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THE INFLUENCE OF PHYTOHORMONES ON SEED DORMANCY AND GERMINATION IN DESERT PLANTS: A COMPREHENSIVE REVIEW

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ABSTRACT

The fundamental processes of seed dormancy and germination enable plants to survive, procreate, and persist in desert ecosystems characterised by erratic rainfall, extreme temperatures, and a scarcity of resources. Here, seeds go through a number of hormonal and physiological changes that prevent them from germinating unless the right circumstances are met, which is extremely uncommon. Gibberellins (GA) and abscisic acid (ABA) are the two primary antagonistic hormones that control the dormancy–germination switch; one promotes radicle protrusion and seedling growth, while the other supports quiescence and stress tolerance. Furthermore, in addition to their interactions, auxins, cytokinins, ethylene, brassinosteroids, and jasmonates also influence hormone sensitivity, reserve mobilisation, and mechanical barrier deterioration. Reactive oxygen species (ROS) and nitric oxide (NO), two very small molecules, can function as environmental cues that trigger hormonal cascades. Desert plants are so well-equipped that they can alter the way their hormones are metabolised while still managing to keep their seeds in the subterranean soil, allow them to cycle through dormancy, and allow them to germinate shortly after the rain, albeit briefly.

Recent molecular mechanisms have shown that transcription factors, hormone carrier proteins, and catabolic enzymes are involved in the precise regulation of these processes, and ecological studies have identified dormancy heterogeneity and bet-hedging as two strategies for plant survival in those conditions. We should welcome and use this type of information for climate change adaptation, dryland agriculture, and restoration ecology. This review's integration of genetics, ecology, and hormone regulation is a potent tool for advancing the field of seed biology and, in turn, for enhancing the management of desert ecosystems through the application of creative techniques.

INTRODUCTION

Desert ecosystems are the most harsh, severe, unstable, and unpredictable types of ecosystems on our planet. Here water shortage, radiance, and extreme temperatures are the basic environmental factors that are highly selective with regard to life-history strategies that ensure their survival both spatially and temporally; in this context, the role of annual plants and seeds appear to be very important since seeds serve as very strong dispersal and persistence units that provide the populations with a possibility to travel through the difficult periods and tap the good or favorable ones, therefore it becomes necessary to know the seed survival strategies, particularly the ones referring to dormancy and germination, so as to be able to explain plant acclimatization, community changes, and restoration that are viable in arid lands [1]. Seed survival strategies adopted by desert flora are represented by seed heteromorphism and bet-hedging by means of soil seed banks having varying degrees of persistence, variability in dormancy states both spatially and temporally (dormancy cycling), and morphological or physiological features of the seed coat (testa) that along with controlling water intake also provide the embryo with protection; these strategies together are the means which populations use to survive against episodic rainfall thus ensuring recruitment that is staggered thus the risk of cohort failure in stochastic desert climates is minimized [2]. Dormancy cannot merely be seen as a lifeless stop of growth but an evolved and adjustable feature is the seed dormancy that stretches from physical dormancy which is caused by water-impermeable testa layers to physiological dormancy that is regulated by internal metabolic and hormonal states and this regulation occurs in a way that seedlings on emergence should be the ones to have the highest probability of survival, thus the individual fitness as well as population persistence in deserts are directly affected where favorable conditions are short-lived and unpredicted [3]. Seed dormancy and germination phenology from the ecological standpoint are the factors that decide the community composition, the types of interactions between the competing species, and the ability of ecosystems to recuperate after being disturbed, the reasons which are seed bank composition and the percentage of seeds that germinate in any recruitment event being the main determinants of these short- and long-term vegetation trajectories in arid and semi-arid regions [4].

Basically, the choice between staying dormant and starting germination is managed by a system of phytohormones and signaling molecules that are connected. ABA (Abscisic Acid) and GA (Gibberellins) are the two main components of this system that are in opposition to each other. While ABA supports and enforces dormancy in the period of seed development and in cases when imbibition happens under unfavorable conditions, GA activates embryo growth and germination when the environment is suitable, so the change in the ABA:GA ratio acts as a biochemical switch that changes the developmental fates of a seed depending on the nature of the environmental inputs (moisture, temperature, light) [5]. Auxin is steadily becoming recognized as a crucial regulator that, in addition to ABA and GA, can enhance dormancy and work with ABA signaling pathways. Hormone metabolism and signaling cascades during imbibition are influenced by small reactive molecules like nitric oxide (NO) and reactive oxygen species (ROS), while ethylene, brassinosteroids, cytokinins, and strigolactones can cause dormancy release or seed sensitization to GA [6].

The hormonal networks in the desert are responsive to the tiniest environmental cues that impact them. To name a few, fluctuating temperatures between day and night, wet-dry cycles, the onset and severity of the rainfall all interact with hormone synthesis and catabolism (for instance ABA biosynthesis and CYP707A-mediated ABA catabolism) to trigger dormancy depth and germination windows—these are the very mechanisms that cause dormancy cycling and the seasonal germination pulses that have been observed in arid annuals and ephemeral communities [7]. The seed coat dermatologic is the first line of defense and at the same time, an active maternal tissue that provides nutrients such as hormones and metabolites to the embryo; in many legumes and other hard-seeded species the physical dormancy imposed by the testa (hardseededness) comes from the cuticles, suberin or phenolic impregnation, and macrosclereid structures that prevent imbibition until the environmental conditions or mechanical, thermal, or biological processes make the coat permeable thereby linking the external habitat changes with the internal hormonal state of the seed [8]. The point is that the testa is less talkative. It carries out functions like synthesizing and transporting ABA, auxin, and cytokinins, regulating antioxidant metabolism and transfer cell differentiation, as well as cell wall degrading activities through the action of hydrolytic enzymes. At the same time, structural features (cracks, light-line, pits) in it dictate the sites of water entry that influence the phase transitions of imbibition and the timing of the rupture of the testa—events that are linked to the embryo growth potential regulated by GA [9].

Some of the environmental signals that are familiar in desert ecosystems like microbial action, high or fluctuating temperature, pulses of moisture, fire or solarization can change the physical dormancy of desert seeds or the ABA: GA balance to germination. Because of that, the interaction of physical and physiological mechanisms is what keeps the seeds viable in seed banks in the soil for such a long time, at the same time, they still have the ability for quick recruitment when the conditions are favorable [10]. On the population scale, maternal effects, phenotypic plasticity, and genetic variation in the dormancy-related pathways that allow local adaptation are the main factors: the seed produced in different maternal environments or in different seasons may differ in dormancy intensity, testa properties and hormone content; thus, producing heterogeneous seed banks that distribute the germination risk over time and that's how they stabilize the populations in front of environmental unpredictability [11]. From a practical viewpoint, of course, the identification of hormonal and structural controls of dormancy has real implications for the restoration of the degraded desert lands, seed storage ex situ as well as seed management of invasive or weedy species: the manipulations that change ABA catabolism, GA sensitivity, or that can simulate natural dormancy-breaking cues can help reveal the germination synchrony for revegetation, and at the same time, hardseededness and testa chemistry can be a guide scarification and pre-treatment strategies for sowing native species [12]. Without a doubt, desert seed survival strategies combine (state) the use of physical defenses, hormone-mediated developmental gating, and life-history variation in a way that is somewhat ecologically tuned. Research linking testa chemistry and anatomy to hormonal networks like ABA, GA, auxin, ethylene, brassinosteroids, cytokinins, and ROS/NO, as well as to field-scale germination patterns, is a first step in understanding how desert plants coexist and how we can apply this understanding to conserve and restore areas impacted by the ongoing climate change [13].

Additionally, understanding the relationship between dormancy cycling and yearly rainfall patterns provides insight into plant population dynamics and climate change adaptation [14], while recent advances in molecular genetics suggest that hormone biosynthesis genes, transcription factors, and chromatin remodeling are the primary determinants of dormancy depth and germination timing [15]. The influence on dormancy release is also a result of interactions between soil microbial communities and seed coats. Additionally, when there have been infrequent precipitation events, germination may be possible in small pockets due to the deterioration of seed coats brought on by microbes or the weakening of the testa [16].

The ability of desert annuals to remain in the desert for a long time is based on seed heteromorphism, where morphologically different seed types from the same parent plant differ in the depth of dormancy and dispersal characteristics, thus further diversifying the recruitment strategies [17]. Physiological experiments reveal that the abandonment of dormancy in desert seeds is in principle the case when ABA levels are lowered and GA sensitivity is increased due to the seasonal variation, a process that is very rapid if the temperature changes are involved, as it is in the case of shallowly buried seeds [18]. Reactive oxygen species (ROS) generation in seed imbibition acts as a positive signal which partly brings about the weakening of the shell mechanical resistance and seed promotion via GA signaling, thus combining environmental stress and developmental control [19]. This switch is controlled by the interdependence of the ethylene and ABA systems, where ethylene encourages shell breaking and radicle extension when water availability is adequate [20]. In order to maintain dormancy, auxin transport and perception in seeds interact with ABA. However, if GA content is increasing, they can promote the release of dormancy in desert seeds through the elongation of embryo cells, illustrating the complexity of hormonal balance in desert seed fate [21]. Brassinosteroids support germination by negating the ABA effect and raising ROS production, conversely cytokinins energize cell division in the embryonic zone and, both of them, are acting downstream of GA signaling [22]. The research on strigolactones has most commonly focused on their function in parasitic plant seed germination; however, new evidence confirms their interaction with light and temperature cues in desert annuals to modulate the dormancy release [23]. In addition to NO, other small reactive molecules which can be signaling intermediates and thus have the capability of dormancy breaking by the induction of ABA catabolism genes and the enhancement of GA responsiveness are [24]. Synthetic phytohormone networks and environmental stimuli that are deployed in concert constitute a finely balanced system that allows desert biota to realize maximal fitness in the harshest of all earthly environments, thus representing the evolutionary sophistication of seed dormancy and germination as adaptation strategy [25].

2. Seed Dormancy and Germination in Desert Plants:

Seed dormancy and germination in desert plants are the main adaptive strategies which have an impact on survival and recruitment in the harshest ecosystems on earth, where the amount of rain is not predictable and the temperature is extreme. The varieties of dormancy seen in desert areas are different and consist of physical dormancy (PY), physiological dormancy (PD), combinational dormancy (PY + PD), morphological dormancy (MD), and morphophysiological dormancy (MPD), with each one giving different ecological benefits under random conditions [26]. Seeds of desert regions and the Great Basin perennials are mostly a mixture of PD and PY seeds. For example, in hot deserts like the Pilbara and Great Sandy Desert of Australia, the seeds are mainly PY and PD and dormancy has been found in up to 88% of the surveyed perennial species that is majorly physiological and about 30% showed seed coats that are impermeable which is characteristic of physical dormancy [27]. Cold desert perennials of the Great Basin mostly display PD which is usually resolved by natural cold stratification during a long winter or by dry after-ripening in summer [28]. The ecological significance of these dormancy mechanisms is, they are capable of staggering germination over multiple seasons, which is a typical bet-hedging strategy that lowers the risk of entire cohorts dying during drought years. For instance, herbs seeds from the perennials in the Great Basin were found to be associated with delayed germination niches that made the recruitment to be linked with favorable late winter and spring conditions hence the seedling establishment potential was increased [30]. In desert restoration attributes, however, the situation is quite different since dormancy turns into a big trouble because restoration practitioners need quick, safe, and predictable germination to have ground cover and outcompete invasive species; therefore, it is very important to deal with dormancy through treatments. [31]

The environmental cues that greatly influence the dormancy cycle and germination are the changeable temperatures, moisture in the soil, and the exposure to fire-related signals like the smoke-derived karrikinolide (KAR1). These have all been proved to stimulate dormancy loss and germination in Australian desert perennials [32]. Among 43 species from the Great Sandy Desert, Commander et al.'s study found that just by introducing KAR1 germination could be triggered in almost a quarter of the species representing different life forms. Besides that, the release of the germination temperature and the increase of the germination speed was also observed [33]. The same goes for the externally applied gibberellic acid (GA3), which is a perfect example of a biochemical mimic of a natural stratification process that has been proven to be effective in the awakening of the seeds of cold desert taxa that are in dormancy [34]. The environmental filters like rainfall in the season have the power of imposing the strong selective pressure on the characteristics of the seeds: seeds that germinate quickly after ephemeral rains are the ones that will have a competitive edge, though this strategy can go wrong at a time when the soil moisture is not sufficient for establishment thus emphasizing the adaptive equilibrium that exists between dormancy depth and germination responsiveness [35]. The distribution of dormancy classes is also distinctly different by life form, in this case, the two, shrubs, and perennials not only have a larger degree of PD, but also of physiological dormancy while the populations of annuals, in most cases, are more variable in dormancy levels within them, hence strengthening the survival of populations under the regime of rainfall that are not predictable [36]. Restoration practitioners working in hot and cold deserts have always had to deal with the problem of ecological variability by adjusting the dormancy-breaking techniques to the ecology of the target flora [37]. As an example, one can mention that cold desert legumes with PY were able to be scaled operationally by pneumatic scarification while post-mining rehabilitation in Triodia pungens, the keystone grass in Pilbara, was very much improved due to priming with KAR1 that enabled establishment to take place [38]. It is this way that the desert dormancy phenomena end up performing the function of risk-widening agents and at the same time the population synchronization with the environmental niches that are the most favorable while the restoration efforts when not managed properly are still being obligated by dormancy to the use of different methods that include the understanding of ecology and seed enhancement technologies [39].

The chart in figure 1 portrays that physiological dormancy (PD) is the major seed dormancy type most commonly found in desert ecosystems by far, with physical dormancy (PY) as the next most frequent group making about one-third of the species. The reason why these two types dominate the dry areas is that they allow the plants to have the flexibility of postponing germination until the environmental conditions become suitable. The frequency of combinational dormancy (PY+PD) is lower, however, it includes those seeds that have twofold protective mechanisms, whereas morphological (MD) and morphophysiological dormancy (MPD) do not only occupy the least portion but also are the furthest from hot deserts, which agrees well with the nonexistence of underdeveloped embryos. The fraction of non-dormant seeds that is quite small shows that some of the species are those which are able to germinate quickly just after the rain - thus they can utilize the water that is quickly lost. To sum up, the prevalence of PD and PY indicates that the evolutionary processes of staggered germination and risk-spreading as survival and reestablishment strategies in the desert's off-and-on climate have been deeply engrained in these species.

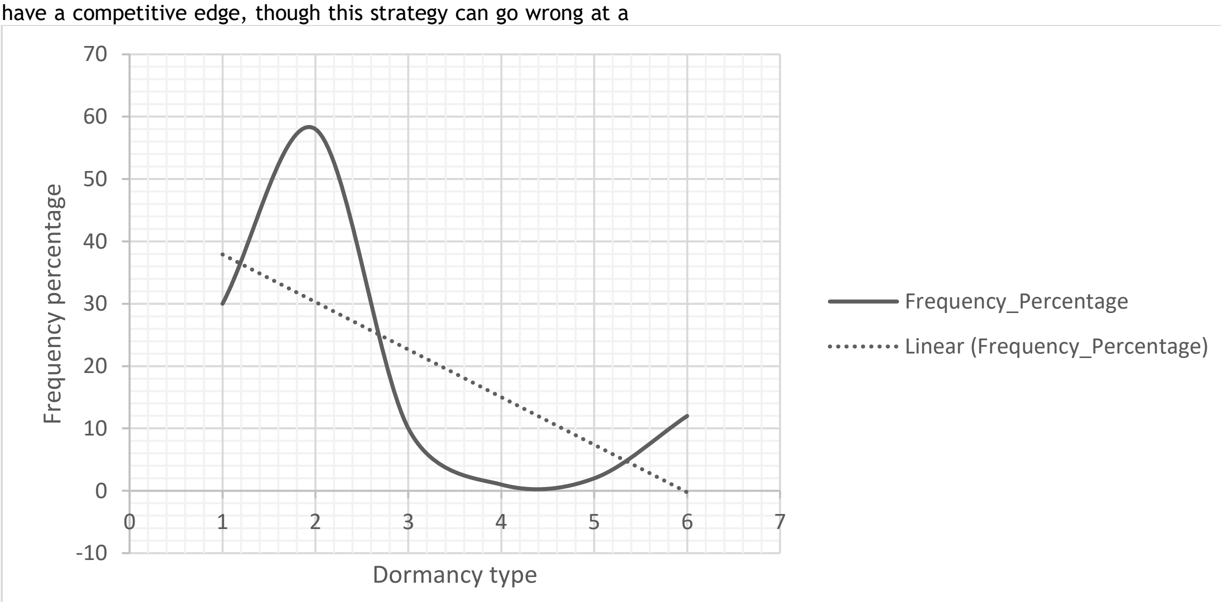

Figure.1 relative frequencies of different seed dormancy types in desert plants, illustrating that those with physiological dormancy (PD) and physical dormancy (PY) are the most common, while the occurrence of combinational (PY+PD), morphological (MD), and morphophysiological dormancy (MPD) is lower. The figure combines data from Commander et al. (2017) and Kildisheva (2019).

3. Phytohormones in Seed Dormancy and Germination:

Phytohormones are the main operators of the seed dormancy-germination decision, working as one very interconnected network, wherein abscisic acid (ABA) and gibberellins (GAs) represent the most antagonistic module: ABA is the promoter of dormancy at seed maturation stage and when seeds are imbibed under unfavorable conditions, on the other hand, GAs lead embryo growth as well as endosperm weakening resulting in radicle emergence besides, biosynthesis, catabolism (e.g., CYP707A-mediated ABA breakdown) and sensitivity changes are implemented simultaneously to alter the dynamic ABA:GA balance which ultimately changes environmental signals to developmental outcomes [40]. Besides, that, auxins, jasmonates (JAs), ethylene, brassinosteroids, cytokinins, and strigolactones are the participants in dormancy depth and germination responsiveness which modulation is the main role of ABA/GA metabolism or signaling by these hormones: On the one hand, auxin may become the factor which is able to confirm dormancy through the enhancement of ABA signalling as well as the reduction of GA responsiveness, on the other, ethylene and brassinosteroids are the groups of substances which usually oppose ABA effects and facilitate germination via the easy biochemical pathways i.e. those which make GA action more effective or just simply remove the blocks existing in embryo growth [41,42]. The context-dependent characters of jasmonates in some species and tissues are illustrated by the fact that JA (and its precursor OPDA) antagonizes dormancy and promotes germination in certain cases, whereas in others it supports dormancy by activating ABA responses via modules such as JAZ–ABI3/ABI5 or by associating with the DELLA proteins like RGL2 thus showing that the tissue-specificity of JA impacts and that these effects are intimately connected to core ABA–GA regulators [43,44].

Small reactive molecules reactive oxygen species (ROS) and nitric oxide (NO) are considered principal upstream integrators of environmental input (light, temperature, moisture) that modulate hormone metabolism: ROS/NO may facilitate ABA catabolism and GA signaling, besides ROS-mediated weakening of the seed covering layers also diminishes the mechanical barrier to radicle protrusion, thus redox state is effectively coupled with hormonal control of germination [45]. Along with the spatial distribution of hormones in seed tissues, the role of the seed coat and endosperm should not be underrated. Besides being mere physically barriers, they are active hormone reservoirs and sites of biosynthesis/accumulation, capable of imposing or releasing dormancy by supplying or sequestering ABA, JA, and auxin, or by acting as sinks that modulate embryo hormone exposure during imbibition and after-ripening [46]. Molecular genetics gives us back the image of the same physiology: transcription factors (ABI3/ABI5), DELLA repressors (RGL2), and hormone transporters choreograph tissue-specific reactions so that variations in ABA biosynthesis or catabolism, GA biosynthetic gene expression, and auxin transport lead to changes in dormancy depth or germination competence [47]. Light quality/quantity, alternating temperatures, wet-dry cycles, smoke-derived karrikins, and soil nitrate are some of the environmental signals that affect this network by changing hormone synthesis and sensitivity (for instance, light increases GA3ox expression and lowers ABA levels), thus enabling dormancy-cycling and seasonal recruitment windows that are very important for unpredictable desert and agricultural areas [48].

Widely, the knowledge of cellular-level interactions is the main cause which enables scientists to apply the most suitable dormancy-breaking methods (scarification, stratification, GA or KAR1 treatments, redox manipulation) that are tailored to hormone profiles of species-specific tissues and ecological strategies and this is the essence of crop management (e.g., sunflower seed coat–endosperm interactions controlling dormancy) and of degraded drylands restoration where germination synchronization is the factor that determines the establishment success [49].

Seed dormancy mainly depends on the concentration of Abscisic Acid and auxin in tissues, whereas Gibberellic Acid has a very strong promotive effect on germination as is illustrated in figure.2. The role of jasmonates is such that they can take any position between the extremes, being dependent on the context and hence are found to be interacting with both ABA and GA signaling pathways.

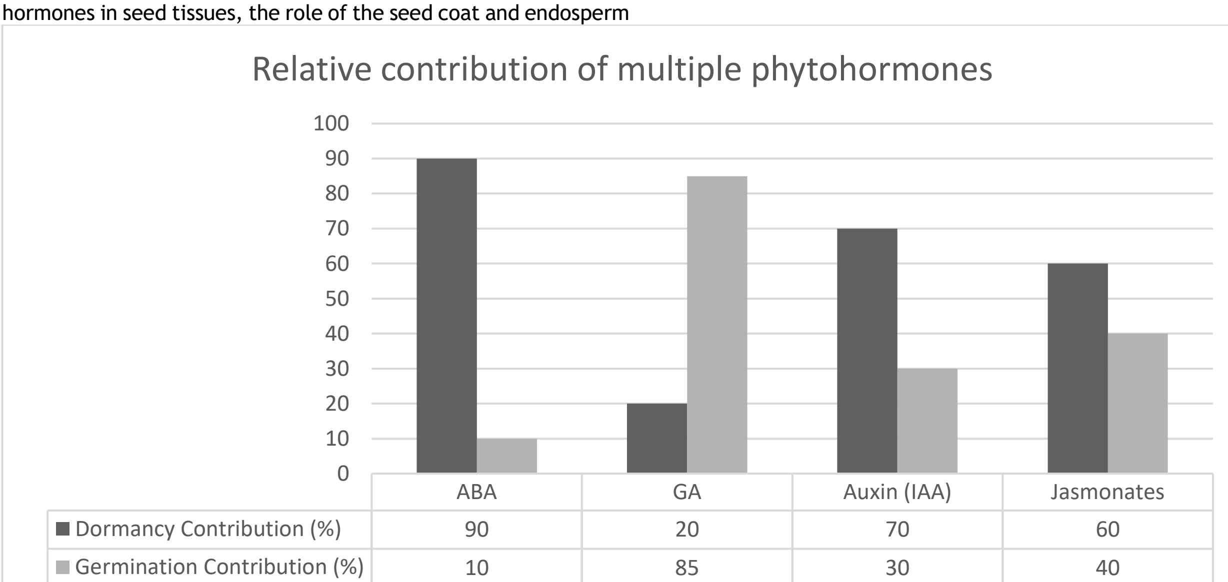

Figure.2 Relative contribution of ABA, GA, auxins, and jasmonates in regulating seed dormancy and germination.

4. Abscisic Acid (ABA): The Central Regulator of Dormancy:

Abscisic acid (ABA) is the main hormone that organizes seed dormancy, with its retention during seed development being necessary to the whole process of dormancy in all kinds of plants. In case of cereals and Arabidopsis, the maxima of ABA production catalyzed by 9-cis-epoxycarotenoid dioxygenase (NCED) correspond to the late stages of seed development, thus ensuring the continuation of dormancy [50]. It has been proven that in wheat and barley cultivars with dormancy, the concentrations of ABA in the embryo stay high for a longer time than in the lines that are not dormant, which implies that the role of ABA in the maintaining of seed quiescence is of a central nature [51]. ABA transmission signal includes PYR/PYL/RCAR receptors, PP2Cs, and SnRK2 kinases, which lead to the activation of transcription factors such as ABI3, ABI4, and ABI5 and thus to dormancy-related gene networks [52]. The most important point is that stress tolerance is increased by ABA also. It is done through the induction of LEA proteins, antioxidant enzymes, and osmoprotectants, which make it possible for seeds to be very well-protected in the case of unfavorable surroundings [53]. Stress signals such as drought or high temperature, for example, very frequently increase the process of ABA synthesis, which, in turn, leads to the strengthening of dormancy and acts as a barrier to the early germination of seeds [54]. Though, one cannot say that seed dormancy is a stagnant phenomenon; it is a matter of ABA breakdown through ABA 8'-hydroxylases action which is encoded by CYP707A genes that cause ABA reduction during imbibition or after-ripening thus making it possible for dormancy to be released

[55]. Environmental signals such as light, temperature, and reactive oxygen species (ROS) also drive ABA decomposition and activate germination [56]. The case of increased ROS generation during imbibition that leads to HvABA8′OH1 expression in barley, thus bringing about ABA decline and dormancy relief is an example [57]. Therefore, ABA is a dormancy keeper and a stress integrator at the same time, whose levels that are fluctuating between biosynthesis and catabolism are essentially for the adherence of seed conduct to the environmental factors [58].

5. Gibberellins (GA): Promoters of Germination:

Gibberellins (GAs) relate to ABA as the promoters of germination and hence, they activate those parts which refer to a successful growth and the use of the seed reserves available. The development of GA includes plastidial terpene synthases (CPS and KS) and cytochrome P450 enzymes which (KO and KAO) lead to the production of GA12 that is further changed into the bioactive GA1, GA3, and GA4 [59]. Besides, GA biosynthetic genes, e. g. GA20ox and GA3ox expression in the embryo and aleurone are factors that developmental and environmental cues i.e. both kinds of signals regulate [60]. Desert plants' GA biosynthesis and signaling are modified so much that GA still decides when to germinate by taking only the correct moisture signals as a trigger [61]. By GA recognition through GID1 receptors, the elimination of DELLA repressors occurs, which results in the empowerment of such factors as GAMYB that themselves turn on the genes which code the hydrolytic enzymes e.g., α-amylase [62]. The enzymes described break down starch and other carbohydrate storage in proteins and, thus, offer energy for radicle protrusion [63]. The antagonism between GA and ABA is very important at this stage: while ABA keeps the seed in the dormancy state, GA signaling acts opposite to ABA by enabling ABA receptor degradation and bringing about the activation of antagonist transcriptional networks [64]. Furthermore, the DELLA proteins, by having the opportunity to physically interact with ABI3 and ABI5, thus, they are the ones which set the stage for regulation between dormancy and germination by altering the intensity of the GA and ABA [65]. When water penetrates cereal grains, the embryo is filled with GA and the aleurone gland receives the message to secrete α-amylase and proteases allowing for the nutrients to be used during germination [66]. Situations of drought or salinity negatively affect GA biosynthesis and signaling which in turn delays a germination that is characterized to be an adaptive strategy [67]. In general, GA acts as the key player commissioning reserve mobilization, growth promotion, and ABA antagonism to successfully achieve germination [68].

6. Auxins and Their Role in Seed Behavior:

Though auxins are mostly identified with the increase and progression of the plant, the scientific studies reveal that these substances are necessary for seed dormancy and germination as well, with a major role in the modulation of ABA and GA pathways. The main auxin indole-3-acetic acid (IAA) influences the development of dormancy by enhancing the biosynthesis of ABA as well as ABA sensitivity, especially during seed maturation [69]. The mechanism involves the event of the auxin-regulated transcription factors such as ARFs, which mediate the activity of the metabolic genes of ABA both directly and indirectly [70]. One piece of evidence is that high levels of auxin in the seeds that are still developing may delay germination by the stabilization of ABI3 and ABI5, thereby strengthening the role of ABA as the dormancy promoter [71]. On the other hand, the reduced auxin signaling is associated with a decrease in ABA levels and an onset of germination that occurs earlier [72].

Furthermore, auxin is known to interact with GA pathways, whereby it practically plays the role of an inhibitor in GA biosynthesis and works as a stimulator of GA catabolism, consequently, the ABA/GA ratio is maintained at the point of dormancy [73]. The interplay between auxin and ABA happens not only at the metabolic level but also at the signaling one. An example of the ARF–ABI transcriptional modules is the integration of environmental signals into dormancy regulation. Nevertheless, there are situations when auxins encourage the germination, as they become the factors of the cell elongation process in the embryonic tissues after ABA levels drop, thus, suggesting a double role depending on the ABA–GA balance [74]. Auxiliary research has also linked the protein transporters such as PIN to the translocation of IAA during seed development which in turn affects hormonal gradients that locate the depth of dormancy [75]. Eventually, auxins take the role of the modulators rather than the direct initiators of dormancy or germination, as they are the ones to combine the given environmental and developmental cues for the sophisticated ABA/GA antagonism [76].

7. Cytokinins: Breaking Dormancy and Promoting Germination:

Cytokinins (CKs) stand as one of the essential regulators that bring about seed dormancy release and germination, are to be considered as going through the antagonism with Abscisic acid (ABA) and the synegry with Gibberellic acids (GAs). The Cytokinin mode of action is through the histidine kinase receptors that initiate phosphorelay cascades resulting in the activation of the response type-B regulators which among other things, increase the transcription of genes related to cell division, reserve mobilization, and germination [76]. A study in cereal grains suggests that CKs not only decrease ABA sensitivity but also destabilize the ABI3 and ABI5 factors that co-mediate dormancy maintenance [77]. Moreover, the CK treatment is also responsible for induction of the α-amylase and protease genes in the aleurone layers, thus, these enzymes ably hydrolyze the reserves in coordination with GA [78]. In water deficit conditions, CKs help to maintain cellular hydration, stabilize membranes and elevate antioxidant enzyme activities leading to the strengthening of germination [79]. The desert plants where unexpected rainfalls cause very short germination periods rely on high CK activities at the time of water supply to automatically and quickly gain the seedlingsâ€™ water [80]. CK signaling cross talks with ROS to bring about ABA degradation by CYP707A-mediated hydroxylation and thus eases germination [81]. The analysis of mutants defective in CK biosynthesis or perception indicates that germination is delayed while exogenous CK treatment can effectively cause dormancy to be released [82]. Therefore, CKs act as the major hormonal signals that can suppress the action of ABA, co-opt other hormone pathways like GA, and impel the seeds to maintain their dormancy-breaking capacity during drought conditions [83].

8. Ethylene and Its Role in Desert Plant Seeds:

Ethylene (ET) is known as a dormancy-breaking hormone that opens up germination, especially in the presence of stress or when a seed is surrounded by mechanical barriers. ET, which is made during seed imbibition, works with auxins and GA signaling to speed up radicle protrusion. In halophytic seeds, the use of ethylene-releasing compounds, such as ethephon, is very helpful in overcoming salinity-induced dormancy and in partially recovering germination, even at the level of salinity that is close to twice seawater. One of the main reasons why the usage of ethylene is very effective in the overcoming of seed dormancy is because it diminishes the secondary and the light-induced dormancy and increases by the seed coat weakening the possibility of the radicle to emerge. In the case of desert species, where thick testa or mechanical resistance are the only reasons for germination, it has been noticed that ET, together with GA, works in a very effective way to break these barriers . Gradually, drought or osmotic stress also become the main reasons for higher production of endogenous ET, which totally neutralizes the inhibition of ABA and activates the enzymes for cell wall loosening. In support there are experiments in halophytes and arid-adapted plants that indeed ethylene, although less effective in removal of innate dormancy, is the most important factor that alleviates environmental stress constraints on germination. This feature of ethylene allows desert seeds, on the one hand, to be able to double germination and synchronization with environmental windows of the most favorable conditions and, on the other hand, to be able to improve their establishment under the most unpredictable moisture regimes.

9. Brassinosteroids and Jasmonates in Germination:

Brassinosteroids (BRs) and jasmonates (JAs) are gradually being identified as key factors that regulate seed dormancy and germination. BRs, which have been identified as the main actors in the cell elongation process and skotomorphogenesis, also give a go-ahead to germination by negating the inhibitory effect of ABA [91]. In Arabidopsis, BRs can help seed germination in the case of GA-deficient or GA-insensitive mutants, thus, be there a strong overlap with GA in terms of a common function to seed germination [92]. Furthermore, mutations in BR signaling units such as det2 and bri1 lead to an increase in the ABA sensitivity. This points out that BR signals are necessary to go around the blockade of dormancy [93]. JAs, which are primarily stressors, affect seed germination through altering ABA sensitivity and connecting GA pathways. On the other hand, extremely stressful conditions combined with very high JA concentrations can stop seed germination. Concurrently, there will be moderate JA signaling, which is in charge of the seed's ability to pass through the mechanical barrier and use up the almidon reserve [95]. Furthermore, both BRs and JAs can maintain a multi-hormonal network that is ideal for germination in desert conditions that can change quickly, in addition to showing synergistic effects with GA and ethylene. Their identification in the seed demonstrates the intricacy of hormone interactions that go beyond the traditional ABA–GA antagonistic model and suggest a more extensive framework for dormant regulation [97].

10. Environmental Stress, Hormonal Balance, and Desert Adaptations:

Hormones are the primary mediators between seed dormancy and germination, which are greatly impacted by environmental factors that harm the environment, such as drought, extremely high or low temperatures, and salty water. Dormancy results from increased ABA production under drought and salinity conditions; however, when conditions improve, GA and ethylene signaling plays a part, enabling germination [98]. Desert species' hormonal regulation is flexible enough to allow for rapid changes in the ABA-GA-ET balance based on the water condition, which is a situation of temporary water availability [99]. Temperature variations also affect hormone metabolism. In this case, it is discovered that high heat encourages the synthesis of ABA, while cool temperatures boost GA's responsiveness.

The communication between different hormones such as cytokinins, BRs, and JAs enhances the integration of the stress signals, thus allowing seeds to calculate the suitable time for germination. Such a change ensures that the species are going to survive in areas that lack water as it is synchronizing germination with very short periods of good conditions, which stands for an excellent example of hormonal plasticity as a major adaptive trait [100].

11. Molecular and Genetic Insights:

The molecular research findings that seed dormancy and germination are the main processes having interconnected gene expression networks as their characteristics, these networks being linked to hormone signaling pathways. Genes connected with ABA such as ABI3, ABI5, and CYP707A regulate the depth of dormancy, on the other side GA biosynthetic (GA20ox, GA3ox) and signaling genes (GID1, DELLA) are the main factors that determine the initiation of germination [76]. On the basis of the ethylene-responsive transcription factors such as EIN2 and ERF1 that stress-induced germination modulate and through ABA suppression they are connected [77]. Commonly, desert-adapted species are characterized by their one-of-a-kind transcriptional signatures, where the stress-inducible promoters in these species result in the higher expression of ABA catabolic genes during the period of rainfall [78]. Seed morphogenetic events including DNA methylation and sRNAs add one more layer of control over the environmental responsiveness of hormonal sensitivity and seed behavior under variable climates [79]. Experiments on genome-wide expression conducted on halophytes and xerophytes corroborate the view that hormonal dialogue is being orchestrated at the level of transcriptional activities thus allowing organisms to respond quickly to the signals coming from the environment [80].

12. Practical Applications and Ecological Implications:

Knowing the hormonal control of dormancy and germination is a tool with which one can achieve restoration ecology, climate adaptation strategies, and agriculture. First of all, in restoration works pre-treatments with ethylene, GA, or cytokinins can depose dormancy and germination of desert species so a seedling becomes established properly can be predicted [81]. Second, in the case of agriculture the use of hormone-based priming can provide more viable seeds in the salinity and drought conditions with BRs and CKs being the leading agents for plant stress resistance as a result [82]. Moreover, desert plants, through their hormone-mediated adaptations, have become sources of ideas for us to create the type of crops that can survive in the harshest parts of the climate [83]. Last but not least, by identifying the hormone plasticity, the scientists are able to come up with earth-friendly plans to re-vegetate the depleted lands, facilitate the seedlings' healthy growth, and fight change in the climate [84].

13. Future Directions and Research Gaps:

Though there have been many improvements and breakthroughs, the gaps that exist in our knowledge of the way hormones regulate the seed biology of desert plants are still quite significant. The next research that would be necessary will definitely have to be focused on the implementation of integrative omics strategies, such as transcriptomics, metabolomics, and proteomics, for decoding hormone crosstalk in the case of an extreme desert stress [85]. The relationship between hormones, which is also the multi-hormonal one, involving ABA, GA, ET, BR, and JAs needs to be broken down at the molecular level so that the interactions between their synergistic and antagonistic effects become clear [86]. Genetics should be focused on discovering the key regulatory factors of desert-adapted species, as the new alleles may be at the base of the enhanced hormonal plasticity [87]. Moreover, an editing technique, as in CRISPR-mediated alteration of hormone biosynthesis or the signaling pathway genes, may be a way to create crops with dormancy personalities adapted to dry regions [88]. Ecological studies, apart from being very useful, are also crucial in assessing the effects that climate change scenarios have on seed dormancy dynamics and germination patterns in desert ecosystems [89]. Deepening primary understanding of the natural world will be a byproduct of this, along with the possibilities of wide scale ecological and agricultural tech innovations that can be utilized in the fight against global change [90].

CONCLUSION

Due to the harsh and unpredictable nature of the desert environment, seed dormancy and germination in desert plants have evolved into evolutionary innovations. Phytohormones are the primary regulators of these changes at the cellular level, with the ABA-GA antagonistic balance essentially determining both the degree of dormancy and the capacity for germination. By creating a system that can detect environmental changes like temperature fluctuations, moisture bursts, and salt stress, auxins, cytokinins, ethylene, brassinosteroids, and jasmonates also add to the vast regulatory network. The hormonal cross-talk required for dormancy maintenance and release is regulated by transcription factors such as ABI3, ABI5, and DELLA in conjunction with enzymes like NCED and CYP707A, according to molecular data. Additionally, small RNAs and epigenetic modifications enhance control over these processes by enabling prompt adaptive responses to the brief desert conditions. Conversely, from an ecological perspective, desert plants are able to endure an unpredictable environment because of their adaptations to seed coats, heteromorphism, and dormancy cycling. Although it complicates restoration ecology because predictable and synchronized germination is typically required, the bet-hedging strategy is crucial for population stability and community resilience. Techniques like seed priming, hormone treatments, and smoke-derived stimulants are increasingly being used to overcome these barriers and offer scalable solutions for crop climate adaptation and the revegetation of degraded drylands. To make the lab findings applicable in the field, future methods that integrate ecological research, omics technologies, and molecular genetics will be needed. In the era of rapidly accelerating climate change, the application of phytohormonal knowledge to dormancy and germination will first and foremost be a great tool to improve our understanding of plant adaptation to deserts. It will also give us powerful tools for biodiversity conservation, sustainable agriculture, and ecological restoration.

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