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**Review Paper**

# Overcoming Germination Barriers in Teak (*Tectona grandis*) by Exploring Drupe Anatomy

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**ABSTRACT:** The teak tree is being grown worldwide for its most valuable timber. The drupe is a compound seed structure that contains 0–4 seeds. The seeds are inside the quadrilocular, hard endocarp known as the stone, surrounded by a thin exocarp and a thick corky mesocarp. The indehiscent drupes are sown as such in the nursery to raise the seedlings. Although some of the drupes initiate germination within ten days of sowing, it may take up to one year to germinate the entire lot. Only 25–35 percent of seeds germinate within 10–90 days of sowing. The poor, erratic, and sporadic germination leads to the production of highly heterogeneous seedlings. Continuous research has been conducted over the past century to standardize appropriate pre-sowing treatments. Four treatments have been experimented *with:* alternate soaking and drying, with and without active ingredients, removal of the exocarp and mesocarp, and heat treatment. Most studies used alternate soaking and drying treatments, followed by removing the exocarp and mesocarp. Thus, most researchers believed that the pericarp of the drupe was the primary factor affecting germination. Many reports also claimed that seeds from older drupes registered better seed germination than those from fresh drupes. Other than drupe characteristics, factors related to seed *per se* (*e.g.*, seed dormancy, seed viability, seed vigour) may also influence seed germination of teak drupes. Based on an extensive review of research conducted on drupe germination, the candidate factors that may affect the seed germination of teak drupes have been adjudged and subjected to comprehensive analysis. Against this back drop, it is concluded that an appropriate drupe treatment protocol to overcome the barriers of teak drupe germination requires a 4-step protocol: i) Size grading of the drupes with sieves of > 9 mm diameter to remove the empty drupes in a seed lot to a certain extent ii) Removal of the mesocarp of the drupes, either by mechanical or biological methods, to overcome mechanical dormancy iii) Exposure of endocarps (after removal of mesocarp) to dry heat for an optimum temperature and duration, to facilitate the 'after-ripening' of the embryo and finally iv) Priming of teak endocarps to enhance the seed vigour status.

**Keywords:** Teak, Seed germination, Fruit structure, Mechanical seed dormancy, After-ripening, Dormancy breaking

## INTRODUCTION

Teak (*Tectona grandis* Linn. f.) is one of the world's most valuable and widely planted timber-yielding species. Tectona *is* derived from the Portuguese word *teca*, a derivative of the Greek word *tekton,* which means 'carpenter,' and g*randis*, in Latin, means large [1]. This tree species belongs to the family Lamiaceae (previously under Verbenaceae), is commonly called teak or Indian oak, or Bangkok teak. Teak wood is considered one of the tropics' finest and most economically valuable timbers. The tight grain, golden colour, and high oil content of the wood lay the foundation for the aesthetic appeal of teak. The wood demonstrates high resistance to termite damage due to sesquiterpenes [2]. The wood is of lower weight, has higher tensile strength, and is durable; therefore, it is widely used in shipbuilding, fine furniture, and decorative objects. Global areas of planted teak forests declined from 5.7 million ha. in 2000 [3] to 4.3 million ha. in 2010 [4] of which 83% are in Asia, 11% in Africa, and 6% in tropical America.

This typically deciduous tree is indigenous to India and Southeast Asia region, and its natural distribution is found in tropical or subtropical regions [5, 6], where it grows up to a height of 45 m [7] (Fig. 1). Teak grows best in moist tropical climates with a pronounced dry season (3-6 months), even though it tolerates a range of climates [8]. Therefore, it has been introduced to Indonesia, Sri Lanka, Vietnam, Malaysia, East and West Africa (Tanzania, Ivory

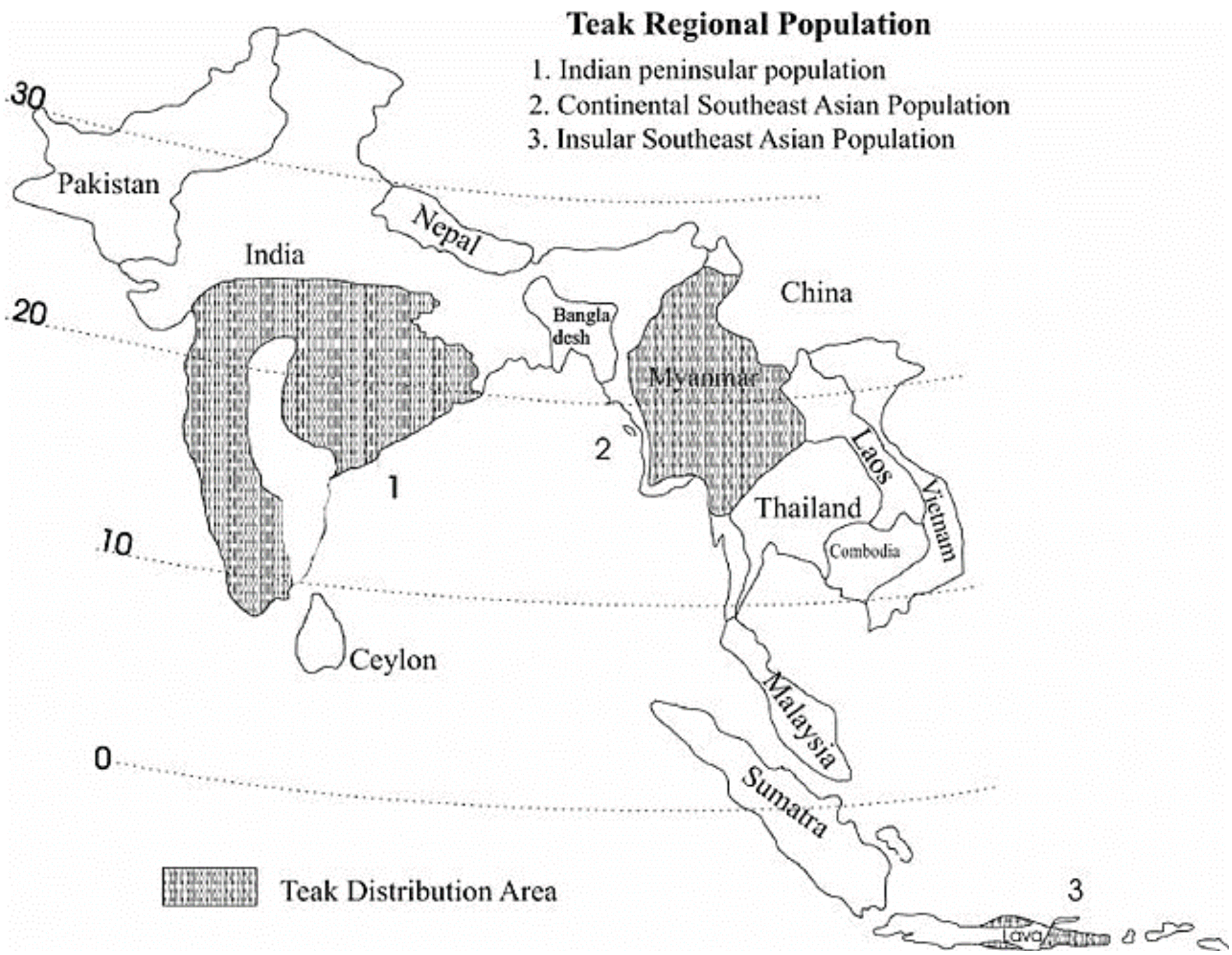


**Figure 1.** Natural distribution of teak across the globe [66]

Coast, Nigeria, Ghana, and Togo), The Caribbean (Cuba, Puerto Rico, Panama, Trinidad, and Tobago), South America Brazil and Central America (Costa Rica) [9, 10].

Teak has been cultivated for timber production for over 500 years [11]. Although the techniques such as rooting of coppice [12] and forced softwood shoots [13] have shown promise for exploitation at the nursery level, the popular method of propagating teak is only through fruits called ‘drupes.’ However, irregular, protracted, sporadic, and meager seed germination rates are a significant problem for the teak plantation industry.

The teak tree starts to flower after six years, but profusely only after 15 years [14]. Although teak flowers abundantly, the fruit set is only about 1-2% since the flowering period coincides with the monsoon, leading to hampered pollination. Besides the low flower-to-fruit ratio, teak has a meager ovule-to-seed ratio [14]. Teak flowering occurs between June and September, and it takes 150 to 200 days to complete the fruit development and maturation process. The fruit, called ‘drupes,’ ripen on the mother tree between November and January (40), and the matured drupes fall gradually over 3-4 months during the dry season [15]. Some drupes may remain hanging on the tree throughout the summer.

Teak is a light-demanding species. The natural regeneration of teak is immensely influenced by annual rainfall, competition from the undergrowth, and the occurrence of forest fires. Based on these aspects, teak forests in India have been classified into five categories [16, 17] (Table 1).

It is thus evident that forest fire has a significant and positive correlation with the natural regeneration of teak, except in very dry teak forests, wherein the deficient annual rainfall, compounded with annual fires, has

**Table 1.** Classification of teak forests in India based on occurrence of undergrowth and forest fire

| Sl. No. | Category of Teak Forest | Annual Rainfall (mm) | Characteristics | Natural Regeneration |
|---|---|---|---|---|
| 1 | Very Moist | >2500 | 10 % teak, dense undergrowth, no forest fire | Very little regeneration |
| 2 | Moist | 1600-2500 | 10-25 % teak, dense undergrowth, no forest fire | Fair but patchy regeneration |
| 3 | Semi-moist | 1300-1600 | 20-60 % teak, moderate undergrowth, occasional fires | Fairly adequate regeneration |
| 4 | Dry | 900-1300 | 50 % to almost pure teak stand, Light undergrowth, frequent fires | Group natural regeneration |
| 5 | Very dry | <900 | Medium population of teak, scanty undergrowth, annual fires | No natural regeneration |

negatively affected the natural regeneration. Forest fire favours natural teak in at least two ways [4]. Fire helps to remove the outer layers of teak drupes, such as the exocarp and mesocarp, and leaves behind the naked endocarp ready for germination. However, the seeds inside the drupes are not affected by fire because of the protective pericarp. After forest fires, the naked endocarps left behind in the fire-cleared forest floor show better potential for germination and unhindered seedling establishment. Further, removing undergrowth favours the germination and growth of teak seedlings due to the availability of more sunlight and the avoidance of competition. However, the sustained growth of the teak seedlings is threatened by fire or drought, which may occur in the following seasons. Teak seedlings usually become fire-resistant only after eight years, when they develop the insulating bark [4]. Under such circumstances, the teak drupe germination behaviour could have evolved as a precautionary measure to enable sporadic and protracted germination during the monsoon rains, where water availability is ensured, risk of fire has been avoided, and a conducive atmosphere for growth has been created [18]. Teak drupe germination behaviour is an essential tool to guarantee the continuous recruitment of teak seedlings, ensuring sustained natural regeneration in the dry forest ecosystem.

Although teak drupe germination behavior favours continuous recruitment of the teak seedlings to ensure sustained natural regeneration under a hostile dry forest ecosystem, nursery growers are often intimidated and discouraged by the dormancy behavior of teak drupes. In order to enhance the seed germination potential of teak drupes, continuous research has been carried out for more than a century. Even as early as 1921, many attempts had been made to improve the germination of teak seed; unfortunately, to date, a breakthrough has yet to be made [19].

Under all these contexts mentioned above, this review aims to highlight the biological barriers associated with the germination of teak drupes, which shall form the basis for developing an appropriate drupe treatment to ensure a quick, synchronous, and higher percentage of teak germination.

## I. Fruit and seed structure

The 5 to 20 mm globose-shaped yellowish or brownish fruit of teak is a dry drupe classified as a compound seed structure [20] (Fig. 2). The dry drupe consists of a thin pubescent exocarp and a thick leathery, spongy, and corky mesocarp surrounding the hard, woody endocarp called ‘stone’ (Fig. 3). The stone’s surface is rough, with protuberances and ridges, which cause an almost complete integration with the mesocarp. The whole structure is loosely enclosed within a membranous epicarp originating from the flower’s calyx. The fruit has two circular pores of approximately 1 mm diameter in the proximal end, where the fruit connects to the pedicel. The two proximal pores penetrated only up to a central cavity associated with the placental axis that has no direct connection with the loculi where the seeds are placed (Fig. 4) [21]. The endocarp is quadrilocular. Each locule possesses a ‘valve’ covering the seeds inside the locule; when the ‘valve’ is removed, it fully exposes the seed

**Figure 2.** Mature teak drupes

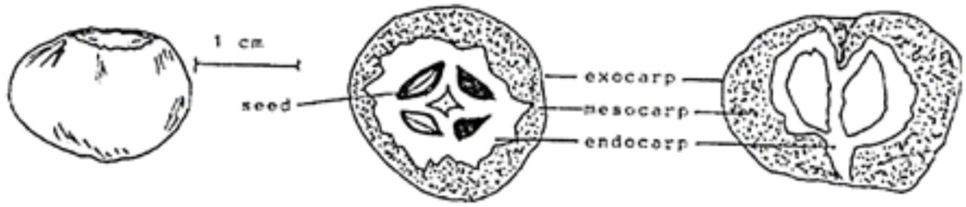


**Figure 3.** Compound seed structure of teak drupes [39]

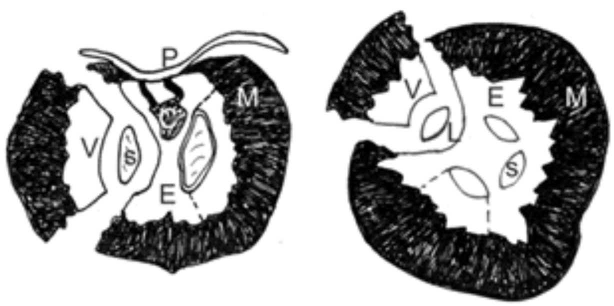


**Figure 4.** Longitudinal and transverse sections of a teak fruit showing features: central cavity, E: endocarp, M: mesocarp, P: pore, S: seed, V: valve. Sutures connecting valves to endocarp is shown by broken line [74]

and another half of the locule (Fig. 2). The number of drupes per kilogram varies from 1150 to 2800 / kg.

The drupe may contain fully or partially formed seeds, sometimes only the testa, or no seed. Therefore, a teak drupe may contain 0-4 seeds (Fig. 3), although one seed is the most common [22]. The presence of seeds in all four seed chambers is a rare phenomenon. The fully developed seeds are pyriform in shape and exalbuminous. Various authors have reported a high percentage of emptiness: 34% [23], 30.8% [24], 33 % [25], 13 to 86 % [26], and 23 % [14]. The average number of fruits with one, two, three, four, and empty fruits was found to vary among the reports (Table 2). The variation may be attributed to drupe size (31; 59) or provenance [27]. The provenance studies conducted by collecting teak drupes from 30 sources spread over India, Bangladesh, and Laos, and studied the seed filling percentage [27]. He recorded an average percentage of 37, 43.9, 15.3, 3.4, and 0.5 drupes in empty, one, two, three, and four-seeded drupes, respectively. The highest filling was observed in Siruvani, Nilambur, and Parambikulam (India) (32.27 %), while the lowest was observed in Chittagong (Bangladesh) (12.35 %). The emptiness varied from 19.2 % (Nilambur, India) to 70.8 % (Kalakkad, India). The Nilambur (48.1%), Konni (23.28%), Tura (38.5%), and Bagafa (25.5%) sources exhibited a higher germination percentage. The sources like Tarai (0.8%), Dehradun (0.3%), Kariar Road (0.75%) and Wimberligunj (0.50%), and Sampangi (0.50%) recorded poor germination.

The teak drupe may vary from 5 mm to 20 mm in diameter. However, the effect of drupe size on seed germination was reported to be limited. Drupes that belonged to the size category of > 9.0 mm diameter recorded higher germination potential [28, 29].

### II. Germination behaviour of teak drupes

The teak seeds cannot be easily separated from the indehiscent quadrilocular dry drupes with a hard endocarp. Therefore, the teak drupes are sown in the nursery as such. Teak drupes initiate germination from 10 days of sowing, but continue germinating for months together. It has been widely reported that 25-35 percent of teak seeds germinate 10-90 days after sowing, while sporadic germination may occur several years after sowing [23, 30, 31, 32]. The presowing seed treatment of subjecting the drupes to alternate soaking and drying

**Table 2.** Variations in seed filling proportion in teak drupes

| S. No. | Percentage of fruits: Empty drupes (%) | One seeded drupes(%) | Two seeded drupes (%) | Three seeded drupes (%) | Four seeded drupes (%) | Reference |
|---|---|---|---|---|---|---|
| 1 | 34 | 44 | 16 | 4 | 2 | [13] |
| 2 | 37 | 43.9 | 15.3 | 3.4 | 0.5 | [73] |
| 3 | 0 | 42 | 33 | 22 | 10 | [3] |
| 4 | 39 | 54 | 4 | 0 | 0 | [59] |

six times (3 days) and sowing in moist sand, exposed to sunlight [20]. The optimum temperature for germination is 30°C. The first and final count of seed germination is fixed as 14 and 28 days after sowing, respectively. The dormancy period was reported as 1-2 years, whereas the storage period under ambient conditions was reported as two years.

The pattern of germination in teak drupes was closely observed [33]. He observed that the germination of imbibed seeds enclosed inside the teak drupes occurs once the 'valves' on the endocarp open. During germination, the endocarp cracks along the wall of the seed chamber [23]. He also observed that the opening of the fruits was noticed even if no seed was present in the respective chamber. He attributed it to the mechanical expansion and contraction of the endocarp at varying vapour pressure created during imbibition. The 'cracking along the wall of the seed chamber' during seed germination was because of lifting a valve-like structure covering the seed present in each locule of the quadrilocular drupe [21]. He described that germinating seeds emerged from the locule of the endocarp by pushing open the corresponding 'valve,' which eventually detached from the endocarp (Fig. 4). This phenomenon represented the 'post dispersal dehiscence' of teak fruits to release the germinating seeds through valves with the help of pre-formed sutures [21].

### III. Pre-sowing seed treatments to enhance germination potential

Teak being an economically significant tree, continuous attempts have been made to improve the germination of teak seed through pre-sowing treatments [19], but with slight improvement. The different types of treatments that have been attempted over the century by several researchers have been reviewed and presented under four categories , *viz.,* i) soaking without active ingredients, ii) soaking with active ingredients, iii) removal of exocarp, mesocarp, and endocarp, and iv) heat (Table 3).

**Table 3.** Details of treatments imposed on teak drupes to enhance seed germination potential

| Sl. No. | Recommended Treatments | Reference |
|---|---|---|
| **I.** | **Soaking and drying treatments without active ingredients** | |
| 1 | Soaking in a pond for 36 h + alternate soaking and drying for 2-3 weeks | [6] |
| 2 | Soaking for 2-3 days + alternate soaking and drying for several times | [86] |
| 3 | Soaking of 8-12 months stored seed in a stream for 72 h | [88] |
| 4 | Soaking in a running stream for 12 hours and drying in sun for 12 h. The process can be repeated for 1-2 weeks | [36] |
| 6 | Soaking in a stream for 96 h and drying for one week | [60] |
| 7 | Soaking for 2 days, drying for 1 day and repeating the procedure four times | [89] |
| **II.** | **Soaking and drying treatments with active ingredients** | |
| 8 | Soaking & Drying (5 days) + Soaking in $H_2O_2$ (1.5%) (12h) | [56] |
| 9 | Soaking & Drying (5 days) + Soaking in $KNO_3$ (4.5 %) (12h) | [57] |
| 10 | Soaking in $H_2SO_4$ (1h) + $KNO_3$ 1% (48h) | [51] |
| 11 | Soaking & Drying (5 days) + Soaking in$KNO_3$ (2 %) (12h) | [58] |
| 12 | Splitting of drupe in micropylar end +soaking in $GA_3$ (20 ppm) (6 days) | [33] |
| 13 | Soaking & Drying (5 days) + Soaking in $CaOCl_{2-}$ 6% (12h) | [54] |
| 14 | Soaking of seeds in running water (24h) | [63] |
| 15 | Soaking & Drying (5 days) + Soaking in Ca $(OH)_{2-}$ 6% (12h) | [55] |
| 16 | Soaking (24h) + Sun drying (24h) | [82] |
| 17 | Soaking (24 h)+ Sun drying (1 week) | [4] |
| **III.** | **Removal of exocarp and mesocarp** | |
| *a)* | *Manual removal* | |
| 18 | Pericarp removal enhanced germination compared to pericarp cracked, hot water and cold-water soaking treatments | [2] |
| 19 | Mechanical scarification + alternate soaking & drying (7 days) | [84] |
| 20 | Mechanical scarification (6 min) + Soaking in $GA_3$ 250 ppm (12 h) + humid incubation (3 days) | [80] |
| *b)* | *Biological removal* | |
| 21 | Complete consumption of exocarp (and mesocarp) of teak drupes by termite (white ant) within 10 days | [13] |
| 23 | Termite feeding of teak drupes | [16] |
| *c)* | *Fire* | |
| 25 | Burning dry grass over teak fruits is a long established pre germination treatment | [78] |
| **IV.** | **Heat** | |
| 26 | Dry-heating either at 50°C for 1-5 weeks or at 80°C for 48 h or at 110 º C for 12 h | [76] |
| 27 | Dry heating at 80! for 48 h | [39] |
| 28 | Oven heating at $80^{0\ C}$ (6 h) | [75] |

The above studies reveal that among the four categories of treatments, 'alternate soaking and drying' with or without active ingredients have been predominantly recommended by many researchers. Although chemicals such as thiourea, $H_2O_2$, $KNO_3$, $CaOCl_2$, and Ca $(OH)_2$ have been recommended in various studies, the germination improvement obtained by these treatments has not exceeded 50 percent, similar to that of 'soaking and drying' treatments. It is, therefore, inferred that the mode of action of the treatments was only to facilitate the 'softening' of the exocarp, mesocarp, and endocarp which surround the seed [21]. The third category of treatment, *i.e.,* removal of these parts through mechanical methods, biological treatments, or fire, has also been shown to improve the seed germination performance of teak drupes. All three categories of treatments were aimed at altering the intactness of the pericarp, which encloses it. The fourth category of treatment involving exposure of drupes to heat has also been found to be effective by a few researchers, although it has no role in softening the pericarp. It is therefore perceived that other than fruit pericarp, factors related to seed *per se* (*e.g.*, seed dormancy, seed viability, seed vigour) may also influence the seed germination potential of teak drupes.

**Comprehensive assessment of candidate factors influencing teak seed germination**

In light of the various reports made on teak germination, it can be inferred that teak drupe germination is being influenced by candidate factors such as i) seed filling/ emptiness, ii) seed viability/ dead seeds, iii) seed dormancy, iv) immature seeds and v) very low vigour seeds. The results reported and the inferences made by various authors are discussed hereunder to develop a holistic hypothesis on the mechanism underlying teak drupes' sporadic and protracted germination.

**i) Emptiness of drupes:** In teak, the proportion of empty drupes in a seed lot may vary from 19.2 to 66.4 %, depending on the provenance [27]. Even if the drupes belonged to the same provenance, the emptiness of drupes varied from 32 to 46 %, depending on the drupe size [29]. Thus, the presence of empty drupes can be a major cause for poor germination of teak. However, since teak drupe is quadrilocular, the presence of double, triple, and four-seeded drupes may compensate for empty drupes (Table 1). Thus, it is imperative to select the superior provenance and big-sized drupes to obtain a higher percentage of multi-seeded drupes to obtain a maximum number of seedlings from the teak drupes sown.

**ii) Seed viability:** Among the 30 provenances studied, the seed viability percentage ranged from 55 to 96.67 percent [27]. The vast difference among the 30 provenances was attributed to the age of the drupes collected for the study. In four months, old drupes, only about 0.04 –0.05 percent of seeds were found to be non-viable, as revealed by the TZ staining test [21]. Teak drupes may have a long viability period since many reports suggested that one-year-old drupes recorded higher germination percentages than fresh ones [22, 34, 35, 36, 37]. Thus, seed viability may not cause poor germination potential of teak drupes.

**iii) Seed dormancy:** Seed dormancy is defined as a viable seed's (temporary) inability to germinate under conditions otherwise favourable for germination [38]. The poor, sporadic, and protracted germination of teak drupes has been reported to be caused by various forms of dormancy [39]. The candidate dormancy types reported concerning teak drupes are physical, chemical, mechanical, morphological [36, 40, 41], and combined dormancy due to the presence of two or more types of dormancy mechanisms [39].

*a. Physical dormancy:* It is a state of some seeds wherein impermeability of the seed coverings or seed coat is caused by a layer of thick-walled, cutinized macro scleroid cells that acts as a barrier for water imbibition and prevents seed germination. The thick corky mesocarp and stony endocarp of teak drupe might prevent the entry of both water and gas and inhibit the initiation of the germination process, resulting in physical dormancy [42]. The stony impermeable endocarp of teak might cause seed dormancy [43, 40]. The endocarp and the mesocarp of teak drupes possessed a layer of palisade cells with thick walls and externally covered by waxy cuticle, ultimately causing physical dormancy [44]. However, soaked teak drupes in dyed water and confirmed that the water moved through numerous mesocarp cavities and the endocarp's minute pores to reach the locules within six hours of soaking [21]. Since the pericarp of teak drupes is fully permeable to water, it can be concluded that physical dormancy cannot cause poor germination of teak drupes.

*b. Mechanical dormancy:* The pericarp of the fruit or the seed coat may be permeable to water; however, the mesocarp and endocarp may be very strong, causing a mechanical barrier to swelling of the seed and protrusion of the radicle resulting in mechanical dormancy. The thick pericarp of the drupe does not soften sufficiently for the embryo cells to grow and germinate even after imbibition by the drupes, suggesting that mechanical dormancy might be a cause of poor seed germination in teak [45]. *ex-situ* seeds extracted from the drupes germinated up to 62 ± 2 % under *in vitro* conditions, while *in-situ* (intact drupes) seeds germinated only up to 32 ± 2 % within 16 days after sowing [21]. Since removing the endocarp and mesocarp had improved germination, they proposed that mechanical dormancy caused by the endocarp could be a prominent cause for teak seeds' poor seed germination potential. However, [23] proved that opening of 'valves' present on the endocarp is achieved only due to expansion and contraction of the endocarp at varying vapour pressure generated in the water-soaked drupes and had no connection with the germination of seeds present inside the locule. [23] cautioned that the exocarp (and mesocarp) might retard the opening of the valves closing the seed chamber. This inference draws support from the reports that 'removal of mesocarp by termite' helps to improve the rate of seed germination as well as seed germination percent [23, 46] or fire [42]. Direct and negative correlation existed between mesocarp weight and seed germination, revealing that the more significant the mesocarp portion, the greater will be the germination inhibition [27]. The adverse effect of mesocarp on seed germination and the methods of removing it for better seed germination [47, 48, 49]. Therefore, the mechanical dormancy in teak drupes may not be caused by the endocarps [21]. However, there is a high probability that the thick corky mesocarp encircling the endocarp might offer a mechanical barrier to the opening of the 'valves' and prevent the germination of the seeds inside the locule. In natural ecosystems, the felty mesocarp that undergoes destruction due to fire or biological decomposition may eventually lead to sporadic and protracted germination. In many of the experiments conducted on teak germination (Table 3), long-term alternate soaking and drying have been reported to be effective in improving seed germination which may be attributed to the weakening of the thick mesocarp. Based on these revelations, it is inferred that mechanical dormancy caused by the mesocarp and endocarp might be one of the significant causes for the poor germination potential of teak drupes.

*c. Chemical dormancy*: Chemical dormancy occurs when chemical inhibitors in the pericarp or seed coat prevent seed germination or embryo growth [18]. The soluble substances extracted from the mesocarp of teak drupes have been reported to inhibit the seed germination of other crop plants [1, 20, 26 and 66] and led to the hypothesis that chemical dormancy might be a cause for poor seed germination of teak. However, no direct estimation of inhibitors in teak drupes or their effect on teak seed germination has been reported. Therefore, further research is required to ascertain the presence of chemical dormancy in teak drupes.

*d. Morphological dormancy:* Morphological dormancy refers to the inability of seeds to germinate immediately after dispersal due to the presence of rudimentary embryos, which require more time to undergo further embryo differentiation and growth to reach the 'critical' size inside the dispersed seed [50]. The underdeveloped seeds exhibiting morphological dormancy will have a minute embryo with an embryo: seed ratio (E: S) of < 0.5 [51]. Once imbibed to initiate germination, the minute embryo shall initiate elongation and growth inside the seed. Usually, about 30 days are required to complete the embryo's growth after dispersal to initiate germination [51, 52, 53].

In the case of teak, true seeds extracted from the drupes recorded 62±2 percent germination within 8 DAS under in vitro conditions [21]. Besides, the seeds enclosed in the teak drupes (*in vivo*) showed the first signs of germination within 6 DAS. Thus, although the time taken for completion of teak germination may extend even upto a year, yet initiation of germination of seed lot commenced within 8-12 days [21, 22, 29]. Since the size of the embryo inside the seed is well developed, and a portion of the seeds in a lot is germinable immediately after sowing, it shall be inferred that teak seeds have completed the morphological growth at the time of dispersal and are devoid of morphological dormancy (Fig. 5). However, the delayed germination of some parts of the seed lot might be due to other physiological impediments, such as the requirement of 'after ripening' of the seeds after seed collection.

**iv) After ripening:** After-ripening is the physiological process in the seed after dispersal from the tree, without any associated morphological changes, resulting in post-harvest maturity essential for normal seed germination. After-ripening is sometimes classified as a kind of dormancy [42]. Various reports have confirmed that fresh seed lots of teak record a meagre rate of germination compared to one-year-old drupes [22, 34, 35, 36, 37]. Fresh drupes of teak required 24 days to initiate germination, while one-year-old drupe required only 16 days, with the corresponding germination of 4 and 29

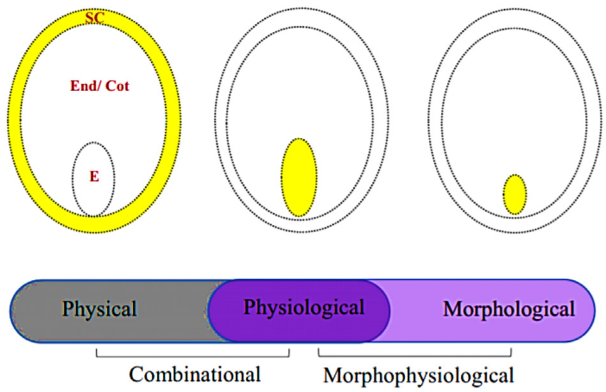


**Figure 5.** Depiction of seed dormancy classes [61,10]. The reason for dormancy is shown in yellow. E- embryo; End/Cot- endosperm/ cotyledon; SC- seed coat [34].

i) *Physical dormancy* is caused water-impermeable layers of palisade cells in the seed or fruit coat [8]; ii) *Physiological dormancy* is a condition wherein the seeds have fully developed embryos at the time of dispersal, yet may fail to germinate because the embryo lacks the growth potential [9], unless they are subjected to external treatments; and iii) *Morphological dormancy* is a state wherein seed contain undifferentiated rudimentary embryos which do not require a dormancy-breaking treatment per se in order to germinate; they simply need time to grow to full size and then germinate [8].

percent, respectively [54]. The protracted germination behaviour may be due to insufficient ripening of the embryo, leading to a requirement for the after-ripening process [42, 55].

The requirement of an after-ripening period draws support from [56], who found that ground-collected drupes (32.0 percent) germinated better than crown collected (2.75 percent), with a relative increase in speed of germination as well as seedling growth and inferred that crown collected drupes required more prolonged duration of after-ripening compared to ground collected drupes, owing to lower maturity level. Later, [54] reported that teak drupes exposed to 40oC and 100 % RH conditions for 13 days improved the seed germination from 18 percent (control) to 53 percent, probably due to the facilitation of the after-ripening process. Four-month-old seed lot of teak contained seeds with differential maturity levels as revealed by the seed coat colour, viz., light brown or slightly green testa was present in a single seed lot [21]. The seeds with green testa might be slightly immature compared to those with light brown testa. Thus, the seeds in a single lot may be heterogeneous in maturity level. Eventually, the fully mature seeds with brown seed coats may be capable of germinating immediately after sowing, and the rest of the seeds may germinate as and when they complete the ‘after-ripening’ process, which may extend even up to one year after sowing. It is therefore concluded that the protracted and sporadic germination of the teak drupes might be a function of the heterogeneous maturity level of seeds present in a lot since the seeds will tend to germinate as and when they complete the after-ripening process.

**v) Low seed vigour:** Due to continuous flowering, plant species exhibiting indeterminate growth habits, such as teak, usually produce buds, flowers, and fruits simultaneously on the same plant. The seed-filling and development period of late-formed flowers is very short compared to early-formed flowers [57]. Correspondingly, the filling of storage reserves in late-formed seeds is comparatively lower, and it mainly manifests in poor seed vigour and failure to germinate [58]. In a single drupe, some seeds were well developed and fleshy, while the other seed was found to be shriveled in nature, revealing that partitioning of resources may not be equal among all the seeds present in a drupe [59]. A cutting test on the ungerminated teak drupes after 20 weeks of sowing and observed that most of the seeds were rotten by the end of the experiment [60]. Therefore, one of the most probable reasons for the low germination percentage of teak drupes could be very low vigour seeds produced due to lower assimilate availability and intense competition among the developing seeds.

The research reports made on teak seed germination have underscored the effect of size grading (to eliminate empty drupes), alternate soaking and drying of drupes or removal of mesocarp and endocarp (to eliminate mechanical dormancy), and dry heat treatment or dry storage of drupes (to accelerate after-ripening) on germination of teak drupes. However, since only one kind of drupe treatment had been imposed at a time in all the experiments conducted (Table 3), it could have led to the incomplete elimination of multiple candidate factors resulting in lower-than-expected improvement in drupe germination potential. Based on the above discussions, it is concluded that characteristics related to drupe and seed influence teak germination are as follows: Drupe characteristics are i) the proportion of empty drupes in a seed lot might reduce the seed germination percentage, ii) mechanical dormancy due to the large corky mesocarp and endocarp may lead to sporadic seed germination. The seed characteristics are i) differential maturity levels necessitating an ‘after-ripening period’ for late-formed seeds may lead to protracted germination, ii) the presence of low vigour seeds which are shriveled may not

**Table 4.** Effect of mechanical scarification on removal of fruit parts and seed germination characteristics of Teak (Tectona grandis)

| Treatments | Days to initial germination | Seed Germination (%) | Root length (cm) | Shoot length (cm) | Dry matter production (g / seedling) | Vigour Index |
|---|---|---|---|---|---|---|
| Control(Cow dung Slurry) | 15.6 | 4.1 | 2.0 | 5.1 | 0.582 | 2.44 |
| 2 min | 14.5 | 4.8 | 2.4 | 5.6 | 0.602 | 2.89 |
| 4 min | 14.3 | 5.0 | 4.5 | 6.2 | 0.610 | 2.93 |
| 6 min | 8.0 | 17.6 | 4.9 | 6.5 | 1.261 | 22.45 |
| 8 min | 0 | 0 | 8.5 | 10.4 | 0 | 0 |
| Mean | 10.48 | 6.3 | 4.4 | 7.1 | 0.611 | 6.142 |
| SEd | 0.274 | 0.215 | 0.113 | 0.151 | 0.016 | 0.230 |
| CD (5%) | 0.599 | 0.469 | 0.246 | 0.329 | 0.036 | 0.502 |

A B C

**Figure 6.** Germination of teak seeds from drupes scarified in mechanical scarifier for 6 min and incubated in humid conditions for 10 days. A) A view of the teak seed germinating inside the locule, after the ejection of the valve. B) Teak seedling dispersed after emergence. C) A view of the empty locule, after seedling dispersal [80]

germinate but eventually decay, leading to low seed germination percentage (Fig. 7).

Anent to the above hypothesis, experiments were conducted to compare the effect of different durations of scarification with a mechanical scarifier machine by adopting 2 min, 4 min, 6 min, and 8 min scarification [61]. The drupes scarified for 6 min recorded the highest germination, germination speed, dry matter production, and vigour index compared to those scarified for 2,4, and 8 min (Table 4) (Fig 2, 6). However, 8 min scarification resulted in the valve opening and damaged the seeds forming empty locules. The results revealed that complete removal of the mesocarp and partial scarification of the endocarp by scarifying the teak drupes for 6 min in a

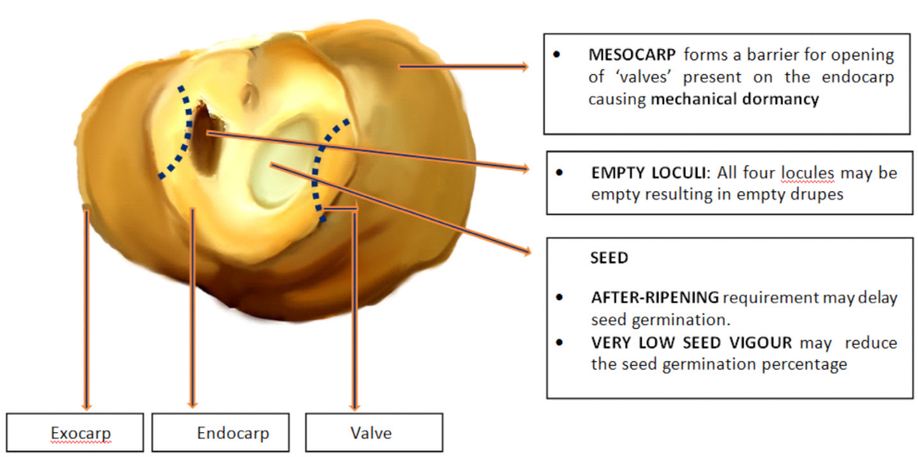


**Figure 7.** Sporadic, protracted and poor germination behavior of Tectona grandis is attributed to certain drupe and seed characteristics. A) Drupe characteristics: 1. Mesocarp forms a barrier to seed germination by preventing the opening of the 'valve' present on the endocarp over the seed 2. Empty drupes: Large percentage of teak drupes are found to be empty (upto 39 percent), B) Seed characteristics: 1. After ripening requirement of seeds 2. Very low seed vigour


**Figure 8.** Treatment protocol for teak (Tectona grandis) drupes to overcome multiple barriers and enhance seed germination potential

mechanical scarifier had led to optimum destruction of the mesocarp, thereby paving the way for the opening of the 'valve' present on the endocarp leading to quicker seed germination from teak drupes (Fig. 7). Thus, it was proven that mechanical restriction offered by the mesocarp caused a significant barrier to seed germination of teak drupes.

Against this back drop, it is concluded that in order to overcome multiple barriers of seed germination of teak drupe, a 4-step drupe treatment protocol is required : i) Size grading of the drupes with sieves of > 9 mm diameter to remove the empty drupes in a seed lot to a certain extent ii) Removal of the mesocarp of the drupes, either by mechanical or biological methods, to overcome mechanical dormancy iii) Exposure of endocarps (after removal of mesocarp) to dry heat for an optimum temperature and duration, to facilitate the 'after-ripening' of the embryo and finally iv) Priming of teak endocarps to enhance the seed vigour status (Fig. 8).

## CONCLUSION

Seed germination of teak drupes is found to be governed by multiple factors. Empty drupes, mechanical restriction caused by large corky mesocarp and endocarp, differential maturity levels of seed in a lot, and the presence of shriveled low vigour seeds are the major factors that cause low seed germination potential in teak drupes. Response of seeds to pre-germination or sowing treatments depends on how closely such treatments resemble the ecological characteristics of the natural habitat of the species in question. In the case of teak drupes, under natural conditions, removal of the mesocarp is achieved through termite feeding, while 'after ripening' of seeds might be accomplished during storage of seeds under ambient conditions in the soil seed bank. When exposed to moist, humid monsoon season conditions, such drupes may undergo invigoration and culminate in seed germination. Thus, imposing the teak drupes to a treatment consortium involving size grading, removal of mesocarp, partial scarification of endocarp, after-ripening, and seed priming has the potential to overcome the barriers and increase the speed of germination and seed germination percentage of the teak drupes to increase the production of high-quality teak seedlings.

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## REFERENCES

1. COWEN DV (1965). Flowering trees and shrubs in India. Thacker & Co., Ltd., Fort Bombay.
2. MALESKAR AR (1983). Forester's companion. India Forest Handbook. Jugal Kishore and Co., India.
3. LADRACH W (2009). Management of teak plantations for solid wood products. ISTF News, Special Report, December 2009.
4. KITTINANDA SP (1967). Natural regeneration of teak in Lampang. In: Proc 1st For Conf, Royal Forest Department, Bangkok.
5. KADAMBI K (1972). Silviculture and management of teak. School of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, Bulletin **24**, pp. 137.
6. TIWARI CK, S SHARMA AND RK VERMA (2004). Effect of fungicides and plant growth hormones on germination of teak (*Tectona grandis*). *J Trop For Sci,* **16(1)**: 25-34.
7. WEAVER PL (1993). *Tectona grandis* L.f. Teak. Verbenaceae. Verbena family. USDA Forest Service, International Institute of Tropical Forestry; 18 p. (SO-ITF-SM; 64).
8. KAOSA-ARD A (1981). Teak: its natural distribution and related factors. *Nat Hist Bull Siam Soc*, **29**: 55-74.
9. HEDEGART T (1976). Breeding system, variation and genetic improvement of teak (*Tectona grandis* Linn.f.). In: Burley, J., Styles, B.T. (Eds.), Tropical Trees. Academic Press, London.
10. KEOGH RM (1979). Le teek, essence forestiere ideale pour l'Amerique tropicale: les plantations de teck aux Antilles, en Amerique Centrale, au Venezuela et en Colombie. Unasylva, **31**: 13-19.
11. EVANS J AND J TURNBULL (2004). Plantation forestry in the tropics. 3rd ed. Oxford University Press, Oxford, UK.
12. PALANISAMY K AND K SUBRAMANIAN (2001). Vegetative propagation of mature teak trees (*Tectona grandis* L.). *Silvae Genet,* **50(5-6)**: 188-191.
13. AKRAM M AND F AFTAB (2009). High frequency multiple shoot formation from nodal explants of teak (*Tectona grandis* L.) induced by thidiazuron. *Propag Ornament Plant,* **8**: 72-75.
14. PALANISAMY K, M HEGDE AND YI JAE-SEON (2009). Teak (*Tectona grandis* Linn. f.): A renowned commercial timber species. *J For Sci,* **25(1)**: 1-24.
15. KAOSA-ARD A (1998). Overview of problems in teak plantation establishment. In: Kashio, M., White, K. (Eds.), Teak for the Future, Bangkok: RAP Publication 1998/5, FAO Regional Office for Asia and the Pacific, pp. 49-60.
16. CHAMPION HG AND SK SETH (1968). A Revised Survey of the Forest Types of India: 113-117, 181-184. Manager of Publications, Delhi.
17. SETH SK AND MAW KHAN (1958). Regeneration of teak forests. In: Proceedings of the All-India Teak Study Tour, F.R.I., Dehra Dun, pp. 107-120.
18. HARTMANN HT, DE KESTER, FT DAVIES AND RL GENEVE (1997). Plant propagation: principles and practices. Prentice Hall, Upper Saddle River.
19. TROUP RS (1921). The Silviculture of Indian Trees, Vol. II. Oxford University Press, Oxford.
20. ISTA (1976). International Seed Testing Association: rules for seed testing and evaluation. *Seed Sci Technol,* **13**: 356-513.
21. SLATOR NJ, AN CALLISTER AND JD NICHOLS (2013). Mechanical but not physical dormancy is a cause of poor germination in teak (*Tectona grandis* L.f.). *New For,* **44**: 39-49.
22. DABRAL SL (1976). Extraction of teak seed from fruit, their storage and germination. *Indian For,* **102**: 650-658.
23. BRYNDUM K (1966). The germination of teak. *Nat Hist Bull Siam Soc,* **21(1-2)**: 75-86.
24. KAMRA S (1976). Use of X-ray radiography for studying seed quality in tropical forestry. *Stud For Suec,* **131**: 34.
25. KUSHALAPPA KA (1977). Teak plantations in Thailand. *Indian For,* **103**: 323-328.
26. GUPTA BN AND A KUMAR (1976). Estimation of potential germinability of teak (*Tectona grandis* L.f.) fruits from twenty-three Indian sources by cutting test. *Indian For,* **102**: 808-813.
27. SIVAKUMAR V, K PARTHIBAN, BG SINGH, V GNANAMBAL, R ANANDALAKSHMI AND S GEETHA (2002). Variability in drupe characters and their relationship on seed germination in teak (*Tectona grandis* L.f.). *Silvae Genet,* **51**: 232-236.
28. INDIRA EP, SC BASHA AND KC CHACKO (2000). Effect of seed size grading on the germination and growth of teak (*Tectona grandis*) seedlings. *J Trop For Sci*, **12(1)**: 21-27.
29. MASILAMANI P, VA ALBERT, S VENKATESAN AND P JANAKI (2020). Effect of phosphorus application on growth and stump quality of teak (*Tectona grandis* Linn. f.) seedlings. *Madras Agric J,* **107(10-12)**: 363-368.
30. HEDEGART T (1973). Pollination of teak (*Tectona grandis*). *Silvae Genet,* **22**: 124-128.
31. KEIDING H AND F KNUDSEN (1974). Germination of teak in relation to international provenance testing. For Tree Improv Arboretet Horsholm, Copenhagen **7**: 19-29.
32. KAOSA-ARD A (1994). *Tectona grandis*, Linn.f. - Nursery techniques. *Seed Leafl*, **4A**: 1-33.
33. HILL AW (1933). The method of germination of seeds enclosed in a stony endocarp. *Ann Bot,* **47**: 873-887.
34. DASAPPA S (1990). Nursery techniques in teak (*Tectona grandis* Linn. f.) for afforestation. *My forest,* **26(1)**: 23-31.
35. JOSHI MD AND SP KELKAR (1971). Germination of seed in dry teak (*Tectona grandis* L.). *Indian For,* 214-215.
36. SUANGTHO V (1980). Factors controlling teak (*Tectona grandis* Linn. f.) seed germination and their importance to Thailand. M.Sc. Thesis, Australian National University, Canberra.
37. VICHIEN S, T HEDEGART AND EB LAURIDSEN (1974). Compendium and manual for Teak Improvement Centre staff. Teak Improvement Centre, Ngao, Lampang.
38. ARNOLD RL, RA SANCHEZ, F FORCELLA, BC KRUK AND CM GHERSA (2000). Environmental control of dormancy in weed seed banks in soil. *Field Crops Res,* **67**: 105-122.
39. KEIDING H (1985). Seed leaflet no. 4, teak *Tectona grandis* linn f danida, humlebaek, denmark.
40. SCHMIDT L (2000). Dormancy and pretreatment. In: Guide to Handling of Tropical and Subtropical Seed, Danida Forest Seed Centre, Humlebaek, Denmark.
41. RAJPUT A AND KP TIWARI (2001). Effect of alternate chilling/heating on germination of fresh teak (*Tectona grandis* L.f.) drupes without scarification of felty mesocarp. *Seed Sci Technol,* **29**: 57-64.

42. TIWARI DN (1992). A monograph on teak (*Tectona grandis* Linn.f.). International Book Distributors, Dehra Dun.

43. UNNIKRISHNAN K AND KP RAJEER (1990). On germination of Indian teak (*Tectona grandis*). *Indian For,* **116**: 992-993.

44. DIAS JRM, AL CAPRONI, PGS WADT, LM SILVA, LB TAVELLA AND JP OLIVEIRA (2009). Quebra de dormência em diásporos de teca (*Tectona grandis* L.f.). *Acta Amazon,* **39(3)**: 549-554.

45. KADAMBI K (1972). Silviculture and management of teak. School of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, Bulletin **24**, 137 pp.

46. CHANDRASEKHARA PK PILLAI, MR SRUTHI AND R MAHENDRAN (2014). Seed handling and nursery practices in teak. *Teaknet Bull,* **7(1)**: 2-4.

47. BAPAT AR AND MM PHULARI (1995). Teak fruit treatment machine – A Prototype – II. *Indian For***, 121**: 545-549.

48. BHUMIBHAMON S, B PONOY AND K CHAISURISRI (1983). Publicacion-Especial-Instituto-Nacional-de-Investigaciones-Forestales, *Mexico*, **35**:253-264.

49. CHACKO KC (1998). Termite aided mesocarp removal of teak (*Tectona grandis* Linn.f.) fruits for germination and cost-effective seed handling. *Indian For,* **124**: 134-140.

50. NIKOLAEVA MG (1977). Factors controlling the seed dormancy pattern. In: Khan, A.A. (Ed.), The Physiology and Biochemistry of Seed Dormancy and Germination, North Holland, Amsterdam, pp. 51-74.

51. BASKIN JM AND CC BASKIN (2004). A classification system for seed dormancy. *Seed Sci Res***, 14**: 1-16.

52. FINCH-SAVAGE WE AND G LEUBNER-METZGER (2006). Seed dormancy and the control of germination. *New Phytol***, 171**: 501-523.

53. NIKOLAEVA MG (1969). Physiology of deep dormancy in seeds. Leningrad, Russia: Izdatel'stvo Nauka. (Translated by Z. Shapiro, National Science Foundation, Washington, DC).

54. MASILAMANI P, C DHARMALINGAM AND K ANNADURAI (2002). Effect of natural ageing on germination and seedling vigour of teak (*Tectona grandis* Linn. f.) drupes*. Indian J For*, **25(2)**: 122-126.

55. GUPTA BN AND PG PATHANATH (1975). Factors affecting germination of teak seeds of eighteen Indian origins. *Indian For,* **101**: 584-587.

56. MASILAMANI P, GURUDEV B SINGH AND L MARIMUTHU (1998). Influence of collection methods and treatments of seeds on the germination and seedling vigour of teak. *Bangladesh J For Sci,* **27(2)**: 138-140

57. GBIKPI P AND RK CROOKSTON (1981). Effect of flowering date on accumulation of dry matter and protein in soybean. *Crop Sci,* **21**: 652-655.

58. SAVAGE WE AND GW BASSEL (2015). Seed vigour and crop establishment: extending performance beyond adaptation. *J Exp Bot***, 67(3)**: 567-599.

59. AKRAM M AND F AFTAB (2006). Fruit size and sampling sites effect on dormancy, viability and germination of teak (*Tectona grandis* L.) seeds. *Pakistan J Bot,* **48(2)**: 511-518.

60. NGULUBE M (1986). Preliminary study of germination of pretreated seed of teak (*Tectona grandis*) under nursery conditions in Zomba, Malawi. *For Ecol Manage*, **17**: 147-151.

61. UMARANI R (2021). Development of seed cube technology for mass propagation of teak (*Tectona grandis*). Project Report, Tamil Nadu Agricultural University, Coimbatore, India.