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Seed dormancy and germination strategies in critically endangered *Gymnocladus assamicus* ex P.C. kanjilal: implications for conservation and regeneration

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Abstract
Gymnocladus assamicus, a critically endangered leguminous tree native to Northeast India, faces significant regeneration challenges due to seed dormancy and adverse environmental conditions. The species exhibits physical dormancy caused by a hard, water-impermeable seed coat that hinders natural germination. Research indicates that mechanical scarification and hot water treatment are particularly effective in breaking seed dormancy and significantly enhancing germination rates. Sulfuric acid treatment has also shown promise under both laboratory and field conditions. In addition, seed priming and *in-vitro* propagation have emerged as viable techniques for species recovery and conservation. This review underscores the urgency of addressing external threats such as overexploitation, habitat degradation and limited seed dispersal, all of which further impede natural regeneration. Developing effective germination protocols and mitigating ecological pressures are crucial for the long-term survival of the species. The study presents integrated strategies to improve germination success and advocates for sustainable conservation practices, including regulated harvesting and habitat protection, to ensure the preservation of this endangered tree.

Keywords: *Gymnocladus assamicus*, seed dormancy, hot water treatment, seed priming, *In vitro* regeneration

Introduction

Gymnocladus assamicus - An Endemic Plant of Arunachal Pradesh

The Himalayan soap pod tree, scientifically known as *Gymnocladus assamicus* Kanj. ex P.C. Kanjilal, is a critically endangered species belonging to the family Leguminosae and is endemic to Northeast India (Choudhury *et al*., 2007a) [15]. It has been identified as a priority species under India's National Recovery Programme for conservation (Ganeshaiah, 2005) [21]. The species is classified under the subfamily Caesalpinioideae (DC., 1825) and locally referred to as *Minagmose* or *Dikang* by the Adi tribe, (Bharali *et al*., 2017) [9]. According to the Missouri Botanical Garden (Choudhury and Khan, 2019) [12], the genus *Gymnocladus* comprises six officially recognized species with a global distribution. *G. dioicus* (L.) K. Koch is native to North America, *G. arabicus* Lam. is found in Egypt and *G. angustifolius* (Gagnep.) J.E. Vidal occurs in Vietnam. The remaining three species *viz*. *G. chinensis* Baill., *G. assamicus* Kanj. ex P.C. Kanjilal and *G. burmanicus* C.E. Parkinson are primarily distributed in the tri-junction region of India, China and Myanmar. However, according to the World Database of Legumes (Bisby *et al*., 2005) [10], the genus consists of five taxonomically recognized species, excluding *G. arabicus* and is primarily distributed across Eastern North America and Eastern Asia.

It is believed that the genus originated in Eastern Asia during the Eocene epoch of the Paleogene period and later migrated to North America via the Bering land bridge (Sanjappa, 2002) [38]. In India, the distribution of *G. assamicus* and *G. chinensis* is restricted to the northeastern states (Schnabel *et al*., 2003) [39]. The tree typically remains leafless for approximately two months, from January to February and begins flowering in April. Mature pods persist on the tree until the following flowering season. Male trees usually bloom from late March to early April, while trees bearing hermaphroditic flowers reach full bloom in April (Choudhury *et al*., 2014) [17]. The mature pods of *G. assamicus* yield a soap-like substance that is traditionally used by local tribal communities for household purposes and religious rituals (Choudhury *et al*., 2007c) [14].

Distribution

G. assamicus remains poorly studied due to its extremely limited natural population. The species was first discovered in the Khasi Hills of Meghalaya (then part of undivided Assam) in 1934 (Kanjilal *et al*., 1938) [28] and remained unrecorded for decades, except for two isolated reports from Arunachal Pradesh and Nagaland in Northeast India. It was subsequently rediscovered in the West Khasi Hills district of Meghalaya (Venugopal and Pamidimarri, 2015) [42].

Between 2004 and 2007, Choudhury and his team conducted extensive field surveys across Arunachal Pradesh to assess the distribution of *G. assamicus*, documenting individual trees at each site. Using the quadrat method, they analyzed the associated vegetation to understand the species community structure. Based on preliminary observations, several study plots were selected, considering both the presence of *G. assamicus* populations and ease of geographic access. Nine such plots were identified and three representative sites *viz*. Changfu Moon, Dambla Village and Moishing Village were chosen for in depth analysis of vegetation and microclimatic conditions. Across these nine sites, located in the Dirang Circle of West Kameng District, Arunachal Pradesh, a total of 28 mature *G. assamicus* trees were recorded. Documenting populations of such rare and endangered species is crucial for biodiversity conservation, as it aids in evaluating their conservation status and in developing effective strategies for both *in situ* and *ex situ* preservation.

Species Morphology

G. assamicus is a medium to large deciduous tree that typically reaches a height of 15 to 17 m. It has a horizontally spreading trunk with branches that grow upwards. The bark is greyish-brown, featuring a corky outer layer with a reticulate pattern and parallel furrows. The leaves are compound, bipinnate and alternately arranged, measuring approximately 38–45 cm in length and 20–25 cm in width. Each leaf has a swollen base with indistinct glandules and comprises 10–12 pairs of pinnae, which are either opposite or slightly sub-opposite. These pinnae measure about 10–22 cm long and 6–8 cm wide, each bearing 15–20 leaflets. The leaflets are short-stalked and arranged alternately or sub-oppositely, measuring approximately 2–2.3 cm in length and 0.64–0.67 cm in width. They are oblong to ovate-oblong in shape with minutely pointed tips. The upper surface is nearly smooth, while the lower surface displays fine brown pubescence along the midrib. Each leaflet has 5–8 pairs of primary lateral veins, which are slightly raised above and recessed below. The inflorescence is a terminal raceme with fine pubescence. Male inflorescences are relatively larger, measuring about 13–16 cm long and 5–6 cm wide, with nearly whorled lateral branches bearing 15–20 flowering nodes. In contrast, hermaphrodite inflorescences are smaller, ranging from 4–6 cm in length and 5–6 cm in width. Both male and bisexual flowers are small, tubular, violet-colored and lack fragrance (Choudhury, 2008) [18]. The fruit is a pod, typically 10–16 cm long and 2.5–4 cm wide, containing 4 to 8 small seeds. The seeds are ovoid to subglobose, measuring about 14–15 mm by 15–17 mm and are encased in an extremely hard, black testa. The mesocarp is highly saponaceous, while the pericarp is smooth and fleshy. Upon maturity, the pods remain fleshy and emit a strong, persistent pungent odor. The radicle is relatively small and grows in an erect manner. The wood of *G. assamicus* is moderately hard with a yellowish-white hue, while the pith is soft and spongy, particularly in young shoots (Choudhury, 2008) [18].

Surface Morphology and Biochemistry of G. Assamicus Seeds

Seed germination is primarily regulated by the hardness and impermeability of the seed coat (testa), which induces dormancy and protects the embryo from unfavorable physical and biological influences in adverse environmental conditions (Debeaujon *et al*., 2000) [19]. Many plant species employ seed coat-imposed dormancy as a survival mechanism. Khan *et al*. (1997) [29] established a correlation between seed coat color and dormancy, attributing it to the presence of phenolic compounds. Their study on proso millet (*Panicum miliaceum* L.) revealed that darker seeds had thicker seed coats, resulting in slower water absorption and delayed germination. This adaptation minimized imbibition-related damage and enhanced seed longevity in the soil compared to lighter-colored seeds. The seeds of *G. assamicus* are deep black and likely possess similar chemical properties that inhibit water uptake and delay germination. Beneath the testa lies a stony endodermal layer that transforms into a mucilaginous texture upon imbibition. Surface morphology studies indicate that the hard, impermeable testa serves as the principal barrier to water penetration, thereby retarding the germination process. Hard seed dormancy and delayed germination vary among species and are typically associated with restricted water and gas exchange, the presence of chemical inhibitors, limitations in the release of these inhibitors from the embryo, reduced light permeability and mechanical resistance to embryo expansion (Bewley and Black, 2012) [7]. This type of dormancy is especially prevalent in legumes (Smýkal *et al*., 2014) [40]. However, unlike most legumes, *G. assamicus* thrives in temperate climates (Menon *et al*., 2010) [34] and may have evolved seed coat-imposed dormancy as an adaptation to harsh environmental conditions, facilitating the maintenance of a persistent soil seed bank. Such dormancy mechanisms are often responsible for low germination rates in legumes.

The extremely hard seed coat of mature, dry *G. assamicus* seeds is primarily attributed to the presence of thickened galactomannan or mannan polymers in the endosperm cell walls. Gong *et al*. (2005) [22] reported that embryo emergence in hard seeded species is influenced by the structural characteristics of the micropylar endosperm cell walls, which contain hydrophilic galactomannans that become mucilaginous upon imbibition and enzymatic hydrolysis. Observations of *G. assamicus* seeds indicate the development of mucilaginous coatings after imbibition, supporting the possible presence of galactomannan or mannan polymers in the endosperm (Choudhury *et al*., 2009) [16]. In plant families such as Leguminosae and Malvaceae, hard seed coats with specialized palisade or malpighian layers are known to regulate water uptake prior to germination. These coats become permeable only when a specific region of the malpighian layer is disrupted or split (Baskin *et al*., 2000) [4]. Scanning Electron Microscopy (SEM) studies have shown that the seed coat of *G. assamicus* comprises a continuous layer of densely packed palisade cells (Choudhury *et al*., 2009) [16].

Reproductive Ecology

Understanding the reproductive ecology of rare or endangered plant species is crucial for determining whether the challenges to their survival stem from intrinsic biological constraints or extrinsic environmental factors. Many plant species rely on insects for pollination and animals for seed dispersal. Pollen limitation caused by insufficient pollen availability or a lack of effective pollinators can severely reduce seed production (Pearse *et al*., 2015) [37]. *G. assamicus* is characterized by a limited number of reproductively active individuals, fragmented populations, and a low proportion of seedlings and saplings compared to mature trees (Choudhury *et al*., 2007c) [14]. In addition to biotic limitations, abiotic factors such as climate and soil conditions can directly impact flowering and fruit set. The breeding systems within the genus *Gymnocladus* are known to be complex, ranging from polygamous to dioecious or unisexual floral arrangements. These breeding strategies play a critical role in shaping population dynamics and evolutionary trajectories (Charlesworth, 2006) [11]. Extensive field observations have identified both fruiting and non-fruiting mature *G. assamicus* individuals in their native habitats. However, it remains unclear whether this variability is due to irregular flowering and fruiting cycles or anthropogenic disturbances, such as branch harvesting for firewood. Historically, there has been a lack of detailed information regarding the floral biology, sexual expression, and breeding system of *G. assamicus*, which has limited efforts to develop effective conservation strategies.

Ethno-Botanical and Medicinal Utilizations

G. assamicus holds considerable cultural and practical significance for the Monpa tribes of Arunachal Pradesh due to its wide range of ethnobotanical uses (Choudhury *et al*., 2007b) [13]. Local communities are well-versed in identifying the locations of mature trees and typically collect fully ripened pods either directly from the branches or from the ground. Large-scale harvesting of mature pods is common, with excess pods often stored for extended periods, sometimes lasting up to four to five years. In some cases, pods are collected by cutting tree branches, which results in severe damage to the trees. Among the Monpa people, mature pods are regarded as sacred and are frequently exchanged as gifts. Buddhist monks also accept these pods as religious offerings. The pods are primarily used in monastery rituals and for various domestic purposes, including washing clothes, hands, and utensils. Elder members of the community often prefer using the pods for bathing in place of commercial soaps (Choudhury *et al*., 2007b) [13].

Scientific investigations have revealed that methanolic extracts from *Gymnocladus* pods exhibit anti-HIV properties (Konoshima *et al*., 1995) [31] and specific saponins isolated from the plant have been shown to inhibit HIV replication (Lee and Morris-Natschke, 1999) [32]. In Arunachal Pradesh, forest dwellers also prepare a pod-based decoction to protect domestic animals from leeches and insect bites. Additionally, local communities consume roasted seeds or use powdered seeds to prepare traditional beverages. Extracts from various parts of *G. assamicus* have also demonstrated notable antioxidant activity (Gupta *et al*., 2013) [25].

Population Structure, Regeneration Status and Modes of Regeneration

Choudhury *et al*. (2007c) [14] observed that mature trees of *G. assamicus* outnumbered saplings and seedlings at all surveyed sites except Morshing. The highest numbers of seedlings (160) and saplings (11) were recorded at Morshing in Arunachal Pradesh, whereas in Dambla, reported only a single sapling. Approximately 55% of the seedlings were located within a 4–8 m radius of the mother tree, while saplings were found only between 8–12 m. No regeneration was observed beyond 12 m, indicating limited seed dispersal as a major constraint.

The study attributed the poor regeneration in Changfu Moon and Dambla to anthropogenic pressures such as overharvesting, habitat disturbance and grazing primarily due to their proximity to human settlements. In contrast, the relatively undisturbed environment at Moishing likely facilitated better regeneration outcomes.

G. assamicus regenerates exclusively through seeds. Freshly collected seeds exhibited a germination rate of 42% and retained a viability of 6.7% even after 12 months of storage under standard laboratory conditions. However, seed viability declines progressively with time. Germination usually begins within 10 to 12 days after sowing, although in some cases, seeds have been observed to germinate even after 12 to 13 months (Choudhury *et al*., 2007c) [14].

Seed Dormancy

Seed dormancy and germination are fundamental characteristics that play a pivotal role in plant life history strategies. Dormancy refers to the inability of viable seeds to germinate even under favorable environmental conditions. This adaptive trait serves as a protective mechanism, delaying germination until conditions are optimal for seedling survival and growth. Over evolutionary timescales, seed dormancy has proven to be a critical survival strategy, significantly influencing plant adaptation, persistence, and distribution.

In many plant species, delayed germination results from water-impermeable seed coats that restrict water uptake. Without pretreatment, seeds with hard coats often exhibit irregular and delayed germination, sometimes persisting in the soil seed bank for years. To overcome such dormancy, researchers apply natural or artificial dormancy-breaking techniques to enhance germination (Baskin and Baskin, 1998; van Assche *et al*., 2003) [3, 41].

Seed dormancy is broadly classified into five major types: physiological dormancy (PD), morphological dormancy (MD), morphophysiological dormancy (MPD), physical dormancy (PY), and combinational dormancy (PY + PD) (Baskin and Baskin, 1998) [3]. Of these, physical dormancy is common across 15 angiosperm families (Baskin *et al*., 2000) [4], particularly within the three subfamilies of Fabaceae *viz*. Caesalpinoideae, Mimosoideae and Papilionoideae (Baskin and Baskin, 1998) [3]. This form of dormancy is caused by one or more layers of impermeable palisade cells in the seed or fruit coat, which prevent water absorption (Baskin *et al*., 2000) [4].

The morphological and physiological traits of the seed and embryo play a decisive role in determining germination behavior (Bewley *et al*., 2013) [8]. Emerging research also highlights the importance of epigenetic regulation in modulating seed dormancy and germination (Nonogaki, 2017) [36]. While dormancy imposed by the seed coat can hinder natural regeneration, it can be effectively broken using techniques such as mechanical scarification, hot water treatment, dry heat exposure, acid scarification or other chemical methods.

Successful germination is governed by the complex interplay between a seed's physical state, physiological readiness and its surrounding microenvironment. Understanding the ecological factors influencing seed germination and seedling establishment is essential for gaining insight into plant recruitment and succession, and for informing conservation strategies, particularly in the context of tropical forest restoration. Facilitating timely and site-specific germination is crucial for the regeneration and *ex situ* conservation of endangered species (Herranz *et al*., 2010) [26].

Thick seed coats may have evolved as a defense against insect oviposition, while the presence of phenolic compounds offers protection against microbial attack (Mohamed-Yasseen *et al*., 1994) [35]. In *G. assamicus*, seed dormancy caused by a hard seed coat represents a major intrinsic barrier to germination, often resulting in unsuccessful germination on the forest floor and poor seedling establishment. Despite the ecological and ethnobotanical importance of *G. assamicus*, research on its seed biology remains limited, with insufficient data on dormancy mechanisms, storage behavior and germination ecology (Choudhury *et al*., 2009) [16].

Breaking Seed Dormancy

Research has made significant progress in understanding seed germination and dormancy-breaking techniques, particularly in legumes (Baskin and Baskin, 2004) [5]. In the case of *G. assamicus*, pre-treatments such as mechanical scarification, hot water immersion and chemical scarification with sulfuric acid have been found to enhance germination rates to varying extents. Boiling water treatment for two minutes nearly doubled the germination rate, increasing it to 80% compared to 42% in untreated seeds. Other approaches, including mechanical and chemical scarification, also facilitated faster and more uniform germination compared to untreated seeds (Choudhury *et al*., 2009) [16]. Dormancy in *G. assamicus* is primarily of the physical (PY) type, resulting from water-impermeable layers of palisade cells in the seed coat (Baskin and Baskin, 2003) [6]. Similar findings have been reported in other legume species.

Choudhury *et al*. (2009) [16] conducted an experiment demonstrating that fresh seeds of *G. assamicus* exhibited high viability and germination rates. Tetrazolium (TTZ) tests conducted at zero months indicated 90.00% (±1.50) seed viability, whereas only 41.75% (±1.70) of the seeds germinated during the same period. A significant variation was observed between seed viability and germination percentages across different storage durations. Pre-treatments effectively enhanced germination rates, with untreated seeds showing approximately 42% germination. Mechanical scarification and hot water treatment significantly increased germination ($P < 0.002$), reaching 65-80%. The most notable improvements were observed with mechanical scarification ($F = 126.328$, $P < 0.001$) and hot water treatment for one minute ($F = 258.283$, $P < 0.001$) and two minutes ($F = 190.582$, $P < 0.001$). Additionally, chemical scarification with sulfuric acid for 40 minutes also led to a significant increase in germination ($F = 12.302$, $P < 0.05$). Boiling water treatment proved to be the most effective method for enhancing germination compared to other approaches. This technique also significantly improved seed germination in other legume species. However, some legumes have shown limited responsiveness to boiling water treatments. In natural habitats, *G. assamicus* seeds are sometimes consumed by grazing animals and passage through the digestive tract can aid germination, contributing to regeneration. Laboratory pre-treatments simulate the natural dormancy-breaking mechanisms of *G. assamicus*. The slightly acidic soil at the study site may gradually soften the seed coat, while chewing and rumination by animals can scarify the seeds, improving water absorption and germination. Boiling water treatment is particularly recommended due to its affordability and simplicity.

Seed Priming

Besides boiling, seed priming is a highly effective method for improving seed germination under challenging conditions. It is a traditional and successful approach that enhances seed germination, growth and resilience to both abiotic and biotic stressors (Lutts *et al*., 2016) [33]. Seed germination consists of three distinct phases: imbibition, followed by the activation of metabolism, and finally, cell elongation and radicle protrusion. The initial phases of seed germination, namely imbibition and metabolism activation, can be reversed without affecting the seed's ability to germinate, providing the foundation for seed priming.

In seed priming, pre-sowing treatments are applied to regulate the seed's hydration levels, allowing pre-germinative metabolic processes to occur without triggering radicle emergence. This process not only enhances germination but also activates plant defense mechanisms (Hussain *et al*., 2015; Anderson, 2015) [27, 1]. Primed seeds exhibit higher and more synchronized germination due to several factors such as a shorter lag time during imbibition, activation of enzymes, accumulation of metabolites that enhance germination, metabolic repair during imbibition and osmotic adjustments.

Several seed priming methods, such as hydropriming, osmopriming, chemical priming, nutrient priming, hormonal priming and redox priming, are used across various environmental conditions to enhance tolerance to abiotic and biotic stresses in field and vegetable crops. Growing evidence suggests that primed plants activate cellular defense mechanisms, providing them with increased resilience to subsequent exposure to both biotic and abiotic stresses in the field (Khan *et al*., 2015) [30]. Combining priming with plant growth regulators, such as gibberellic acid, can improve yields, accelerate early growth and offer protection against environmental stress (Gupta and Chakrabarty, 2013) [23]. Gibberellic acid is particularly noted for promoting plant growth and development.

***In vitro* Regeneration of G. Assamicus**

The natural recruitment of *G. assamicus* seedlings in their native habitat is very limited. Restoring the declining population of *G. assamicus* may only be feasible through the application of plant tissue culture techniques. Although leguminous tree species are generally considered difficult to propagate through tissue culture (Anis *et al*., 2005) [2], successful protocols have been developed for several key species. These include *Dalbergia latifolia*, *D. sissoo*, *Sesbania sesban*, *Pterocarpus marsupium* and *Gymnocladus dioicus*. With the exception of research on its ecology (Choudhury *et al*., 2007a, b) [15, 13] and seed biology (Choudhury *et al*., 2009) [16], *G. assamicus* remains largely un-investigated in terms of its morphogenic capabilities. Gupta *et al*. (2013) [24] conducted a study on the *In vitro* regeneration of *G. assamicus*, where they developed a straightforward, reliable and efficient regeneration system using nodal explants. The study found that the highest rate of multiple shoot induction in *G. assamicus* was achieved by using MS basal medium supplemented with benzyl adenine (BA) combined with adenine sulphate (ADS). Additionally, multiple shoot production was enhanced during the second subculture of harvested shoots in optimal medium. The best rooting results were obtained with half-strength MS medium supplemented with indole-3-acetic acid (IAA), and plantlets were successfully acclimatized. This efficient and reproducible protocol offers a viable method for reintroducing this critically endangered species, *G. assamicus*, into its natural habitat.

Conservation Status

The population of *G. assamicus* is extremely small, with fewer than fifty reproducing individuals, which verifies that the species should be classified as "critically endangered" (Frankel *et al*., 1995) [20]. Therefore, implementing active protection measures and continuously monitoring the existing populations should be the top priority. Due to the limited number of mature trees, all populations of the species must be preserved. Rare and endangered species often occur in small populations, which are prone to bottlenecks. To address this, a short-term conservation goal should focus on maintaining or restoring population vigor by strategically managing the remaining genetic diversity to counteract the effects of inbreeding.

The demographic characteristics of *G. assamicus* indicate that seedlings and saplings do not adequately support natural regeneration. Therefore, artificially introducing the species into suitable ecological habitats could be a viable option for restoring its populations. A supplementary regeneration strategy, involving the introduction of nursery-grown seedlings, may help combat declining populations by compensating for the lack of natural regeneration. Key threats to *G. assamicus* include habitat degradation and overharvesting of mature pods. Raising awareness among local communities, preserving existing reproductive individuals, and implementing sustainable pod harvesting practices are crucial for successful preservation. Government agencies, NGOs, and conservation organizations can play a significant role by developing, distributing, and planting nursery-grown seedlings in appropriate habitats. Planting seedlings in home gardens, agricultural lands, or roadside plantations is also recommended, as these locations are generally protected, ensuring better growth and survival of the seedlings (Choudhury *et al*., 2007a) [15].

Summary and Conclusion

The morphology of the seed surface shows that the hard and impermeable testa acts as a barrier to imbibition, thereby hindering germination. Various experiments have demonstrated that the dormancy caused by the seed coat's water impermeability in *G. assamicus* can be overcome through pretreatment methods such as mechanical scarification, boiling water, or acid treatments. Notably, a 2-minute boiling water treatment significantly improved germination compared to other methods. These relatively simple and inexpensive techniques require minimal skill and can be effectively applied for large-scale seedling production and restoration efforts. The laboratory pretreatments mimic the natural processes by which *G. assamicus* seeds break dormancy. It has been noted that humans harvest large quantities of pods, leaving few or no pods/seeds for wild animals. These cumulative factors likely contribute significantly to the poor dispersal, germination, and natural regeneration of the tree. For regeneration and conservation strategies, seed priming and tissue culture methods are highly recommended, as they significantly enhance germination and break seed dormancy. Through *In vitro* propagation and mass propagation, we can regenerate the plant on a large scale. It is necessary to conserve this critically endangered plant as it has many potential applications for mankind. Currently, this plant is experiencing both biotic and abiotic stress, and thus, it is crucial to develop efficient protocols to resist such stressors effectively. Additionally, it is essential to develop effective protocols for the efficient germination and regeneration of this plant, as very few research studies have been conducted on the germination and conservation of *G. assamicus*.

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