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Review Paper

Fresh Seed Dormancy in Groundnut: Mechanisms, Factors, and Implications for Crop Improvement – a Review

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ABSTRACT: Groundnut (*Arachis hypogaea* L.) is a globally important oilseed and legume food crop. However, the absence of fresh seed dormancy (FSD) in the most commonly grown Spanish bunch type varieties presents a significant hurdle to groundnut productivity and quality. Given its economic significance, research is underway to investigate the mechanisms and factors contributing to FSD in model systems, with implications for groundnut cultivation. Recent reviews have emphasized remarkable advancements in unravelling genetic control, molecular mechanisms, and the physiological and environmental factors influencing germination and dormancy across diverse plant species. In this context, we examine the latest research findings concerning FSD in groundnut, placing a stronger emphasis on the genetic factors associated with FSD. Furthermore, we explore the attempts aimed at breeding superior genotypes to enhance groundnut improvement.

Keywords: Groundnut, Fresh seed dormancy, *In vitro* sprouting, Molecular mechanisms, Omics-based insights, Breeding for dormancy

Seed dormancy is a phenomenon where seeds temporarily suspend germination, even in the presence of typically conducive environmental conditions such as appropriate temperature, moisture, and light. This adaptation is vital for seeds to withstand adverse conditions and germinate when environmental factors favour growth. It plays a critical role in regulating plant populations and ensuring the long-term survival of many plant species. Seed dormancy can be classified into four types based on triggers and mechanisms: physiological dormancy, physical dormancy, morphological dormancy, and chemical dormancy [1]. In groundnut, a significant oilseed and legume food crop, the semi-spreading and spreading varieties (Virginia types belonging to subspecies *hypogaea*) often display prolonged dormancy periods. Conversely, Spanish and Valencia bunch varieties (belonging to subspecies *fastigiata*) lack dormancy, leading to *in situ* sprouting in the field if there is rainfall at the time of maturity. It is believed that the fastigiata subspecies of cultivated groundnut underwent a loss of FSD as a result of domestication and human-made selection. *In situ* sprouting can cause a significant yield loss of up to 20-25% [2]. It not only diminishes yield but also adversely impacts seed quality and storability. Therefore, integrating a short dormancy period (3-4 weeks) into widely cultivated groundnut varieties, especially those of the bunch type, may alleviate yield losses due to viviparous germination. Accomplishing this requires a thorough understanding of the mechanisms and factors affecting FSD. In this review, we evaluate the present comprehension of FSD in groundnut, analyzing its physiological, genetic, environmental, and agronomic dimensions. This insight could inform future research directions and provide viable strategies to address FSD, thus promoting groundnut production and sustainability.

What is known in the model plant?

Significant progress has been made, particularly with the model plant *Arabidopsis thaliana*, in understanding the molecular mechanisms underlying the transition between dormancy and germination, driven by developmental and environmental cues [3]. Genetic and physiological inquiries have established a sturdy foundation in this domain, highlighting the pivotal roles of plant hormones like abscisic acid and gibberellins in orchestrating these processes. Additionally, investigations into natural variation and quantitative genetics have pinpointed genetic determinants of dormancy and germination. The utilization of omics technologies, encompassing

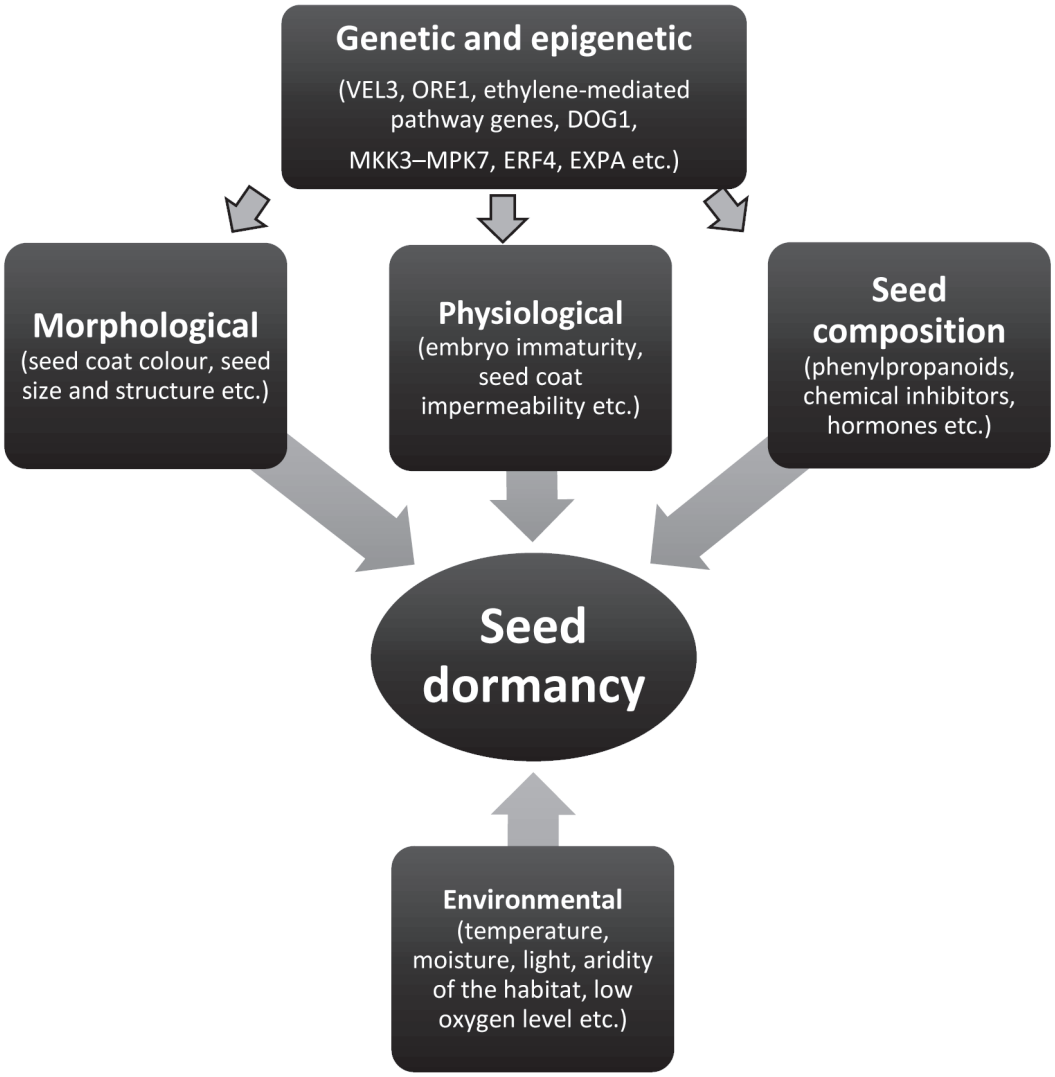

Figure 1. Mechanisms regulating the seed dormancy

transcriptomics, proteomics, and translatomics analyses, has further advanced our understanding by uncovering novel regulatory components governing seed dormancy and germination (Figure 1).

Physiological mechanisms of fresh seed dormancy

The impermeability of the seed coat to water and gases is a common feature contributing to FSD in groundnut. Physical and chemical properties of the seed coat, including thickness, waxiness, and lignification, influence water uptake and gas exchange, thereby affecting germination potential. Woodstock [4] reviewed the imbibition, the uptake of water by the dry seed involving absorption of water by cell wall and protoplasmic macromolecules, i.e., proteins and polysaccharides, wherein water molecules are “held” by electrostatic forces such as hydrogen bonds. Jayasuriya and Phartyal [5] discovered that the percentage of water-impermeable (WI) seed coats escalates in correlation with the aridity of the habitat across 25 species of Fabaceae. Notably, populations from drier regions in India exhibit a greater prevalence of WI seeds compared to those from Sri Lanka.

A compelling study conducted by Zhang *et al.* [6] demonstrated a correlation between seed coat colour and structure with seed dormancy in soybeans. Through scanning electron microscopy analysis, it was revealed that light-coloured seeds exhibited a thin palisade layer with minimal surface deposits, whereas dark-coloured seeds showcased a thicker palisade layer and extensive

honeycomb-like surface deposits similar to those found in wild soybean seeds. Seeds with lighter colours (yellow and green) tended to be less dormant, while those with darker hues (brown and black) exhibited higher levels of dormancy.

Physiological dormancy of the embryo, resulting from the presence of inhibitory substances or developmental arrest, can contribute to delayed germination in fresh groundnut seeds. Sreeramulu and Rao [7] discussed the balance of growth-promoting and inhibiting substances in relation to seed development and dormancy in groundnut, and concluded that the acidic inhibitors are responsible for dormancy in groundnut seeds.

Hormonal regulation and metabolic processes within the embryo are critical factors in triggering dormancy release and facilitating seedling emergence. Abscisic acid (ABA) predominantly regulates dormancy, while gibberellins (GAs) become dominant during germination. Therefore, the balance between ABA and GAs serves as a pivotal switch between dormancy and germination stages [8, 9]. Chen *et al.* [10] identified a fate switch comprised of the MKK3–MPK7 kinase cascade and the ethylene response factor ERF4 that is responsible for the state transition from dormancy to germination. Dormancy-breaking factors activate the MKK3–MPK7 module, which affects the expression of some a-EXPANSIN (EXPA) genes to control seed dormancy.

Oxygen availability and temperature fluctuations influence seed metabolism and dormancy release in groundnut. Low oxygen levels and suboptimal temperatures can prolong dormancy by inhibiting metabolic processes essential for germination. The content of phenyl-propanoids (i.e., phenolics and flavonoids) present in the chickpea seed coat has a significant influence on dormancy. Phenolic acids were generally more highly concentrated in the dormant genotypes [11].

Utilizing automated phenotype analysis, Krzyszton *et al.* [12] found that in Arabidopsis, small seeds exhibited higher levels of both primary and secondary dormancy as compared to large seeds. Notably, large seeds displayed increased expression of translation-related genes associated with germination competency, while small seeds showed heightened expression of various positive regulators of dormancy, notably the DOG1 (DELAY OF GERMINATION 1) gene. This investigation underscored a clear association between the seed size and its physiological attributes. In a related study, Li *et al.* [13] conducted a comparative transcriptome analysis of germinating seeds from two groundnut accessions, A86 (a high-vigour variety) and A279 (a low-vigour variety), revealing differential expression of genes implicated in dormancy regulation, akin to observations made in Arabidopsis.

Environmental and agronomic influences on fresh seed dormancy

Environmental factors, including temperature and moisture levels during seed development and storage, can modulate FSD in groundnut. Optimal environmental conditions favour dormancy release and promote germination, whereas unfavourable conditions may prolong dormancy maintenance. Agronomic practices such as timely harvesting, proper seed drying, and storage management are critical for minimizing FSD and preserving seed viability in groundnut. Post-harvest treatments and conditioning techniques can help accelerate dormancy release and improve seedling vigour. Soil moisture content and texture affect water availability to seeds, influencing dormancy release and germination. Inadequate soil moisture can exacerbate dormancy in fresh groundnut seeds, leading to poor stand establishment. Light conditions during seed development and after harvest can influence dormancy in groundnut. Exposure to light or specific photoperiods may promote dormancy release and stimulate germination.

The impact of heat stress on both seed germination and seedling vigour was examined by Opio and Photchanachai [14]. It was observed that as the temperature of heat stress rose, there was a notable decrease in both seed germination and seed vigour. Despite this, the seed moisture content and the total count of abnormal seedlings remained consistent across all treatments. However, at temperatures exceeding 40±1°C, there was a significant increase in the occurrence of deformed seedlings. Furthermore, exposure to 40°C resulted in a notable induction of dormancy, with a 31% increase compared to control seeds. Beyond 50°C, heat stress had a severe detrimental effect on groundnut seeds, leading to embryonic death. Seeds are also exposed to various factors including moisture, gas composition, and light, which may act independently or collectively to regulate germination and subsequent seedling growth [15].

Genetic regulation of fresh seed dormancy

The genetic regulation of fresh seed dormancy encompasses a multifaceted interplay of various genetic

factors. Numerous genes are involved in controlling the onset and duration of dormancy in seeds, influencing aspects such as seed coat development, hormone metabolism, and signalling pathways. These genetic mechanisms interact with environmental cues to fine-tune the dormancy status of seeds, ensuring optimal conditions for germination and seedling establishment. Different plant species exhibit distinct genetic regulatory networks governing fresh seed dormancy, reflecting their evolutionary adaptations to specific ecological niches and reproductive strategies. Understanding the genetic basis of fresh seed dormancy holds significant implications for agriculture, enabling the development of tailored breeding strategies and molecular interventions to optimize seed quality, storage, and germination performance.

A comprehensive screening was conducted on a significant pool of germplasm, consisting of 200 accessions and 21 cultivars, all falling within the category of Spanish bunch type. The aim was to evaluate pod loss resulting from seed sprouting in the field. The assessment revealed considerable diversity in pod loss attributable to in situ seed sprouting, as well as in FSD across the various accessions and cultivars. Fresh-seed dormancy index (FSDI) exhibited a wide range, spanning from 2% in Chico to 88% in ICGS 44 (the reference with high FSD). Notably, it was observed that the regulation of FSD appeared to be primarily influenced by the testa rather than the cotyledons [16]. Evaluation of 30 varieties belonging to the three different habit groups in three different seasons (*kharif*, *rabi* and summer) showed considerable variability dormancy. Seeds produced in *kharif* season showed the highest degree of dormancy followed by those produced in *rabi* and summer [17].

Various crosses utilizing non-dormant erect bunch cultivars of groundnut as ovule parents and dormant interspecific Virginia bunch derivatives as pollen parents demonstrated significant heritable variation. A high proportion of segregants were observed for dormancy (26%), erectness (39%), and high yield potential (71%). However, the occurrence of plants with both dormancy and an erect habit (9.4%), as well as those with high yield potential (1.4%), was notably low. Therefore, to enhance the recovery of desirable segregants, it may prove beneficial to either increase the size of the segregating population or facilitate intermating among selected segregants [18].

The investigation carried out by Upadhyaya and Nigam [19] aimed to elucidate the inheritance pattern of FSD utilizing three distinct Spanish groundnut genotypes (ICGV 86158, ICGV 87378, and JL 24). Their findings revealed that FSD in these genotypes was governed by a dominant allele of a single gene.

Stored mRNAs play an important role in seed dormancy and germination. Mature dry seeds accumulate more than 10,000 mRNAs during seed maturation process, which are utilized for protein synthesis upon germination. Seed germination may occur in the presence of transcriptional inhibitors, such as cordycepin or á-amanitin suggesting germination process at least are independent of transcription and may rely on long-lived mRNAs for protein synthesis or (re) activation of stored proteins [20]. These stored mRNAs remain translatable after decades of dry storage to ensure successful germination. A seed in the dry state appears to prevent mRNA decay, whereas, in a hydrated environment, transcript half-lives range from minutes to days [21]. It is unlikely that all of the thousands of stored mRNAs are required for the germination process. They will also be involved in housekeeping activities in cells or are remnants of seed developmental processes. This is the developmental phase starting just after the completion of embryo morphogenesis and also when transcriptional inhibitors no longer inhibit the precocious germination of embryos, suggesting the acquisition of transcriptional independence by the embryos [22]. Studies found that stored mRNAs may also be translated at later stages of germination [23].

Omics approaches have provided further insights into the molecular mechanisms underlying FSD in groundnut, revealing dynamic changes in gene expression and protein profiles during seed maturation and dormancy release. FSD in groundnut exhibits considerable genetic variability, with multiple loci controlling dormancy-related traits. Understanding the genetic basis of dormancy can facilitate breeding efforts to develop cultivars with improved germination characteristics. These genetic studies have identified quantitative trait loci (QTL) associated with FSD traits in groundnut, and highlighted the polygenic nature of dormancy regulation. Candidate genes involved in seed coat development, hormone metabolism, and signal transduction pathways have been implicated in controlling dormancy-related traits.

To uncover the genomic regions and genes underlying seed dormancy in groundnut, a recombinant inbred line (RIL) mapping population bred from a cross between Tifrunner, exhibiting dormancy characteristic of the Runner type, and GT-C20, representing the non-dormant

Spanish type was employed [24]. This population was grown in the field over two years, and seeds freshly harvested from these plants were subjected to seed dormancy assessments at intervals of 7, 14, 21, and 28 days post-germination. Genomic analysis was conducted on the RILs using the SNP array 'Axiom_Arachis' 58 K. This investigation revealed two prominent seed dormancy Quantitative Trait Loci (QTLs) located on chromosome A04 and A05, which respectively accounted for 43.16% and 51.61% of the variation in phenotype. Notably, the QTL situated on A05 harboured a potential candidate gene (*Arahy.KB746A*, encoding an ethylene-responsive transcription factor). From the RIL population, individuals exhibiting either complete absence or pronounced levels of dormancy were singled out for further analysis.

A RIL population derived from ICGV 00350 (nondormant) × ICGV 97045 (dormant) was used for QTL-seq analysis to identify the key genomic regions and candidate genes [25]. Two candidate genomic regions spanning 2.4 Mb and 0.74 Mb on the B05 and A09 pseudomolecules, respectively, were identified controlling FSD. Two candidate genes—RING-H2 finger protein and zeaxanthin epoxidase—were identified in these two regions, which significantly express during seed development and control ABA accumulation. The marker GMFSD1 was validated on a diverse panel.

QTL mapping, utilizing a RIL population derived from the cross of ICGV 02266 (non-dormant) and ICGV 97045 (dormant), identified major QTLs on chromosomes Ah01, Ah11, Ah06, Ah16, and Ah17, explaining up to 74.7% of the phenotypic variance [26]. Moreover, leveraging transcriptomic data from dormant (Tifrunner) and non-dormant (ICGV 91114) genotypes, differential gene expression analysis identified histone deacetylases, histone-lysine N-methyltransferase, cytochrome P450, protein kinases, and ethylene-responsive transcription factor as significant regulators involved in hormonal dormancy regulation. Validation efforts encompassed the successful confirmation of six Kompetitive Allele-Specific PCR (KASP) markers across a diverse panel, inclusive of selected RILs from the same population and germplasm lines.

Silva *et al.* [27] studied the correlation between dormancy and the expression of *ARP*, *DMR1*, and *NCED* genes in both upright and runner groundnut seeds. They observed elevated expression levels of *NCED* and *ARP* in embryo tissues derived from runner genotypes. Conversely, heightened expression of *DMR1* was exclusively detected in the endosperm of upright varieties. NCED was proposed as a potential functional molecular marker for identifying dormancy in groundnut seeds. Transcriptional changes at three different developmental stages; the freshly harvested seed (FS), the after-ripening seed (DS) and the newly germinated seed (GS) stages were investigated by comparative transcriptomic analysis in a genotype (belonging to subspecies *hypogaea*) with dormancy [28]. This effort identified the important regulatory mechanisms operating at dormancy release and germination. Recently, Chaudhari *et al.* [29] presented an integrated view of proteomics, phyto-hormone profile, carbohydrate and lipid metabolism to unravel the mechanism of FSD. Activation of ethylene-mediated pathways being the main cause of pre-harvest sprouting, its effects were studied after ethrel administration. Seed storage-related proteins like Arah1, Arah2, AAI- domain containing protein, conglutin, Arah3/4, arachin, glycinin showed elevated expression. A decrease in ABA, SA and JA content while an increase in GA, IAA and kinetin concentration was observed.

How environmental signals perceived by the mother plant are translated to a particular dormancy state in the progeny seed?

Maternal plants are considered to play a pivotal role in regulating dormancy in their progeny. Chen *et al.* [30] reported that seed dormancy is primarily governed by the surrounding tissues of the embryo, namely the endosperm and seed coat in Arabidopsis. VERNALIZATION5/VIN3-LIKE 3 (VEL3) sustains maternal influence over progeny seed dormancy by initiating an epigenetic state within the central cell. This epigenetic programming sets the stage for the depth of primary seed dormancy during seed maturation. VEL3 co-localizes with MSI1 in the nucleolus and interacts with a histone deacetylase complex. Moreover, VEL3 exhibits a preference for pericentromeric chromatin and is indispensable for orchestrating deacetylation and deposition of H3K27me3 in the central cell. The epigenetic imprint established by maternal VEL3 persists in mature seeds, partly governing seed dormancy by suppressing the expression of the programmed cell death-associated gene ORE1.

Mechanisms underlying the dormancy process and controlling the germination (and repressing embryo growth) can operate in the embryo itself but also on the surrounding structures of the seed, all these structures can potentially be targets for changes induced by the

maternal environment that affects dormancy. The environment is expected to trigger certain biochemical and molecular changes that will in turn affect one or several steps of the germination process. These changes may relate to biochemical and physical properties of the seed coats (pericarp, testa) that are non-living in the mature seed, which in turn affect some physiological processes in the embryo (*e.g*. hormone metabolism or signalling). Sensing of environmental conditions before seed development, either in vegetative organs or in the already differentiated floral meristems, involves certain specific dormancy signals that are then transmitted to the seeds or may also result from broader changes in physiology (e.g. altered source-sink relations, or carbon and nitrogen metabolism) that will later impact on seed dormancy.

A few candidates acting as major regulators controlling dormancy by temperature during seed development have been identified and belong to the phosphatidyl ethanolamine binding protein (PEBP) family, which includes evolutionarily conserved family includes well-characterized members such as the 'florigen' FLOWERING-LOCUS (FT), TERMINAL-FLOWER1 (TFL1) and MOTHER-OF-FT-ANDTFL1 (MFT). Interestingly, cold temperatures affecting the mother plant before anthesis can induce deep-dormant states in *Arabidopsis* seeds, and this involves regulation of FT and also FLOWERING LOCUS C (FLC), which is another recognized component of the flowering pathway [31]. Research on the effects of cold temperatures suffered by mother plants by Chen *et al.* [32] provided insights into the accumulation of proanthocyanidin (PA) in seeds and this is mediated by decreasing FT protein levels that otherwise inhibit PA synthesis. Since FT inhibits PA synthesis in the maternal fruit tissues, these authors proposed that cold-induced inhibition of FT results in increased synthesis and transport (by phloem) of PA from the fruit to the developing seeds, where PA finally accumulate in the seed coat affecting the dormancy. A seed-specific, central regulator of seed dormancy and responsible for intraspecific variability for dormancy among *Arabidopsis* accessions is DOG1 (DELAY OF GERMINATION 1). In addition to high levels of DOG1 and ABA, a functional GA signalling pathway is also essential for dormancy promotion by low temperature during seed development [33].

Efforts on breeding for fresh seed dormancy

Seeds represent a critical input in groundnut production, emphasizing the necessity of utilizing high-quality seeds to maximize yield potential. Physiological seed quality, encompassing factors like germination rate, vigour, desiccation tolerance, and longevity, develops progressively during seed maturation. Seeds achieve their optimal physiological quality when all these attributes reach their peak levels. Consequently, breeding new genotypes that exhibit these desirable qualities is crucial for enhancing groundnut production and productivity. Understanding the physiological, genetic, and environmental factors influencing FSD in groundnut is essential for developing cultivars with enhanced germination performance and stress tolerance. Targeted breeding strategies aimed at incorporating dormancy-related traits and harnessing genetic diversity can facilitate the development of improved groundnut varieties resilient to environmental challenges and conducive to sustainable agriculture.

Considerable efforts have been made to identify and breed superior genotypes. Rathnakumar *et al.* [34] identified Spanish bunch germplasm accessions NRCG 14326 (INGR 10032; IC 0548192), NRCG 14336 (INGR 10033; IC 0582477), NRCG 14350 (INGR 10034; IC 0582478), and NRCG 14409 (INGR 10035; IC 0582479) as exhibiting FSD. Kumar *et al.* [35] assessed 35 Spanish bunch groundnut genotypes in 2012 and 2013 to discern fresh seed dormant varieties. They noted substantial genotypic disparities and observed interactions between genotype and year of production regarding germination percentage. Notably, three advanced breeding lines—PBS-12171, PBS-12169, and PBS-18035 were identified which exhibited fresh seed dormancy lasting more than four weeks.

To improve the efficacy and precision of traditional breeding methods through marker-assisted selection, a groundnut mini-core collection underwent evaluation for FSD using an in vitro germination assay over two seasons: the rainy season of 2022 and the post-rainy season of 2022–2023 at ICRISAT (Hyderabad) [36]. Molecular screening of the mini-core accessions with an allele-specific marker GMFSD1 effectively distinguished between dormant and non-dormant genotypes. Among the accessions tested, ICG 5827 (Virginia Runner), ICG 11457 (Virginia Runner), ICG 7000 (Virginia Bunch), and ICG 11322 (Virginia Bunch) from sub spp. *hypogaea* var. *hypogaea*, along with ICG 9809 (Spanish Bunch) from sub spp. fastigiata var. vulgaris, exhibited an FSD period lasting 2 to 3 weeks. These identified accessions hold

promise as potential donors in breeding programs aimed at incorporating dormancy traits and enhancing groundnut production to suit the diverse requirements of cropping systems in various countries.

Mutation breeding has facilitated the development of improved mutant varieties of groundnut such as TG 22, TKG 19A, TG 37A, and TPG 41 [37]. Furthermore, genome editing, a powerful technology for precise DNA sequence manipulation, provides opportunities for introducing FSD in addition to addressing various traits such as phytate reduction, aflatoxin resistance, and abiotic stress tolerance in groundnut [38].

Management strategies to overcome fresh seed dormancy

Management strategies for overcoming FSD involve physical, chemical, and environmental techniques to break dormancy and promote germination. Physical treatments like scarification and stratification disrupt dormancy mechanisms, while chemical treatments alter hormonal balances, and environmental manipulation influences dormancy release. Employing these strategies, individually or combined, effectively mitigates fresh seed dormancy, enhancing crop productivity. Pre-sowing treatments, mechanical scarification, exogenous hormone application, timely planting, appropriate seeding rates, and optimal soil moisture management are essential components of these strategies. The International Seed Testing Association (ISTA) recommends preheating seeds at 40°C for up to 168 hours to break dormancy. However, Wattanakulpakin *et al.* [39] investigated the use of ethephon to accelerate dormancy release, confirming it as a faster alternative method. Iron oxide, graphene oxide, potassium humate and sodium nitroprusside were also useful in breaking the dormancy and enhancing germination in groundnut [40, 41].

CONCLUSIONS

FSD poses a significant challenge to groundnut production, impacting crop establishment, yield, and quality. Considerable progress has been made in elucidating the physiological, genetic, and environmental factors contributing to FSD. Genetic markers and the candidate genes are now available for embarking on innovative strategies to overcome dormancy constraints and improve groundnut productivity. Marker-assisted breeding, genomic selection and gene editing methods can effectively be employed with continued interdisciplinary research efforts and collaborative initiatives to improve FSD and achieve sustainable groundnut production.

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