Review Article

The Chromatin Structure and Seed Function of Land Plants

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Abstract

seed formation is a survival strategy of higher plants that protects the juvenile embryo from unfavorable conditions and facilitates the dispersion of offspring into a new habitat. Plant seeds do not only benefit the ecological fitness of reproduction, but also contribute to the staple foods for human nutrition and caloric intake. A typical seed consists of highly organized structure, including a differentiated embryo, a nourish endosperm, and a protective seed coat or testa, but the physiological characters of individual seed considerably vary among the plant species. In addition, the complex web of environmental and endogenous factors appears to affect the quality and quantity of seed production. The molecular mechanisms underlying seed formation have been uncovered by the recent studies using the model plant Arabidopsis. In this article, we trace the evolutionary history of land plants that have acquired the abilities to create seed, and introduce the recent achievements of plant seed biology. Future perspectives to dissect the relevance between structure and function of plant seeds are also discussed by retrieving the past information of cytological studies.

INTRODUCTION

Plant reproduction is the process to create the new generation of individuals or offspring from the parents. There are two types of reproduction, namely asexual and sexual reproductions. Asexual reproduction proceeds without the fusion of gametes, and involves the regeneration of vegetative parts that are derived from the parent plant, such as stems, roots, or leaves. The plant created by asexual reproduction is genetically identical to the parent plant. Sexual reproduction produces seeds or spores by the fusion of female and male gametes. Genetic recombination occurs in sexual reproduction, and the offspring produced by sexual crossing within a species may carry different genotypes from its parents. Among the land plants, the bryophytes including liverworts, hornworts, and mosses, which are known to be non-vascular plants, produce with spores as the reproductive cell structures. These plants generate the reproductive organs called spore capsules at the tip of the diploid sporophyte, and form the spores by meiosis. When the spore capsules become mature, the spores are released and grow into the haploid leaf-like structures to conduct photosynthesis. The female and male gametes are produced by mitosis in archegonia and antherida, respectively. The motile sperm is released from the antherida and move into the female organs where it fertilizes with the egg cell and produce a zygote. The zygote grows into the sporophyte by mitotic cell division, and again repeats the life cycle.

Fern is a primitive vascular plant but does not produce seeds. Fern develops the reproductive organs called the sporangia on the underside of the fronds that include the spores. When the sporangia rapture, the spores sown on suitable growth conditions start to germinate and form the gametophyte, named prothallia. The prothallia produce both female and male gametes which fuse to create the next generation of sporophyte. Since these plants do not have vital vascular system and require much water to facilitate sexual reproduction, especially in the bryophytes, the plants without seed formation grow in relatively moist environments.

Most of land plants produce the offspring from seeds. The structural differences between spore and seed are referred that a spore is a single cell and tiny, while a seed is a highly organized multicellular organ containing the differentiated embryo, the nutrient reserves, and the seed coats. The origin of seed plants has been a question under debate that still remains unsolved. It is hypothesized that one of the important events leading to ancestor seed plants is an evolution of heterospory [1]. In general, spore-bearing plants create tiny spores equal in size, while heterosporic plants produce two different sizes of spores, dubbed as megaspores and microspores. Megaspores are thought to either become free-living female gametophytes or to later evolve to megasporangia, megagametangia and ovaries by packaged with the sporophytes. Microspores appear to become free-living male gametophytes or to develop into small micro sporangia, microgametangia, and anthers within the sporophytes.

Currently, the seed plants are classified into two groups, namely gymnosperms and angiosperms. Gymnosperms composed of cycads, ginkgo, yews and conifers do not form flowers, in which the ovules or seeds are not enclosed in an ovary.

Angiosperms are flowering plants whose ovules are enclosed in an ovary. There are a total of 720 species of living gymnosperms and at least 250,000 species of angiosperms [2]. Angiosperms account for about 80% of all the living plant species, indicating the significant advantages of angiosperms for ecological fitness on the current conditions of Earth.

ECOLOGICAL BENEFITS OF SEED FORMATION

Fertilization of angiosperms undergoes inside of an ovary. After the fusion of female and male gametes, the zygote of an ovule and a sex cell nucleus from the pollen develops into the small embryonic plant, and suspends the growth. While the triploid endosperm, which is derived from two egg cells and a sperm cell, and the ovule from the mother plant give rise to the nourish and protective tissues in the developing seed, respectively. The resultant seed of angiosperms consists of three basic parts, including a zygotic embryo, a storage endosperm, and a protective seed coat or testa. The nourish functions of angiosperm seeds are occasionally discussed by the analogy of the mammalian placenta that serves to support and nourish the growing embryo until birth [3]. The size, shape, number, color, and appearance of seeds significantly vary depending on the plant species. Seeds serve versatile roles for the ecological fitness of plants, in which key functions are protection of the embryo, dispersal of the offspring into new locations, and avoidance of unfavorable conditions by dormancy. When the fruits reach mature, the included seeds are dispersed away from the parent plants by a variety of ways, such as hitching on animals, drifting in water flow, floating in the wind, and feces of animal foods. Seed dispersal benefits to the sessile plants in order to avoid overcrowding and competition among the same species as well as extend the living habitat into a new place [4].

The spores of mosses and ferns are also carried by the wind and contribute to the dispersal of offspring, but these spores are very easy to germinate when sown to the optimal conditions and never cancel the primary growth once germination is taking place. Seed plants have an ability to prevent germinations during unfavorable conditions, when the possibility for leaving offspring is low. Seed dormancy could promise the time to disperse from the parent plants and extend a survival opportunity of the offspring for many months or years at the given habitat.

Seed dormancy

Seed dormancy is referred to a mechanism that delays or prevents germination until the growth conditions become optimal for the survival of seedling [5]. The seeds at dormancy are incapable of germinating unless all of the dormant agents will be over come even under ideal conditions for the usual non-dormant seeds. The environmental factors that release the seed from dormancy are various depending on the plant species, such as water, temperature, light, oxygen, gases, and photoperiod [6]. It is likely that seed dormancy is categorized into five general classes of morphological, physiological, morphophysiological, physical, and combinatorial dormancy, which are based on the physical barrier of seed coat to take up water, the maturity of embryo, and the physiological dormancy of embryo itself.

Not all plants have an ability of seed dormancy. Seed dormancy

is distributing at a wide range of the plant kingdom. It is known that the levels of seed dormancy are different among the ecotypes within the same species, suggesting that seed dormancy might have been acquired by regional adaptations in each living habitat [7]. Physiological dormancy (embryo dormancy) is frequently lost from seeds during seed maturation for several weeks (dry after-ripening), but some plants retain seed dormancy in maturing dry state and fail to germinate even after imbibition, in which cellular metabolisms are active. The plants can recapitulate physiological dormancy if the surrounding conditions of seeds become adverse and are not favorable for germination (secondary dormancy).

Cold moist and warm stratifications or chemical treatments of plant seeds are horticultural techniques in aiming to break dormancy and synchronize germination by the artificial procedures. The levels of seed dormancy have been declined during domestication and selection of the cultivated plants because of selective pressures by plant breeders or farmers, although the wild ancestors carry seed dormancy. The lack of seed dormancy is beneficial for commercial purposes that keep the life cycle of plants quickly, while precocious germination or sprouting of crop seeds prior to harvest stands serious issues in agricultural production. In the mature dry seed, metabolic activities are low and the cells in seed do not require nutrients, oxygen, and water. Thus, dormancy can also benefit the storability of plant seeds for longer time.

The genes responsible for seed dormancy

Seed dormancy is known to be established during seed maturation and reach to a maximum level prior to harvesting. The precise mechanisms of seed dormancy have been understood mainly using the model dicot Arabidopsis. The Quantitative Trait Locus (QTL) analysis among the local accessions of Arabidopsis revealed that natural variation of seed dormancy is determined by multiple gene locus and different molecular pathways [8]. The Cape Verde Islands (Cvi) accession exhibits a higher level of dormancy than those of the other ecotypes that are generally used in the laboratories, such as Columbia (Col) and Landsberg erecta (Ler), and it provides useful systems for the study of seed dormancy [9]. The Recombinant Inbred Line (RIL) constructed with Ler and Cvi [8,9], the genome-wide profiling of transcriptome [10], and the proteome analyzes at the different states of Arabidopsis seeds [11] accounted for the gene functions responsible for seed dormancy.

The testa-defective mutants, including *transparent testa* (*tt*) and *aberrant testa shape* (*ats*), significantly reduced seed dormancy, indicating the importance of a physical shield for seed dormancy [12]. The mutations of the transcription factors, including *abscisic acid insensitive3* (*abi3*) [13], *fusca3* (*fus3*) [14], *leafy cotyledons* (*lec1* and *lec2*) [15], resulted in the aberrant seed maturations, coupled with the pleiotropic phenotypes including reduced seed dormancy. These transcription factors coordinately regulate the phase transition from the embryonic growth to the seedling development. These observations further support an idea that the correct program of seed development is required to establish proper seed dormancy.

Abscisic Acid (ABA) is a phytohormone that plays a crucial role for induction and maintenance of seed dormancy [16], while

gibberellins (GA) are required for initiation and completion of germination [17]. It is well known that the commence of germination is regulated by the antagonistic effects between ABA and GA. Supporting this idea, the mutations of perception, signaling, metabolism, or catabolism genes for these two ormones substantially affected the levels of seed dormancy and germination [18,19].

The dormancy-specific genes

The most intriguing finding of these studies is the discovery of seed dormancy-specific genes. Delay of Germination 1 (DOG1) has been identified by the major QTL for seed dormancy between Cvi and L*er* [9]. The *dog1* mutant completely lacks seed dormancy and exhibits no other notable phenotypes besides the change ofseed longevity [20]. The DOG1 gene constitutes a small gene family in Arabidopsis and encodes a plant-specific unknown function protein. The homologous genes for DOG1 have been widely found in other plant species, including lowerdormant Arabidopsis accessions, wheat, and barley [21]. Forced expressions of the DOG1-like genes prepared from wheatand barley give rise to increased seed dormancy in lower dormant Arabidopsis. Furthermore, the protein level of DOG1 in maturing Arabidopsis seeds shows a positive correlation with the levels of seed dormancy, and further declines during dry after-ripening [22]. The line of evidences suggests that DOG1 is a key regulator of seed dormancy conserved among the seed-bearing plants.

Longevity is another important trait of plant seeds [23]. Each seed has a limited viability. If proper conditions would not be given, a seed fails to germinate, repeats the cycle of seed dormancy, and finally deactivates. This means the death of a seed. The life-span of seeds is known to vary depending on the plant species, and seed longevity is strongly influenced by non-genetic factors, such as the environmental conditions during seed maturation, the moisture contents, the maturity or quality of harvested seeds, and the post-harvest storage conditions. But seed longevity within the same species appears to be genetically designated.

From the QTL analysis for seed longevity, DOG1 also plays an important role in determining the span of seed viability [24]. The *dog1* mutant showed longer seed viability, associated with the complete loss of seed dormancy. This implies a negative correlation between the depth of seed dormancy and the length of seed longevity. This finding is surprising because of an objection against the previous concept that dormant seed is highly tolerant to biotic and abiotic stresses, and subjects to longer life-span. Further investigations of DOG1 should be needed to shed light on a trade-off that exists between seed dormancy and longevity.

The chromatin control and seed function

The genome DNA in the nucleus is wrapped with core histone and condensed into a complex structure called chromatin. Chromatin structure is highly complex consisted of several subdomains and distinct architectures, and intimately linked with the control of gene function. The recent cytoelectron microscopy and small-angle X-ray scattering (SAXS) analyzes using animal cells suggested that high-order chromatin structures are not common unlike those described in molecular biology textbooks,

and more randomly distributing in mitotic and interphase cells than previously expected [25]. The transcriptionally silenced nuclei of chicken erythrocyte exhibit unusual chromatin structures that are occupied by 30-nm chromatin fibers, indicating cell-type or species-specific chromatin structures [26].

The chromatin modulators play important roles in a variety of nuclear functions by influencing the assembly of chromatin factors through epigenetic modifications. The previous studies for seed dormancy have also predicted the importance of chromatin control [5]. During the screening for reduced seed dormancy in Arabidopsis Cvi, Reduced Dormancy 4 (RED4)/ Histone Mono Ubiquitination 1 (HUB1), HUB2 [27], and RDO2 [28] have been identified. HUB1 and HUB2 encode C3HC4 class RING finger proteins that are responsible for monoubiquitination of histone H2B. RDO2 encodes transcription elongation factor SII (TFSII). The general role of TFSII is suspected to interact with RNA polymerase II (Pol II) and assist efficient transcription by stimulating the potential activities of Pol II that bypass inhibitory blocks against elongation process with a cryptic and nascent cleavage of RNA [29].

HUB1, HUB2, and RDO2 proteins are likely to constitute the large protein complex, named the RNA polymerase-associated factor 1 complex (Paf1C). Paf1C is highly conserved in eukaryotes, and plays critical roles in coupling of elongation process of the Pol II-mediated RNA transcription and chromatin modification [30]. Expression levels of the genes for seed dormancy, including DOG1, are markedly influenced by the mutations of HUB1, HUB2, and RDO2 [27,28], suggesting that the particular Paf1C may act under seed maturation process, and maintains proper expression of a subset of genes responsible for seed dormancy. The recent attempt to identify single nucleotide polymorphisms deeply associated with seed dormancy using 113 accessions of Arabidopsis has also illustrated the involvement of histone deacetylase gene HD2B in dormancy and/or germinability of plant seeds [31].

The chromatin sturucture in plant seeds

The key genes for seed development and dormancy have been uncovered by the recent efforts of molecular genetic approaches, however, it has not yet been elucidated what kind of the changes would be virtually occurred by the actions of these gene functions. Van Zanten et al. examined the morphology of cell nuclei during maturation of Arabidopsis seeds and confirmed a significant decrease of nuclear size in the embryonic cotyledon of maturing seed [32]. The size of nuclei again increased during imbibition and germination, indicating the programed control of nuclear size involved in seed function.The tested seeds showed a similar reduction of nuclear size regardless either low- or high-dormant Arabidopsis accessions. This result suggests that nuclear size reduction should be independent of seed dormancy and possibly implicated with the general function of plant seeds such as drought tolerance. On the other hand, the double mutation of HUB1 and 2 conferred a noticeable impairment of nuclear size reduction during seed maturation, coupled with reduced seed dormancy [32]. This finding implies certain connection with passive histone modifications and nuclear size control.

The nucleus is the master genetic library of the eukaryotic

cell. In the pioneer works of plant science, the relationships between structure and function of nuclei in plant seeds have been well documented by cytological and cytochemical studies [33]. In the quiescent embryo, the cells blocked at mitosis have never been seen and the majority of cells are arrested at the G1 phase. The reasons for G1 arrest are currently explained by the changed cell-cycling activities of D-type cyclins in part [34,35]. There were technical difficulties to observe intact cell structures of the dry seeds due to dryness, compactness, and hardiness of the quiescent embryos, but several microscopic analyzes have compared morphological changes between the quiescent and germinated embryos.

The most common observations among the quiescent embryos were the highly condensed state of chromatin. Loosening and dispersion of chromatin structures were also confirmed during early germination process. Possible factors responsible for chromatin condensation have been speculated due to the severe water loss during desiccation, the elevated concentrations of cations (Mg^{2+} and Ca^{2+}), and the changes of histone subspecies or modifications during seed development [33]. *In vitro* study using the spread chromatin on the solid surface showed larger sizes and thicker fibrils of nucleoprotein granules in nuclei of the quiescent embryo cells, while those structures disappeared in early germination [33]. These observations demonstrated that qualitative changes must occur in some parts of local chromatin structures of plant seeds (Figure 1).

The physiological roles for chromatin compaction

Chromatin compaction is frequently observed for mitosis of eukaryotic cells to maintain the integrity of genome function, but detailed roles for the packaging of genome DNA have not been elucidated particularly in interphase cells. Takata et al. used permeabilized nuclei from HeLa cells that were attached on poly-L-lysine-coated glass surface and examined whether the high-order chromatin structure is involved in the vulnerability for DNA-damaging [36]. The results showed that the frequency of double-strand breaks in compact chromatin after ionizing irradiation was significantly lower than that observed in relaxed chromatin. This finding suggests that chromatin organization plays an important role in genome integrity by changing the susceptibility to cytotoxic stresses for DNA damage, such as γ-rays, heavy ions, and harmful chemicals.

DNA damage is a serious problem for survival of all living organisms. Plant seeds are subjected to toxic DNA damages that naturally occur during desiccation and also storage period [37]. Repair of DNA damage in plant seeds appears to be crucial to maintain genome integrity and prevent decline in seed quality [23]. DNA ligases catalyze the joining of DNA ends and play important roles not only in regular metabolisms but also emergent DNA repair. Arabidopsis possess canonical and novel-class of DNA ligases. Waterworth et al. reported physiological roles for DNA ligases in genome repair during seed imbibition [38]. The genes for type IV (AtLIG4) and novel class (AtLIG6) DNA ligases are expressed early in normal germination of Arabidopsis seeds and also in dormant hydrated Cvi seed. The atlig6 and the atlig6/atlig4 double mutants were hyper sensitive to artificial genome stresses and displayed delayed germination, accelerated aging, and reduced viabilities of seeds. This study provides evidence that the repair of genome damages, which are accumulated
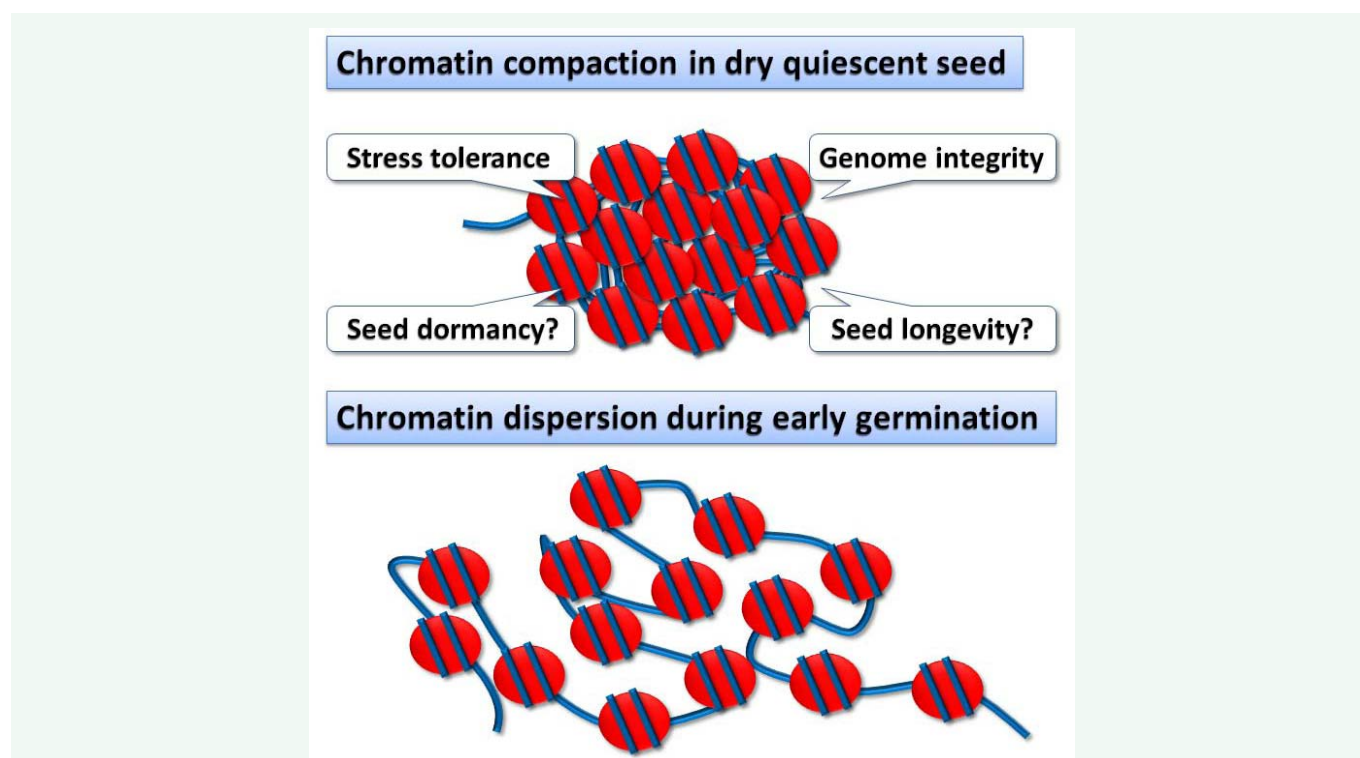

Figure 1 The general feature of chromatin structures observed in dry quiescent and early germinating embryo cells in the plant seeds. The possible roles for chromatin compaction in dry quiescent seeds are denoted [33,36].

Figure 2 The main post-transcriptional modifications of plant core histones. The sites of histone modifications are summarized with reference to the published information [45,48]. The types of histone modifications are depicted in the figure: acetylation (A), methylation (M), phosphorylation (P), and ubiquitination (Ub). The number adjacent with each amino acid represents its position in the histone subspecies.

over seed storage and early imbibition, is important for better performance of seed viabilities, and the protective mechanisms for genome integrity are indeed mobilized in plant seeds.

The analysis of high-order chromatin structure in plant seeds

High-order chromatin structure is organized by numerous factors, including histone variants, histone modifications, DNA methylation, and recruitment of non-histone structural proteins [39]. Research on chromatin dynamics are promising to illustrate how nuclear organization on the molecular level contributes to seed functions. Fluorescent *in situ* hybridization, live-cell imaging with fluorescent protein-tagged probes, and genome-wide Chromatin Immunoprecipitation (ChIP) analyzes are useful techniques to indicate the dynamic changes in chromatin organization [40]. The use of two dimensional polyacrylamide gel electrophoresis (2D-PAGE) in conjugation with Mass Spectrometric (MS) technology became a major tool in a wide range of proteomics studies [41]. Chibani et al. have characterized the mechanisms for seed dormancy in Arabidopsis by proteomics approach using freshly harvested dormant and after-ripened non-dormant Cvi seeds [11]. The data revealed that a specific set of proteins accumulated or disappeared in early imbibition, and some of which were likely associated with the release from seed dormancy. The identified proteins showed only limited correlation with the data obtained from the previous transcriptome analysis [42]. This raises the possibility that the release from dormancy is not depend on transcription response but rather controlled by de *novo* protein synthesis from the stored mRNAs or posttranslational modifications of the preexisting proteins.

Proteomics approach has been also used to dissect posttranslational modifications of the objective proteins [41]. The 2D-PAGE is based on two separation steps, in which the first step usually employs isoelectric focusing. This process is defined to separate differently charged proteins by their isoelectric points on an immobilized pH gradient. Specific histone variants or post-translational modifications in the nucleosome are known to generate distinct chromosomal structures for the regulation of gene function [43], but the conventional 2D-PAGE should not be appropriate for clear separation of histone proteins due to their highly basic nature [44]. To this end, purification of nuclear

fractions and subsequent analysis of subproteomes is the better way to gain useful information for histone analysis.

Zhang et al isolated core histones from the 4-weeks grown Arabidopsis plants and separated into distinct member of histone subspecies by reverse-phase HPLC [45]. The MS/MS analysis of purified proteins provided reliable information of the site and type of post-translational modifications of Arabidopsis core histones (Figure 2). In addition to the canonical modifications of plant histones, including methylation, acetylation, and phosphorylation, they confirmed the ubiquitinated form of histone H2B in the C-terminal sequence (K143, amino acid residue and position). It has not yet been elucidated as to how the ubiquitination of H2B might influence on the nuclear functions of plants, but the ubiquitination of H2B is known to control a broad range of cellular processes [46]. It is noteworthy that the mutation of Arabidopsis HUB1 and 2, which are responsible for monoubiquitination of H2B, resulted in disruption and deregulation of microtubule assembly induced by the treatment of microbe toxins [47]. This finding suggests that H2B monoubiquitination is capable of modulating the dynamics and organization of microtubules and involves the plant defense response. The implications of Jumonji C (JmjC) domain-containing proteins in demethylation of histone H3arginine (A) 2 and H4A3 are also suspected during the light-induced germination of Arabidopsis seeds [48].

The nuclear actin-related proteins are known to participate in regulating DNA compaction to allow basal gene expression and silencing [49]. The nuclear matrix constituent 1-related nuclear proteins, Little Nuclei 1 (LINC1) and LINC2, are important regulators of the nuclear size determination [50]. The gene functions responsible for the determination of plant nuclear size have been explored by the recent studies, but the precise mechanisms controlling in nuclear size and chromatin compaction in response to environmental stimuli or growth periods remain poorly understood. Further investigations are needed to clarify the specific histone variants or modifications leading to the dynamics and organization of plant nuclear architectures. The obtained data might have been applied to better understandings for the relevance between structure and function of plant seed nuclei.

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