

ECOLOGICAL SIGNIFICANCE OF RECALCITRANT SEEDS

Vinay Chamoli¹, Shailendra Tiwari¹, J S Chauhan¹, Anoop Badoni² and Chandan Kumar²

¹Department of Seed Science and Technology, HNB Garhwal University, Srinagar ²Plantica – Indian Academy of Rural Development, Dehradun Corresponding Email: chamolivinay.44@gmail.com

Received: 20 January, 2025 Accepted: 06 February, 2025

Abstract

Recalcitrant seeds, characterized by their sensitivity to desiccation and inability to withstand freezing temperatures, play a critical role in maintaining biodiversity and ecosystem functionality. Unlike orthodox seeds, recalcitrant seeds germinate rapidly after dispersal, allowing them to adapt to specific environmental conditions, particularly in tropical and subtropical ecosystems. These seeds contribute to ecosystem dynamics through specialized dispersal strategies, nutrient cycling, and fostering microhabitats that support diverse plant and animal life. They also enhance ecosystem resilience by promoting rapid regeneration following disturbances. This paper explores the ecological significance of recalcitrant seeds, emphasizing their evolutionary adaptations, role in biodiversity maintenance, and implications for ecosystem stability amidst climate change. The article highlight the need for targeted conservation strategies to protect recalcitrant-seeded species and ensure the sustainability of the ecosystems they support.

Keywords: Recalcitrant seeds, Desiccation, Orthodox seeds, Biodiversity

Citation: Chamoli Vinay, Shailendra Tiwari, J S Chauhan, Anoop Badoni and Chandan Kumar (2025), Ecological Significance of Recalcitrant Seeds. The PLANTA Research Book Series, 6 (1), 1728-1737. www.pgrindias.in

Introduction

ecalcitrant seeds are a unique category of seeds characterized by their sensitivity to desiccation. Unlike orthodox seeds, which can withstand drying and remain viable for extended periods, recalcitrant seeds are unable to tolerate significant loss of moisture. This makes them highly vulnerable to drying conditions. These seeds are typically shed at relatively high moisture content, a feature that is essential for their survival and germination. Due to this requirement, they are incapable of forming a soil seed bank, as they cannot endure prolonged periods of dormancy in dry conditions. However, an interesting adaptation seen in recalcitrant seeds is their ability to form a seedling bank. This allows the seedlings to persist in their environment and germinate successfully even in conditions with limited light availability, an important ecological strategy for their propagation.

Despite their slower germination rates compared to orthodox seeds, recalcitrant seeds share similar temperature optima and maxima for germination. This indicates that while they may be slower to initiate growth, they are adapted to germinate within a specific temperature



range that supports their development. The slow germination process and their sensitivity to drying pose significant challenges for the regeneration and sustainability of plant species producing recalcitrant seeds, particularly under conditions of climate change. With changing environmental conditions, such as increasing droughts and fluctuating temperatures, the vulnerability of these seeds to regeneration failure becomes pronounced. This sensitivity to drought conditions highlights the precarious position of species dependent on recalcitrant seeds for reproduction. The moisture content of recalcitrant seeds is a critical factor influencing their germination. Studies have shown a positive correlation between seed moisture content and the rate of germination. High moisture levels are essential to maintain cellular integrity and support the metabolic processes required for seed development and germination. When recalcitrant seeds experience desiccation, they undergo cellular damage, particularly to the cell membranes. This damage is often irreversible and leads to significant issues such as electrolyte leakage. The loss of cellular stability not only hampers the viability of the seed but also reduces its capacity to germinate and develop into a healthy seedling.

Abscisic acid (ABA), a plant growth regulator, plays a pivotal role in determining the behavior of recalcitrant seeds. ABA is known to influence various physiological and developmental processes in seeds, including dormancy, germination, and stress responses. In recalcitrant seeds, ABA may regulate the balance between dormancy and germination, ensuring that seeds only germinate under favorable conditions. However, the high sensitivity of these seeds to environmental changes can complicate this balance, making them more susceptible to adverse conditions.

Recalcitrant seeds are found in a wide range of tree species, many of which are ecologically and economically significant. These seeds have been part of the evolutionary history of plants for millions of years, with evidence suggesting their presence since the late Cretaceous period. This long-standing evolutionary adaptation demonstrates their resilience and the ecological strategies that have allowed them to persist through various climatic and environmental changes. However, the current challenges posed by climate change, habitat loss, and other anthropogenic factors threaten the survival of species relying on recalcitrant seeds.

The characteristics of recalcitrant seeds present both opportunities and challenges for conservation and agricultural practices. Their inability to withstand desiccation complicates their storage and preservation, making ex situ conservation efforts more complex. Traditional seed storage methods, such as drying and freezing, are unsuitable for recalcitrant seeds, necessitating alternative approaches such as cryopreservation. Moreover, the ecological dependence of these seeds on specific environmental conditions underscores the need for habitat conservation and the development of strategies to mitigate the impacts of climate change on their survival.

Recalcitrant seeds also offer insights into plant physiology and adaptation. Their behavior highlights the intricate mechanisms plants use to survive and reproduce under varying environmental conditions. By studying these seeds, researchers can gain a deeper understanding of plant responses to stress, the role of growth regulators like ABA, and the evolutionary strategies that have shaped plant diversity over time. Such knowledge is invaluable for developing innovative solutions to address the challenges faced by plant species in a rapidly changing world.

Overall, recalcitrant seeds represent a fascinating aspect of plant biology, characterized by their desiccation sensitivity and unique germination strategies. While their ecological significance and evolutionary history underscore their resilience, the challenges posed by their vulnerability to drying and climate change highlight the need for targeted conservation efforts. By understanding the complex mechanism between moisture content,

The Planta RBS, Vol.-6, Issue-1, April 2025: 1728 – 1737 // ISSN: 3048:8494 Chamoli Vinay et.al. (Series Chapter No. – 191 // ISBN: 978-81-965701-4-9) https://www.pgrindias.in

cellular integrity, and environmental conditions, scientific community can work towards preserving the diversity and ecological contributions of species dependent on recalcitrant seeds.

Table 1: List of Some notable species of Recalcitrant seeds

Botanical Name	Common Name	Family	Seed Type
Rhizophora mangle (Red Mangrove)	Red Mangrove	Rhizophoraceae	Recalcitrant
Avicennia marina (Gray Mangrove)	Gray Mangrove	Acanthaceae	Recalcitrant
Castanea spp.	Chestnut	Fagaceae	Recalcitrant
Hevea brasiliensis	Rubber tree	Euphorbiaceae	Recalcitrant
Theobroma cacao	Cacao, Cocoa	Malvaceae	Recalcitrant
Persea americana	Avocado	Lauraceae	Recalcitrant
Durio spp.	Durian	Malvaceae	Recalcitrant
Mangifera indica	Mango	Anacardiaceae	Recalcitrant
Dimocarpus longan	Longan	Sapindaceae	Recalcitrant
Litchi chinensis	Lychee	Sapindaceae	Recalcitrant
Artocarpus heterophyllus	Jackfruit	Moraceae	Recalcitrant
Psidium guajava	Guava	Myrtaceae	Recalcitrant
Olea europaea	Olive	Oleaceae	Recalcitrant
Castanea sativa	Sweet chestnut	Fagaceae	Recalcitrant
Duguetia spp.	Duguetia	Annonaceae	Recalcitrant
Tamarindus indica	Tamarind	Fabaceae	Recalcitrant
Ochroma pyramidale	Balsa	Malvaceae	Recalcitrant
Rhizophora mangle (Red Mangrove)	Red Mangrove	Rhizophoraceae	Recalcitrant

Role of Recalcitrant Seeds in Natural Ecosystems

Recalcitrant seeds hold a vital position in natural ecosystems, particularly in tropical and subtropical regions where they are more commonly found. Their ecological significance is profound, contributing to biodiversity conservation and the maintenance of ecosystem balance. Exploring their role offers valuable insights into their importance in sustaining diverse and dynamic ecosystems. One of the primary contributions of recalcitrant seeds is their role in supporting biodiversity. Many tree species in tropical and subtropical forests rely on recalcitrant seeds for reproduction, making these seeds essential for the survival and propagation of numerous plant species. The plants that grow from recalcitrant seeds often serve as keystone species, providing habitat and food for various animals, insects, and microorganisms. By facilitating the growth of these plants, recalcitrant seeds indirectly support a wide array of species, contributing to intricate ecological networks. Recalcitrant seeds are particularly adapted to environments with high humidity and consistent rainfall. Unlike orthodox seeds, which can remain dormant for extended periods, recalcitrant seeds germinate quickly and rely on moist conditions to survive. This characteristic enables them to establish seedlings rapidly in suitable conditions, playing a critical role in the regeneration of forests. Their ability to germinate in shaded or low-light conditions further enhances their contribution to forest dynamics, as they can thrive beneath dense canopies, aiding in forest

The Planta RBS, Vol.-6, Issue-1, April 2025: 1728 – 1737 // ISSN: 3048:8494 Chamoli Vinay et.al. (Series Chapter No. – 191 // ISBN: 978-81-965701-4-9) https://www.pgrindias.in

stratification and maintaining diverse plant layers. The rapid germination and growth of plants from recalcitrant seeds also contribute to soil health and erosion control. As these plants establish themselves, they stabilize the soil with their roots, preventing erosion and enhancing soil fertility through organic matter deposition. This process is particularly beneficial in tropical ecosystems, where heavy rainfall can lead to significant soil loss without adequate vegetation cover.

Recalcitrant seeds also play a role in carbon sequestration. The plants that grow from these seeds often include large trees with significant biomass, which act as carbon sinks. By supporting the growth of these trees, recalcitrant seeds contribute to mitigating climate change by absorbing atmospheric carbon dioxide. Furthermore, the presence of recalcitrant seeds in ecosystems supports the survival of wildlife species that depend on them as a food source. Animals such as birds, mammals, and insects feed on these seeds and their seedlings, facilitating seed dispersal and enhancing genetic diversity within plant populations. This symbiotic relationship ensures the perpetuation of both plant and animal species, highlighting the interconnectedness of natural ecosystems.

Despite their ecological importance, recalcitrant seeds face threats from habitat destruction and climate change. Their sensitivity to desiccation and reliance on specific environmental conditions make them vulnerable to changing climates and deforestation. Conservation efforts aimed at protecting habitats and understanding the physiology of recalcitrant seeds are essential to ensure their continued role in ecosystem stability. Recalcitrant seeds are indispensable to natural ecosystems, supporting biodiversity, forest regeneration, soil health, and climate regulation. Their unique adaptations and ecological contributions underscore the need for targeted conservation strategies to preserve their role in maintaining the balance and resilience of natural habitats. Here are several key aspects of their role:

Diversity and Adaptation

Recalcitrant seeds are often associated with species that inhabit diverse and dynamic environments, such as tropical rainforests. These environments experience fluctuating moisture levels, temperature variations, and rapid changes in light availability. Recalcitrant seeds, which are desiccation-sensitive, are found in many woody species of tropical forests. These seeds are shed at a high moisture content, do not form a soil seed bank, and are dependent on regeneration under low light levels. The ability of large recalcitrant seeds to germinate in low light is an important adaptation associated with the formation of a seedling bank. Recalcitrant seeds have been found in 721 species, 297 genera, and 84 families, with the trait appearing in numerous lineages since the late Cretaceous. The transition from orthodox to recalcitrant seeds is less frequent than vice versa, and recalcitrant seeds spend less time in the recalcitrant state compared to orthodox seeds in the orthodox state². Climate change, particularly increases in temperature and drought, can negatively affect the success of ex situ conservation and cryopreservation of recalcitrant-seeded species. However, some recalcitrant-seeded species may benefit from increased temperatures and water stress, leading to better adaptation to drying and increased success in propagation and cryopreservation. Recalcitrance is associated with certain ovule/seed characters, such as bitegmic and crassinucellate ovules, nuclear endosperm development, and extensive vascularization of the integument/seed coat, which are considered ancestral character states in dicotyledons. The presence of recalcitrant seeds in such ecosystems reflects the adaptation of plants to these conditions. These seeds germinate quickly after dispersal, taking advantage of favourable conditions for growth and establishment.



Seed Dispersal and Succession

Seed dispersal and succession play pivotal roles in the ecological functioning of recalcitrant seeds, influencing their distribution, establishment, and contribution to ecosystem dynamics. These seeds, sensitive to desiccation and reliant on moist environments, exhibit unique adaptations and ecological behaviors that impact how they are dispersed and how they contribute to ecological succession.

Recalcitrant seeds often rely on biotic agents for dispersal, as their high moisture content and relatively large size limit their ability to be dispersed by wind or other abiotic means. Animals such as birds, mammals, and rodents play a critical role in transporting these seeds to suitable germination sites. In many cases, the seeds are consumed as a food source, with undigested or partially digested seeds deposited elsewhere via animal feces. This process not only aids in dispersal but also enhances germination by exposing the seed to optimal conditions, such as nutrient-rich soil.

Some species of recalcitrant seeds have evolved mutualistic relationships with specific dispersers. For instance, certain large-seeded tropical plants depend on large mammals like elephants for effective seed dispersal over long distances. These dispersers are essential in maintaining the genetic diversity and spatial distribution of plant populations. However, the decline of key disperser species due to habitat loss or hunting poses significant challenges for the dispersal and survival of plants producing recalcitrant seeds.

Recalcitrant seeds are integral to various stages of ecological succession, particularly in forested ecosystems. Their ability to germinate rapidly under favorable conditions allows them to establish seedlings in newly disturbed or regenerating areas. For example, after natural disturbances such as storms, landslides, or human activities like logging, recalcitrant seeds contribute to the initial wave of vegetation that stabilizes the soil and creates a microenvironment conducive to further plant colonization.

These seeds often give rise to species that play a foundational role in forest structure. By forming a dense understorey or canopy layer, plants germinated from recalcitrant seeds provide shade, regulate microclimatic conditions, and create habitats for other organisms. Over time, this facilitates the establishment of more diverse and complex plant communities, driving succession toward a mature ecosystem.

Despite their ecological significance, the dispersal and succession processes involving recalcitrant seeds face several challenges. Habitat fragmentation and climate change disrupt the availability of suitable dispersal agents and germination sites, reducing the effectiveness of natural dispersal mechanisms. Furthermore, the sensitivity of recalcitrant seeds to desiccation makes them particularly vulnerable in changing climates, where increased droughts and temperature fluctuations can hinder their germination and establishment.

To support the role of recalcitrant seeds in seed dispersal and succession, targeted conservation efforts are crucial. Protecting natural habitats and ensuring the survival of key disperser species are essential steps. Additionally, understanding the physiological requirements and ecological interactions of recalcitrant seeds can inform restoration efforts, particularly in degraded landscapes where these seeds can play a transformative role in reestablishing vegetation cover and biodiversity.

Overall, seed dispersal and succession are central to the ecological success of recalcitrant seeds. Their reliance on biotic dispersers and their contribution to forest regeneration highlight their importance in maintaining ecosystem dynamics and biodiversity, underscoring the need for their conservation in the face of environmental challenges.



Microhabitat Creation

Recalcitrant seeds play a significant role in microhabitat creation, contributing to the establishment and maintenance of localized environmental conditions that support diverse plant and animal communities. Their unique traits, such as sensitivity to desiccation and rapid germination, enable them to influence their immediate surroundings in ways that promote ecological balance and biodiversity.

When recalcitrant seeds germinate, the resulting seedlings often form dense clusters that modify the microenvironment. These clusters provide shade, reduce soil temperature, and retain moisture, creating a more favorable environment for other organisms. The shading effect is particularly beneficial in tropical and subtropical forests, where intense sunlight can hinder the growth of shade-intolerant species. By moderating light availability, plants grown from recalcitrant seeds help maintain the layered structure of forest ecosystems, supporting diverse plant life at various strata.

The establishment of seedlings from recalcitrant seeds also contributes to soil stabilization and fertility. Their roots bind the soil, reducing erosion and enhancing water retention. Additionally, organic matter from fallen leaves and decaying plant material enriches the soil, creating nutrient-rich microhabitats that support the growth of other plants and microorganisms. These localized improvements in soil quality foster a cycle of regeneration and growth, facilitating the development of a stable ecosystem.

Plants originating from recalcitrant seeds often provide critical resources for wildlife. Their presence can create small habitats that shelter insects, birds, and small mammals. The seeds themselves, as well as the plants they grow into, serve as food sources, supporting the survival of these organisms. In turn, these animals contribute to seed dispersal and pollination, reinforcing the ecological interdependence within these microhabitats.

In disturbed or regenerating areas, recalcitrant seeds play a crucial role in initiating the recovery process. By germinating quickly and establishing vegetation cover, they create microhabitats that allow other species to colonize the area. This process not only aids in restoring the ecosystem but also ensures the survival of species dependent on the microhabitats created by these plants. The capacity of recalcitrant seeds to influence their surroundings underscores their ecological importance. Their role in creating and sustaining microhabitats highlights the intricate relationships between plants, soil, and organisms within an ecosystem. However, the challenges posed by habitat loss and climate change threaten their ability to perform these functions, making conservation efforts essential for preserving their ecological contributions.

Ecosystem Resilience

Recalcitrant seeds contribute significantly to ecosystem resilience by supporting biodiversity, facilitating regeneration, and maintaining ecosystem processes. Their unique characteristics, such as desiccation sensitivity and rapid germination, allow them to play a critical role in ensuring the stability and adaptability of ecosystems, particularly in tropical and subtropical regions.

By germinating quickly under favorable conditions, recalcitrant seeds enable the rapid establishment of vegetation, which is essential in recovering from natural disturbances such as storms, floods, or human-induced activities like deforestation. The plants that arise from these seeds often act as pioneer species, stabilizing the soil, reducing erosion, and creating a microenvironment that promotes the growth of other plants. This regenerative capacity enhances the ecosystem's ability to bounce back after disturbances, contributing to long-term stability.



Recalcitrant seeds also support species diversity, which is a key component of ecosystem resilience. Many of the plants that grow from these seeds serve as keystone species, providing habitats and food resources for a wide range of organisms. This interconnectedness fosters ecological redundancy, where multiple species perform similar roles, ensuring that ecosystem functions continue even if some species are lost. For example, plants from recalcitrant seeds may sustain populations of pollinators and seed dispersers, whose activities are essential for maintaining plant diversity and ecosystem productivity.

The ability of recalcitrant seeds to germinate in shaded or low-light conditions further strengthens ecosystem resilience by enabling forest regeneration beneath existing canopies. This characteristic supports the development of stratified forests, which are more resistant to environmental stressors such as drought or temperature fluctuations. The diverse plant layers created by these seeds enhance ecosystem functions, including carbon sequestration, nutrient cycling, and water regulation, all of which are crucial for maintaining resilience in the face of climate change.

In addition, plants grown from recalcitrant seeds contribute to long-term ecosystem health by enriching the soil with organic matter and improving its structure. The nutrient-rich environment they create supports the growth of other plant species and microorganisms, fostering a dynamic and self-sustaining system. This process ensures the ecosystem's capacity to adapt to changing conditions and continue providing essential services.

However, the sensitivity of recalcitrant seeds to desiccation and their dependence on specific environmental conditions make them vulnerable to climate change and habitat degradation. Their decline could compromise the resilience of ecosystems that rely on them. Conservation efforts, including habitat protection and research into the ecological requirements of recalcitrant seeds, are critical to preserving their role in maintaining ecosystem stability and adaptability.

Recalcitrant seeds exemplify the intricate relationships within ecosystems, where their growth and survival are intertwined with broader ecological processes. Their ability to promote biodiversity, facilitate recovery, and enhance ecological functions underscores their importance in building and maintaining resilient ecosystems.

Adaptation strategies of Recalcitrant Seeds in Ecosystems

Genetic Diversity and Evolutionary Strategies

Plants with recalcitrant seeds often exhibit high genetic diversity within populations. This diversity allows them to respond to environmental changes and adapt to varying conditions over time. The presence of recalcitrant seeds in ecosystems represents an evolutionary strategy that balances risks associated with seedling establishment in challenging environments and opportunities for rapid growth and reproduction under favourable conditions.

a) Adaptation to Moist Environments

Recalcitrant seeds are predominantly found in species inhabiting moist tropical and subtropical environments. Their sensitivity to drying is an evolutionary adaptation to these humid climates where the risk of desiccation is minimal. This adaptation ensures that seeds remain viable and ready for



Fig. 1: Shorea robusta seeds (Sal) (Source: Indiamart)

The Planta RBS, Vol.-6, Issue-1, April 2025: 1728 – 1737 // ISSN: 3048:8494 Chamoli Vinay et.al. (Series Chapter No. – 191 // ISBN: 978-81-965701-4-9) https://www.pgrindias.in

germination when environmental conditions are favourable, particularly moisture availability. For instance, species such as the tropical tree *Shorea robusta* produce recalcitrant seeds that thrive in the consistent humidity of tropical rainforests.

b) Rapid Germination and Seedling Establishment

One of the most notable ecological features of recalcitrant seeds is their propensity for rapid germination. Unlike orthodox seeds, which may remain dormant until conditions are suitable, recalcitrant seeds often germinate soon after dispersal. This rapid germination is advantageous in stable environments where the conditions for seedling establishment, such as adequate moisture and temperature, are consistently met . For example, the seeds of the mangrove species



Fig. 2: Avicennia marina

Avicennia marina exhibit immediate germination,

allowing seedlings to establish quickly in the dynamic intertidal zones they inhabit . (Source of Fig.-2: https://www.asergeev.com/pictures/archives/compress/2015/1645/12.htm)

c) Contribution to Continuous Reproduction

Recalcitrant seeds support continuous reproductive cycles in ecosystems where seasonal changes are minimal. In tropical rainforests, where environmental conditions remain relatively constant throughout the year, the ability of recalcitrant seeds to germinate without a dormancy period enables ongoing regeneration and maintenance of forest structure and biodiversity. This continuous reproduction is crucial for sustaining the dense and diverse vegetation typical of these ecosystems.

4. Maintenance of Biodiversity

The unique germination requirements and characteristics of recalcitrant seeds contribute significantly to the maintenance of plant biodiversity. These seeds support species that might not survive if their seeds required dormancy and desiccation tolerance. This promotes a variety of plant life, which in turn supports diverse animal and insect populations, creating a complex



Fig. 3: African oil palm (Elaeis guineensis)

and interdependent web of life. For instance, the African oil palm (*Elaeis guineensis*) produces recalcitrant seeds that contribute to the rich biodiversity of tropical African forests. (*Source of Fig. 3: Franz Eugen Köhler, Köhler's Medizinal-Pflanzen*)

5. Specialized Seed Dispersal Strategies

Plants producing recalcitrant seeds often rely on specific dispersal mechanisms, frequently involving animal dispersers. The mutualistic relationships between these plants and their dispersers are critical for seed propagation. Animals such as birds, mammals, and insects that feed on these seeds play a crucial role in transporting them to suitable germination sites. This dispersal strategy not only aids in plant propagation but also enhances



genetic diversity by spreading seeds across wider areas. The Brazil nut tree (*Bertholletia excelsa*), for instance, relies on agoutis to disperse its large, recalcitrant seeds.



Fig. 4: The Brazil nut tree (Bertholletia excelsa) (Source: wikipedia)

6. Role in Nutrient Cycling

Recalcitrant seeds contribute to nutrient cycling within their ecosystems. Since they are not adapted for long-term dormancy, recalcitrant seeds that do not germinate decompose relatively quickly. This decomposition process returns valuable nutrients to the soil, supporting the overall health and fertility of the ecosystem. The rapid breakdown of these seeds helps maintain soil quality and promotes the growth of other plant species.

7. Implications for Climate Change Resilience

Understanding the ecological significance of recalcitrant seeds is increasingly important in the context of climate change. As global temperatures rise and precipitation patterns shift, the habitats of many recalcitrant seed-bearing plants are under threat. Conservation efforts targeting these species are critical for maintaining the resilience and functionality of ecosystems that rely on them. Preserving the genetic diversity and adaptive potential of these plants is essential for ensuring ecosystem stability in the face of environmental changes.

Conclusion

Recalcitrant seeds play a vital role in their ecosystems through rapid germination, support of continuous reproduction, maintenance of biodiversity, specialized dispersal strategies, and contribution to nutrient cycling. Their ecological significance underscores the need for targeted conservation strategies to ensure the survival of these sensitive species amidst the challenges posed by climate change. By appreciating and protecting the unique characteristics of recalcitrant seeds, we can help sustain the complex and dynamic ecosystems that depend on them.



References

- Ana Carolina Ruiz Fernández, Pedro León-Lobos, Samuel Contreras, Juan F. Ovalle, Sershen, K. van der Walt, Daniel Ballesteros. (2023). The potential impacts of climate change on ex situ conservation options for recalcitrant-seeded species. *Frontiers in forests and Global change*.
- Ashley Subbiah, Syd Ramdhani, Norman W. Pammenter, Angus H.H. Macdonald, Sershen. (2019) Towards understanding the incidence and evolutionary history of seed recalcitrance: An analytical review. *Perspectives in Plant Ecology, Evolution and Systematics*. Vol 37. 11-19,
- Corley, R. H. V., & Tinker, P. B. (2015). The oil palm. John Wiley & Sons.
- Farrant, J. M., Pammenter, N. W., & Berjak, P. (1993). Seed development in relation to desiccation tolerance: A comparison between desiccation-sensitive (recalcitrant) seeds of *Avicennia marina* and desiccation-tolerant types. *Seed Science Research*, 3(1), 1-13.
- Fenner, M., & Thompson, K. (2005). The ecology of seeds. Cambridge University Press.
- Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13(1), 201-228.
- Hugh W. Pritchard, Sershen, Fui Ying Tsan, Bin Wen, Ganesh K. Jaganathan, Geângelo Calvi, Valerie C. Pence, Efisio Mattana, Isolde D.K. Ferraz, Charlotte E. Seal. (2022) Regeneration in recalcitrant-seeded species and risks from climate change. *Plant Regeneration from Seeds*, Academic Press. 259-273.
- Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *American Naturalist*, 104(940), 501-528.
- Khatoon, H., Pant, A., Rai, J.P.N. (2017). Plant Adaptation to Recalcitrant Chemicals. In: Shukla, V., Kumar, S., Kumar, N. (eds) Plant Adaptation Strategies in Changing Environment. *Springer, Singapore*. https://doi.org/10.1007/978-981-10-6744-0_11
- Peres, C. A., & Baider, C. (1997). Seed dispersal, spatial distribution and population structure of Brazil-nut trees (*Bertholletia excelsa*) in southeastern Amazonia. *Journal of Tropical Ecology*, 13(4), 595-616.
- Probert, R. J. (2000). The role of temperature in the regulation of seed dormancy and germination. Seeds: The Ecology of Regeneration in Plant Communities, 261-292.
- Tweddle, J. C., Dickie, J. B., Baskin, C. C., & Baskin, J. M. (2003). Ecological aspects of seed desiccation sensitivity. *Journal of Ecology*, 91(2), 294-304.
- Walck, J. L., Hidayati, S. N., Dixon, K. W., Thompson, K., & Poschlod, P. (2011). Climate change and plant regeneration from seed. *Global Change Biology*, 17(6), 2145-2161.
- Whitmore, T. C. (1998). An introduction to tropical rain forests. Oxford University Press.