process that starts with fertilization and ends up in maximum fresh weight and dry weight accumulation. At the end of this, seed maturation begins and it continuous till harvest (Harington, 1972). For the proper ensure of seed quality in terms of viability and vigour, the studies on seed development and physiological maturity is considered to be significant. End of seed filling period is the point at which maximum seed quality is attained (Tekrony and Hunter, 1995; Tekrony and Egly, 1997; Kowslowsky, 1972). Storage starts only from the moment when the seed is mature. Physiological maturity is the most accepted measure, where the seed get reached its maximum dry weight and can be used for storage. Seeds at physiological maturity with high moisture content can be dried to low moisture content without loss in viability (Indira and Darmalingam, 1996). Environmental factors play a critical role in describing seed quality both before and after physiological maturity (Delousche, 1980). Some studies proved that factors like temperature, water stress or excessive rain, nutrient shortage, pest incidence can influence the seed quality during seed development and maturation (Demir et al., 2008).

The stage of maturity at harvest is one of the most important factors that can influence the quality of seeds (Carvalho and Nagakawa, 2012). Obtaining seeds of quality is associated with the proper time of collection. For collecting good quality seeds, there must be a proper knowledge about the time of collection. It is necessary to follow the physical and physiological characters of fruit/seed development (Oliver, 1974). When seeds are collected before maturation, they possess a low potential of germinability, storage, as well as poor quality as they are not completely developed in terms of reserve components. Hence, an important aspect of seed production is the correct determination of physiological maturity and the ideal harvest moment, in order to reduce the losses caused by exposed weathering, pest attack and infection by microorganisms. Through this, the maturation process and its relations with recommendable period for harvest should be perfectly known (Silva et al., 2011).

3. A Throwback to Crop Physiological Maturity

Among the studies on physiological maturity of crop species, the major focus was on certain attributes like fruit colour, dry matter and seed vigour. A sum up of major works carried out in this area are as follows.

3.1. Fruit colour

Studies on yellow Passion fruit states that seeds obtained from yellowish fruits showed better performances in tests of vigour having higher speed, uniformity and emergence percentage. They also concluded that the refractive index of the fruits epicarp is a valid and easy method for determining the physiological maturity of the seeds (Ligia et al., 2008). Relation between fruit colour and maturity was again supported by the research carried out in *Jatropha curcas* seeds. The study inferred that those seeds from yellow and brownish-yellow-colored fruits have greater vigour and maintain physiological quality for a longer time compared to seeds extracted from brown fruit, i.e., the dry fruit (Jimenez Garcia et al., 2013). Fruit and seed color of *Cnidosculus quercifolius* was not a good indicator of seed physiological maturity. As little changes were observed on fruit color and more changes were observed in the seed coat color that was white in the initial crops. Seeds were found brown from 51 to 65 days after flowering, but were again white after 72 days of flowering (Uleberg et al., 2012). These findings were corroborated by another study stating that fruit color changing during ripening is associated with degradation of chlorophyll and anthocyanin biosynthesis, which are a class of flavonoids synthesized from the phenylpropanoid pathway responsible for giving reddish and bluish colors and purple shades in fruits (Lillo et al., 2008). The phenylpropanoid pathway responds to various environmental stimuli, such as temperature, photoperiod (Zoratti et al., 2014) and soil fertility (Harington, 1972). In particular light, this is the main factor that contributes to the accumulation of flavonoids in fruits (John et al., 2009). Therefore, the higher incidence of radiation may result in increase in anthocyanin concentration in the epicarp, justifying that the plasticity of the morphometric characteristics of the seeds is shaped by the environment and not by the fruit development stage.

3.2. Fruit/Seed dry matter content:

Seeds reach physiological maturity when their dry matter content attains maximum value (Demir and Ellis, 1992). In mungbean studies, dry weight was significant in treatment combination of varieties and dates of harvest for which minimum viability in seeds generally coincides with maximum dry weight attainment (Carvalho and Nagakawa, 2000). For some plant species, the seed physiological maturity is reached simultaneously with the moment when the seed has its maximum dry mass; while for other species such event may occur before or after that moment. Once the maximum dry mass attained, the deterioration process is initiated leading to a progressive reduction in the physiological quality of the seeds. Such process can be a threat to physiological quality of seeds, once these may be exposed to weathering, pest attack and infection by microorganisms (Carvalho and Nagakawa, 2012). The highest dry weight serves as the point of physiological maturity since this time, all the assimilates necessary for the development and germination of the seeds are translocated towards the developing seeds. Hence after the point of physiological maturity, deterioration of the seeds could occur because of the environmental stresses which could contribute to the deterioration of the seeds quality (Demir et al., 2008). Term physiological maturity sometimes coincides with the term mass maturity. The maximum quality of a seed is associated with the accumulation of dry matter, also called mass maturity. Seeds that are not completely mature are also possessing capacity of germination. However, such seeds do not generate plants as vigorous as those collected at the point of physiological maturity. Mass maturity occurs close or at the same time of physiological maturity of the seeds, stopping the transfer of plant dry matter to the seeds, reaching maximum physiological potential or quite near of reaching it (Jerry et al., 1973).

On contrary, there was some opinion that the determination of physiological maturity on the basis of measuring maximum seed dry weight accumulation was found to be tedious, time consuming and unsatisfactory for routine use (Anonymous, 2002; Anonymous, 2009). In physiological maturity of seeds and colorimetry of fruits of *Jatropha curcas,* there was no significant change in fruit dry weight after fruit pigmentation. Hence, the authors came into the conclusion that the dry matter of fruits/ seeds was not an effective indicator of physiological maturity in seeds of *J. curcas.*

3.3. Seed vigour

Seed vigour can be defined as 'seed properties that determines potential for fast and uniform emergence, and development of seedlings under a wide range of field conditions (Zakaria et al., 2009). In any seed lot especially agricultural species, losses of seed vigour are related to a reduction in the ability of seeds to carry out all the physiological functions that allow them to perform (Harington, 1972). Generally, low germination speed, high sensibility to stresses of seeds and seedlings during germination process, and plants with slow, low and irregular growth or with less root development, are typical characteristics of seed with low physiological potential. Each biotic or abiotic factor that affect seed vigour during seed's development, subsequently will affect production especially when seeds produced under stress condition (Tekrony and Egly, 1997).

For seed producers, the production of high vigour seeds is an inevitable strategy in order to improve the field performances. According to some researchers (Tekrony and Hunter, 1995; Ellis and Pietafilho, 1992), mass maturity formerly described as physiological maturity is a good sign of achieving maximum seed vigour on the mother plant (Golezani and Hosseinzadeh, 2009). Seed vigor studies in faba bean resulted that a peak of vigour obtained at about mass maturity or slightly after this stage. At earlier harvest seed vigour was low due to immaturity and on later harvests because of aging (Patric and Stoddard, 2010).

In Pea plants, harvesting the seed before the attainment of physiological maturity recorded lesser viability and vigour potentials due to a greater number of immature seeds with relatively low degree of embryo development and high moisture content (Savita et al., 1997). Production of high-quality seeds could be facilitated by the harvesting of a seed with maximum vigour at kernel maturity. Correlations were worked out among kernel maturity indices and seedling vigour parameters including percent germination, root and shoot dry weight in a mature corn seed. Although the germination was high over all the harvest dates, both root and shoot dry weight was maximum only at maturity stage (Jerry et al., 1973). Works on crop plants such as Sun flower, Maize, Jatropha, Tomato, Soybean, Red clover Mung bean, Mustard, Lentil, Dill etc. have shown that the physiological maturity could be considered as the key driver for maximum viable seed collection. The main profits for applying concept of physiological maturity on crop seeds are only the production of good quality seeds and majority of the crop seeds are coming under the orthodox category.

4. Recalcitrant Seeds-challenges

Recalcitrance or nature of rapid loss in seed viability among forest seeds is being a great challenge in tropical forestry particularly in the context of climate change. This seed behaviour is more common to the plants which grow in evergreen and riparian ecosystems where atmospheric humidity is higher to maintain seed viability for a reasonable period from week to a few months. However, the erratic weather changes, especially warm conditions existing over a period of time *in situ* found sensitive to recalcitrant seeds and affects their viability apart from seed pests and fruit/seed predation. Thus, maintaining and conserving the existing plant resources, particularly habitat specific threatened plants, an appropriate germplasm conservation is essential. Of the different strategies available to meet this goal, seed storage can be a relatively cheaper, reliable method to hold viable germplasm until field gene bank or plantations are established (Jose et al., 2002; Jose et al., 2013). The main purpose of storing seeds is to a have a viable seed supply when it is needed for regeneration.

Recalcitrant tree species of tropical countries are of high economic importance. Many of them are multipurpose trees including fruit trees of which the products have manifold uses. The populations of these tree species has been declined considerably because of over exploitation by human interference on logging, wood harvesting (Nair et al., 2007), edible fruit collection, habitat degradation and finally natural regeneration of the recalcitrant tree species is found to be very poor (Roby et al., 2013).

5. Rapid Loss in Viability

Recalcitrant seeds possess a remarkably short lifespan, particularly when stored in open conditions. Certain species of the family Dipterocarpaceae and Euphorbiaceae have viability lasts only for a few days or months, eg. *Dipterocarpus bourdillonii* (Swarupanandan et al., 2013) and *Aporosa lindleyana* (Anilkumar et al., 1996). *Shorea robusta,* which is common in both moist and dry forests, whose seeds remain viable only for 7–10 days (Saha et al., 1992; Umarani et al., 2015). Seeds of *Gluta travancorica* lose their viability within a month under ambient conditions (Jose et al., 2004). Among wild nutmegs (*Myristica malabarica, Myristica fatua* var. *magnifica, Myristica beddomei, Gymnacranthera farquhariana* and *Knema attenuata*), the recalcitrant nature of seeds and inability of clonal reproduction are the major causes for the dwindling of the population size (Ranjith and Jose, 2016; Anilkumar et al., 2002). Under natural conditions, the seed viability of *Hydnocarpus macrocarpa* lasts only for seven days (Jose et al., 2014). Along with this seed predation and poor natural regeneration leads to the endangerment of these species. Some important recalcitrant species of tropical forests (*Artocarpus hirsuitus, Calophyllum inophyllum, Dysoxylum malabaricum, Gluta travancorica, Syzygium cumini, Syzygium travancoricum)* possess seed viability for 7 days to one month in natural conditions (Pillai and Pandalai, 2015).

The exact cause for viability loss in recalcitrant seeds is the synergistic effect of a large number of metabolic processes. The exposure of seeds to lower and higher temperatures cause structural changes at cellular and tissue levels and it is reflected by the increased leakage of ions, sugars and proteins. The damage in cells may initiate uncontrolled free radical attack and decrease enzymatic and non-enzymatic protein protection to the embryo. A number of protective enzymes like peroxidase, polyphenol oxidase and superoxide dismutase have been reported in recalcitrant seeds (Chaithanya and Naithani, 1994; Babu et al., 2010)

6. Fruit/ Seed Predation

Fruit and seed predation are the most important interactive relationship in the environment that enables the continuity of the ecosystem. Even though sometimes this may adversely affect the existence of some species particularly those with recalcitrant nature. Natural regeneration of this category is found to be very poor due to the short viability period of the seeds and lack of ideal habitat conditions. In addition to this, the fruit/seed predation is thought to be an added disadvantage for these kinds of species. Studies on many recalcitrant species like, *Garcinia morella, Knema attenuata, Myristica beddomei, Myristica malabarica, Persea macrantha,* showed that the natural regeneration of the species is highly affected by the tree level predation by certain mammals and birds and ground level predation by rodents (Pandurangan, 2003). In *Garcinia imberti,* an endangerd species of souhern Western Ghats also facing a decline in natural germination due to high level of fruit predation (Anto et al., 2018).

7. Seed Pest

Fungi and bacteria do damage in flowering as well as fruiting stages of species in general and recalcitrant species in particular. Insects and fungi are probably responsible for the most serious seed losses of certain species. As fruits of these species may shed with high water content and are susceptible to fungus and bacterial attack which may leads to seed viability loss and poor soil seed bank further affecting natural regeneration. In *Dipterocarpus bourdillonii*, 31.9% of matured fruits were destroyed by weevils and 7% by fungal infestation. Finally, the percentage of fruits with viable seeds was only 7.4 where as in the case of *Humboldtia bourdillonii*, in its reproductive cycle, weevils interfere in two stages, inflorescence stage and fruit maturing stage. Through the infestation, about 13% of the seeds become dead or nonviable (Swarupanandan et al., 2013). The seed pest infestation in tropical trees especially in recalcitrant species significantly affects the germination and eventually leads to poor natural regeneration as in the case of *Dipterocarpus retuses* (Senthilkumar et al., 2009), and *Humboldtia vahliana* (Jose et al., 2008) In *Gluta travancorica*, 25-30% of matured fruits were found destroyed by Nut Weevils (Jose et al., 2004, Jose and Pandurangan, 2013). Seed infestation in *Knema attenuata* (Pandurangan, 2003) and *Cyanometra beddomei* (Jose et al., 2016) leads to the loss of large seed lot per year. The above mentioned are certain case studies of recalcitrant species. A thorough research on this area is to be needed.

8. Recalcitrance vs. Seed Physiological Maturity

Literally recalcitrance and physiological maturity are two independent concepts. But when it comes under the conservation aspect of tropical forest trees these two terms can be presented on a common platform, as they could be relatable. According to Kew data base, among the 345 species of tropical forest trees belonging to 15 families, more than 52% of the tree species were found to be recalcitrant (Kew, 2011; Kettle, 2012). Taking into the consideration all the above consequences i.e; rapid loss of seed viability, fruit/ seed predation, seed infestation altogether causes drastic germplasm loss and genetic resources available to these species.

9. Conclusion

Recalcitrant forest seeds having limitations of short viability period and susceptibility to predation and pests affects the natural regeneration of seeds leading to species endangerment. Identification of biochemical factors at physiological maturity of seeds along with fruit morphological characters is considered as optimum harvest practice for recalcitrant forest seeds. This practice can extend the shelf life of recalcitrant seeds as compared to conventional harvest practices.

10. Acknowledgement

The Authors obliged Dr. Syam Viswanath, the Director, KSCSTE-Kerala Forest Research Institute, Peechi for facilities provided. The first author acknowledges CSIR, New Delhi for the award of Junior Research Fellowship and University of Calicut, for the registration of Ph.D Degree.

12. References

Anilkumar, C., Babu, K.P., Krishnan, P.N., 2002. Seed storage and viability of *Myristica malabarica* Lam. An endemic species of Southern western Ghats, India. Seed Science and Technology 30, 651–657.

Anilkumar, C., Thomas, J., Pushpangadan, P., 1996. Storage and germination of seeds of *Aporusa lindleyana* (Wight) Bailon, an economically important plant of Western Ghats (India). Seed Science and Technology 25, 1–6.

Anonymous, 2009. International rules for seed testing. International Seed Testing Association, Switzerland. New York, USA: John Wiley and Sons Inc 3–98.

Anonymous, 2002. Seed Vigour Testing Handbook. Contribution No. 32 to the Handbook of Seed Testing 2002. Association of Official Seed Analysts, NE, USA.

Anto, M., Jothish, P.S., Angala, M., Anilkumar, C., 2018. Fruit predation and adaptive strategies of *Garcinia imberti* an endangered species of southern Western Ghats. Current Science 115, 2315–2321.

Babu, K.P., Anilkumar, C., Salim, N., 2010. Biochemical aspects of desiccation induced viability loss in *Myristica malabarica* Lam. seeds. International Journal of Plant Science 5, 664–668.

Barbedo, C.J., Marcosfilho, J., 1998. Tolerancia a dessecacaoemsementes. ActaBotanicaBrasilica12, 145–164.

Calvi, G.P., Aud, F., Ferraz, I.D.K., Pritchard, H.W., Kranner, I., 2017. Analyses of several seed viability markers in individual recalcitrant seeds of *Eugenia stipitata* McVaugh with totipotent germination. Plant Biology 19, 6–13.

Carvalho, N.M., Nakagawa, 2012. Journal of Seed Science Technology and Production, 5th Ed, Funep, Jaboticabal.

Carvalho, N.M., Nakagawa, J., 2000. Seeds: science, technology and production. FUNEP, Jaboticabal, SP, Brazil.

Chaithanya, K.S.K., Naithani, S.C., 1994. Role of superoxide, lipid peroxidation and superoxide dismutase in membrane perturbations during loss of viability in seeds of *Shorea robusta* Gaertn.f. New Phytologist 126, 623–627.

Chandrsekhara Pillai, P.K. Pandalai, R.C., 2015. Storage practices in recalcitrant tropical forest seeds of Western Ghats. KFRI Research Report No. 496, 285.

Delouche, J.C., 1980. Environmental effects on seed development and seed quality. Horticultural Science 15, 775–780.

Demir, I., Ashirov, A.M., Mavi, K., 2008. Effect of seed production environment and time of harvest on Tomato (*Lycopersicon esculentum*) seedling growth. Research Journal of Seed Science 1, 1–10.

Demir, I., Ellis, R.H., 1992. Changes in seed quality during seed development and maturation in tomato. Seed Science Research 2, 81–87.

Ellis, R.H., Pieta Filho, C., 1992. Seed development and cereal seed longevity. Seed Science Research 3, 247–257.

Ellis, R.H., Hong, T.D., Roberts, E.H., 1990. An intermediate category of seed storage behaviour. Journal of Experimental Botany 41, 1167–1174.

Farnsworth, E., 2000. The ecology and physiology of viviparous and recalcitrant seeds. Annual Review of Ecology Evironment and Systematics, 107–138.

Figliolia, M.B., Kageyama, P.Y., 1994. Maturacao de sementes de Inga uruguensis Hook et Arn. emflorestariparia do Rio Moji Guacu, municipio de Moji Guaçu, SP. Revista do Instituto Florestal, Sao Paulo 6, 13–52.

Fiona, R.H., Robin, J.P., 2013. Advances in seed conservation of wild plant species: a review of recent research. Conservation Physiology 1, 30.

Golezani, K., Hosseinzadeh, M.A., 2009. Changes in seed vigour of faba bean (*Vicia faba* L.) cultivars during development and maturity. Seed Science and Technology 37, 713–720.

Hamilton, K.N., Offord, C.A., Cuneo, P., Deseo, M.A., 2013. A comparative study of seed morphology in relation to desiccation tolerance and other physiological responses in 71 Eastern Australian rainforest species. Plant Species Biology 28, 51–62.

Harington, J.F., 1972. Seed storage and longevity, In Seed Biology: Kozlowski TT (Ed.). Academic Press, New York 145–245.

Hasina, G., Khan, A.Z., Khalil, S.K., Rehman, H.U.R., Anwar, S., Saeed, B., Akbar, F.H., 2013. Crop growth analysis and seed development profile of wheat cultivars in relation to sowing dates and nitrogen fertilization. Pakisthan Journal of Botany 45, 951–960.

Hong, T.D., Ellis, R.H., 1996. A protocol to determine seed storage behavior. Rome: International Plant Genetic Resources Institute. Technical Bulletin 1, 55.

Indira, K., Dharmalingam, C., 1996. Seed development and maturation in fenugreek. Madras Agriculctural Journal 83, 239–240.

Jerry, D., Eastin, Joe, H., Hultquist, C.Y., Sullivan, 1973. Physiologic Maturity in Grain Sorghum. Crop Science 13,175–178.

Jimenez–Garcia, S.N., Guevara–Gonzaleza, R.G., Mirandalopezb, R., Feregrino-Perezc, A.A., Torres–Pachecoa, I., Vazquez-Cruz, M.A., 2013. Functional properties and quality characteristics of bioactive compounds in berries: biochemistry, biotechnology, and genomics. International Food Research Journal 54, 1195–1207.

John Anurag, P., Chaurasia, A.K., Rangare, N.R., 2009. Physiological maturity in mungbean (*vigna radiata* L. Wilczek) cultivars as influenced by differing harvest dates. Agriculture Science Digest 29, 182–185.

Jose, P.A., Pandurangan, A.G., 2013. Seed storage studies on *Gluta travancorica* Bedd. – An endemic and threatened tree of Southern Western Ghats. Indian Journal of Forestry 36, 349–352.

Jose, P.A., Mohanan., N., Hussain, A., 2008. New record of seed Pest *Cryptorhyncus indicus* Motschulsky (Coleoptera: Curculionidae) in *Humboldtia vahliana* Wight. Indian Forester 134, 849–850.

Jose, P.A., Pandurangan, A.G., Mathew, G., 2004. Impact on insect –pest incidence on natural population of *Gluta travancorica* Bedd..– A rare and endemic tree of Southern Western Ghats. Non–Timber Forest Products 11, 99–102.

Jose, P.A., Pandurangan, A.G., Thomas, J., Pushpangadan, P., 2002. Seed storage studies on *Ochreinauclea missionis* (Wall.ex.G.Don) Ridsd. – An endemic tree of Western Ghats. Seed Research 30, 275–278.

Jose, P.A., Kuruvila, S.T., Binoy, N.M., 2016. New record of seed pest, *Alcidodes Sp. Indet* (Coleoptera: Curculionidae) in *Cynometra beddomei* Prain – An endemic, endangered legume tree of Southern Western Ghats. Indian Journal of Forestry 39, 133–135.

Jose, P.A., Sumod, M., Robi, A.J., 2014. Conservation through restoration of *Hydnocarpus macrocarpa* (Bedd.) Warb – an endemic and endangered tree of Southern Western Ghats. In: Proceedings of the Twenty–six Kerala Science Congress, Kerala State Council for Science, Technology and Environment, Thiruvananthapuram, Kerala. 28– 31 January, Kerala Veterinary and Animal Science University, Wayanad. 2619–2622.

Swarupanandan, K., Indira, E. P., Muralidharan, E. M., Pandalai, R. C., Jose, P. A., & Sanjappa, M. (2013). Species recovery of *Dipterocarpus bourdillonii* and *Humboldtia bourdillonii*, two critically endangered endemic trees of Western Ghats. Final Project Report 463, 86.

Kettle, C.J., 2012. Seeding ecological restoration of tropical forests: priority setting under REDD. Biological Conservation 154, 34–41.

Kowslowsky, 1972. Seed Biology, Vol. I, Vol. II, Vol. III. Academic Press, New York.

Lígia, M.M.S., Ivor Bergemann, D.A., Valderez, P., Matos Ricardo, A.V., Izaque Francisco, C.D.M., 2008. Physiological maturity of *Cnidosculus quercifolius* Pax, K. Hoffm. Seed Science and Technology 36, 15–20.

Lillo, C., Lea, U.S., Ruoff, P., 2008. Nutrient depletion as a key factor for manipulating gene expression and product formation in different branches of the flavonoid pathway. Plant Cell and Environment 31, 587–601.

Liu, L., Lai, Y., Cheng, J., Wang, L., Du, W., 2014. Dynamic quantitative trait locus analysis of seed vigor at three maturity stages in rice. Plos One 9, 115732.

Mehta, C.J., Kuhad, M.S., Sheora, I.S., Nandwal, A.S., 1993. Studies on seed development and germination in chickpea cultivars. Seed Research 21, 89–91.

Nair, P.V., Ramachandran, K.K., Swarupanandan, K., Thomas, T.P., 2007. Mapping biodiversity of the *Myristica* swamps in Southern Kerala., KFRI Research Report No. 326, 245.

Oliver, W.W., 1974. Seed maturity in white fir and red fir. USDA. Forest Service. PSW Research Paper, Berkeley 99, 1–12.

Pandurangan, A.G., 2003. Rescue and restoration of endemic and RET medicinal plants of Agasthyamalai, Kulamavu, Wayanad MPCAs, Kerala, India. Final Project Report, Tropical Botanic Garden and Research Institute, Thiruvananthapuram.

Patrick, J.W., Stoddard, F.L., 2010. Physiology of flowering and grain filling in faba bean, Field. Crop Research 115, 234–242.

Pritchard, H.W., Daws, M.I., Fletcher, B.J., Gamene, C.S., Msanga, H.P., Omondi, W., 2004. Ecological correlates of seed desiccation tolerance in tropical African dry land trees. American Journal of Botany 91, 863–870.

Ramya, M., Yogeesha, H.S., Bhanuprakash, K., Gowda, R., Veere., 2016. Physiological and biochemical changes during seed development and maturation in onion (*Allium cepa* L.). Vegetable Science 39, 157–160.

Ranjith, C.V., Jose, P.A., 2016. Conservation of wild nutmegs of the Western Ghats of Kerala: A model study for the restoration of dwindling tree population. In: 28th Kerala Science Congress held from 28–30 January, at University of Calicut. 2390–2401.

Robert, E.G., 2020. Seed Quality: Basic Mechanisms and Agricultural Implications,CRC Press, 60, 76

Roberts, E.H., 1973. Predicting the storage life of seeds. Seed Science and Technology, Zurich.1, 499–514.

Roby, T.J., Jose, J., Nair, P.V., 2013. *Syzygium travancoricum* (Gamble) – a critically endangered and endemic tree from Kerala, India – threats, conservation and prediction of potential areas; with special emphasis on Myristica swamps as a prime habitat. International Journal for Environmental Science and Technology 2, 1335–1352.

Saha, P.K., Bhattacharya, A., Ganguly, S.N., 1992. Problems with regard to the loss of seed viability of *Shorea robusta* Gaertn. f. Indian Forester 118, 70–75.

Savita, K., Kaur, A., Singh, G., 1997. Comparison of seed quality at physiological maturity and harvest maturity of two pigeon pea (*Cajanus cajan* L. Mill sp.) cultivars. Actaagrobotanica 50, 1–2.

Senthilkumar, N., Bharathkumar, N.D., Singh, A.N., 2009. Record of seed onset pests of *Dipterocarpus retusus* in Hollongapar reserve forests. Journal of Tropical Forest Science 21, 8–12.

Sershen, B.P., Pammenter, N.W., Wesley Smith, J., 2012. Rate of dehydration, state of subcellular organisation and nature of cryoprotection are critical factors contributing to the variable success of cryopreservation: studies on recalcitrant zygotic embryos of *Haemanthus montanus*. Protoplasma 249, 171–186.

Silva, L., Dias, C.F.S., Dias, L.A.S., Hilst, P.C., 2011. Physiological quality of *Jatropha curcas* L. seeds harvested at different development stages. Seed Science and Technology 39, 10–15

Sivasubramaniam, K., Geetha, R., 2012. Recalcitrant seeds causes and effects. Satish serial publishing house, New Delhi., 120.

Sreedevi, R., Manomani, V., 2019. Predicting the optimal stage of maximum seed quality during seed development and maturation in proso millet (*Panicum miliaceum* L.), International Journal of Farm Sciences 9, 89–93.

Tekrony, D.M., Hunter, J.L., 1995. Effect of seed maturation and genotype on seed vigor in maize. Crop Science 35, 857–862.

Tekrony, D.M., Egli, D.B., 1997. Accumulation of seed vigour during development and maturation. In Ellis, R.H., Black, M., Murdoch, A.J., Hong, T.D. (Eds.), Basic and applied aspects of seed biology, , Kluwer Academic Publishers, Dordercht, 369–384.

Tura, B., 2018. Biology of seed development and germination physiology, Advances in Plants & Agriculture Research 8, 336–346.

Uleberg, E., Rohloff, J., Jaakola, I., Trost, K., Junttila, O., Haggman, H., Martinussen, I., 2012. Effects of temperature and photoperiod on yield and chemical composition of northern and southern clones of bilberry (*Vaccinium myrtillus* L.). Journal of Agricultural Food Chemistry 60, 10406–10414.

Umarani, R., Aadhavan, E.K., Faisal, M.M., 2015. Understanding poor storage potential of recalcitrant seeds. Current Science 108, 2023–2034.

Walters, C., Berjak, P., Pammenter, N., Kennedy, K., Raven, P., 2013. Preservation of recalcitrant seeds. Science 339, 915–916.

Xia, K., Zhu, Z.Q., 2021. Characterization of physiological traits during development of the recalcitrant seeds of *Quercus serrata*. Plant Biology 23, 1000–1015.

Yesica, C.M., Javier, F.B., Nora, V.G., Daniel, J.M., Deborah, P.R., 2019. Physiological maturity as a function of seed and pod water concentration in spring rapeseed (*Brassica napus* L.). Field Crops Research 231, 1–9.

Zakaria, M.S., Ashraf, H.F., Seragm, E.Y., 2009. Direct and residual effects of nitrogen fertilization, foliar application of potassium and plant growth retardant on Egyptian cotton growth, seed yield, seed viability and seedling vigour. Acta Ecologica Sinica 29, 116–123.

Zoratti, l., Karppinen, K., Luengoescobar, A., Haggman, H., Jaakola, L., 2014. Light-controlled flavonoid biosynthesis in fruits. Frontiers in Plant Science 5, 1–16.