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## Chapter

# Seed Dormancy Challenges in the Production of Medicinal and Underutilized Leafy Vegetables

*Thobile Perseverance Mkhwanazi, Gugu Cynthia Maseko and Zakheleni Palane Dube*

## Abstract

Seed dormancy has played a significant role in the adaptation and evolution of seed plants, by ensuring germination under favorable conditions, avoiding extreme weather periods, and other unfavorable conditions. While its biological significance is clear, dormancy acts as a delaying mechanism, making it difficult to simultaneously plant and properly maintain the population of the most important indigenous high-quality plants, consequently inhibiting mass cultivation and adoption. Several genetic and environmental factors influence dormancy, and different crops and or crop varieties including those of medicinal and indigenous vegetables exhibit varying degrees of dormancy. Breaking of dormancy will make a significant contribution towards ensuring consistent germination and cultivation of these crops. It is also important to observe and understand the types of dormancy exhibited by these as this can provide a guide for effective methods of breaking it. This book chapter will comprehensively discuss the types and challenges of seed dormancy associated with wild medicinal plants and indigenous vegetables, with special mention of cancer bush and jute mallow, as well as some pre-sowing treatments that can be used to break their dormancy. It further examines the potential of technological advances such as gene editing, genome engineering, and epigenesis regulation in addressing these challenges and improving cultivation.

**Keywords:** dormancy mechanisms, dormancy management, seed dormancy, seed germination, seed priming, underutilized crops

## 1. Introduction

Medicinal plants and indigenous vegetables have long been used by traditional cultures as alternative approaches to healthcare and nutritional needs [1]. About 75–80% of the world's population, mostly from developing countries, are reported to be dependent on these plants [2]. It is estimated that there are between 10,000 and 53,000 species of medicinal and underutilized crops worldwide, with the majority

still being harvested from the wild [3]. In recent years, as the prices of medicine and food have increased, the use of both medicinal plants and edible herbs as vegetables has become a topic of global importance [4]. To achieve effective and sustainable food production, there is a need for research and cultivation of all underutilized indigenous crops [5, 6].

The higher demand for medicinal plant-based products has resulted in increased overharvesting of plants from wild populations [1]. Together with overexploitation, habitat destruction, climate change, and illegal trading of wild populations over the years have threatened medicinal plants with extinction [7]. According to Julsing et al. [8], only 10% of medicinal species are cultivated, and harvesting these wild species in high volumes without implementing mitigation measures increasingly pressures wild populations, threatening biodiversity. In South Africa, over 700 wild species are actively traded, mostly illegally [9]. The cultivation of most medicinal plants has been proven challenging due to low germination rates that require a specific ecological requirement [10]. It is noted that seed dormancy contributes significantly to these low germination rates [11, 12].

Seed dormancy acts as a delaying mechanism that inhibits germination, making it difficult to plant and properly maintain crop populations in the field simultaneously [13]. It also inhibits mass cultivation, growth, yield, and adoption as viable seeds can remain dormant in the soil for extended periods [14]. Germination-promoting stimuli such as scarification have been found to assist seeds in breaking their dormancy [15]. Previous studies on medicinal and indigenous crops have focused on various agronomical tactics to improve cultivation, including pre-sowing treatments (i.e., seed scarification) to break seed dormancy and stimulate germination [11, 16, 17]. Shaik et al. [18] explored biotechnological tactics such as micropropagation of cancer bush from vegetative plant parts to reduce wild harvesting while improving ex-situ cultivation and resources for acclimatized plants. Investigation on the effect of cultural practices (pruning and fertilizer application) on the growth, biological activities, and chemical properties of cancer bush, finding significant improvements in plant growth [1]. Masenya et al. [19] studied the effect of rhizobia inoculation (both native and commercial strains) on the growth and chemical composition of cancer bush.

Currently, there is limited knowledge concerning the specific requirements for pollination, seed germination, and growth of medicinal plants and underutilized vegetable crops, as most remain in their wild stages with dormant seeds. Farahani et al. [20] reported that dormancy is the main problem preventing the sustainable use of medicinal plants that can germinate in their native arid lands but fail to germinate well under laboratory conditions or when cultivated in the field. However, research suggested that if information on cultivation and economics were available and medicinal plants were properly phased into cultivation, the economic rewards for small-scale farmers could exceed those from maize or sugarcane [2]. The lack of knowledge on the cultivation and economics of medicinal plants is considered a major limiting factor in commercializing traditional medicinal plants [21]. To effectively domesticate and cultivate any plant species, having comprehensive information on seed germination and overcoming dormancy is imperative.

This book chapter explores the challenges of dormancy associated with medicinal and underutilized crop plants, identifies reported mechanisms, and proposes potential actions to overcome them. Finally, it examines the prospects of biotechnology in improving the cultivation of medicinal and underutilized vegetables.

2. Drives to commercialize underutilized medicinal and leafy vegetables

Neglected and underutilized crops as shown in **Tables 1–3** represent an important component of agro-biodiversity with potential to contribute to climate change adaptation, food security, and human health [46]. Over the years, much attention has been paid to exotic crops due to their known inherent agronomic, ecological, economic, and nutritional value. Given the known value of exotic crops, a majority of plant breeders, researchers, and policymakers have constantly ignored the development potential of underutilized crops, which led to their poor value chain. In South Africa, there is a wide range of underutilized crops that are historically popular and used by rural communities such as cancer bush (*Sutherlandia frutescens*), jute mallow (*Corchorus olitorius* L.), *Amaranthus* spp., *Chenopodium album*, and many others as listed in **Tables 1–3** [35]. Some of these crops have been incorporated into human diets since ancient times, especially in sub-Saharan Africa and many Asian countries where they greatly contribute to food and nutrition security and medicinal needs [40]. Their well-documented nutritional quality and climate adaptability compared to the exotic plants have led them being considered as one way to curb the “hidden hunger” that is most prevalent in developing countries, and as a result contribute to the achievement of some of the UN’s Sustainable Development Goals SDG-1 (no poverty), SDG-2 (zero hunger), and SDG-3 (good health and wellbeing) [40]. However, since the beginning of the Green Revolution, many of these local, traditional, and underutilized crops have been replaced by high-yielding staple crops or cultivars developed through modern breeding programs [47]. Typically, underutilized crops do not meet modern standards for uniformity and other characteristics as they have been neglected by

African leafy vegetable	Harvested from wild	Cultivated	Growth season
<i>Abelmoschus esculentus</i> Moench		X	Summer
<i>Amaranthus</i> spp.	X		Summer
<i>Bidens spinosa</i> L.	X		Summer
<i>Brassica rapa</i> L. subsp. <i>chinensis</i>		X	Winter
<i>Chenopodium album</i> L.	X		Summer
<i>Citrullus lanatus</i>		X	Summer
<i>Cleome gynandra</i> L.	X		Summer
<i>Corchorus olitorius</i> L.	X		Summer
<i>Cucurbita</i> spp.		X	Summer
<i>Vigna unguiculata</i> (L.) Walp		X	Summer
<i>Solanum retroflexum</i> Dun		X	Winter
<i>Portulaca oleracea</i> L.	X		Summer
<i>Momordica balsamina</i> L.	X		Summer
<i>Galinsoga parviflora</i> Cav	X		Summer

Source: Ref. [22].

**Table 1.**  
African leafy vegetable commonly harvested from the wild or obtained through cultivation in South Africa.

Common name	Scientific name	Crop type <sup>a</sup>	Plant part used <sup>b</sup>	Human nutrition	Pharmaceutical and nutraceutical properties	Reference
Cancer bush	<i>Sutherlandia frutescens</i> (L.) or <i>Lessertia frutescens</i> (L.) Goldblatt and J.C. Manning	Legume, herb, shrub	St, Lv, F, Pd, R	N/A	Used to treat chickenpox, diabetes, cancer, menopausal symptoms, influenza, rheumatoid arthritis, peptic ulcers, anxiety, clinical depression, HIV infection, and external wounds. Caner bush is amino acids, proline, and alanine.	[19, 23]
Wild ginger	<i>Siphonochilus aethiopicus</i> (Schweinf.) B.L.Burt	Root and tuber	F	Contains fat, sodium, carbohydrates, sugars, protein, and calories.	Used to treat intestinal ailments, relieve stomach aches and cramps, and reduce stress, pain, and anxiety. The rhizomes and roots are chewed fresh to treat asthma, hysteria, colds, coughs and flu, malaria, vaginal thrush, and headache, and it is chewed by women during menstruation.	[24]
Carob	<i>Ceratonia siliqua</i> L.	Tree	Lv, Pd,	Pods are a rich source of carbohydrates (providing animals with a readily available source of energy to fuel their daily activities and metabolic processes) and protein (contributes to muscle development, tissue repair, and overall animal health) and are high in fiber (which plays an important role in maintaining digestive health).	Carob possesses various pharmacological activities, such as antioxidative, anti-diarrhea, antibacterial, anti-ulcer, anti- inflammatory, and anti-diabetic effects.	[25, 26]

Common name	Scientific name	Crop type <sup>a</sup>	Plant part used <sup>b</sup>	Human nutrition	Pharmaceutical and nutraceutical properties	Reference
Drumstick	<i>Moringa oleifera</i>	Herb	Lv, F, F, B, R	Almost all tree parts are eaten or used as ingredients in traditional herbal medicines. This especially applies to the leaves and pods, commonly eaten in parts of India and Africa. Moringa leaves are excellent source of calcium, potassium, iron, magnesium, phosphorus, zinc, vitamin A, B1 (thiamine), B2, (riboflavin), B3 (niacin), B-6, folate, and ascorbic acid (vitamin C), oils, fatty acids, micro-macro mineral elements, and various phenolics.	Provide treatments for inflammation, paralysis and hypertension, rheumatism, arthritis, diabetes and high blood pressure, relieve menstrual pain, stomach pain, heals burned skin and wounds.	[27–29]
Bush tea	<i>Athrixia phylicoides</i> DC.	Herb	St, Lv, F, R	N/A	Used to clean or purify the blood, treating boils, headaches, infected wounds, and cuts, and the solution may also be used as a foam bath. Treatment of various ailments such as boils, acne, colds, loss of voice, and throat infection as a gargle. Significantly high polyphenols, tannins, antioxidants, quercetin, flavonoids, alkaloids, polysaccharides, amino acids, lipids, vitamins, and inorganic elements.	[30, 31]
Bitter gourd	<i>Momordica charantia</i> (L.)	Herb	Fr	N/A	Provides proteins, potassium, iron, and fiber. It is used in the treatment of cancer and as an aphrodisiac.	[32, 33]

Common name	Scientific name	Crop type <sup>a</sup>	Plant part used <sup>b</sup>	Human nutrition	Pharmaceutical and nutraceutical properties	Reference
Hyacinthus	Hyacinthaceae	Lv	Fr, R, Sh	Contains sodium, potassium, carbohydrates, protein, and vitamin C. Also, Hyacinthus is a good source of crude lipids, ash, fiber, proteins and minerals, potassium, and sodium	Used to treat rheumatism, cardiac, urinary infection, dermatological problems, stomach, hemorrhoid, and prostate disease.	[34]
Honeybush	<i>Cyclopia</i> (Vent.) spp.	Herb, legume	Lv	N/A	Helps in reducing digestive problems, arthritis and to treat diabetes, stress relief and relaxation remedy, treat hypertension and hypotension, chest ailments, diarrhea, immune-boosting, blood circulation and blood cleanser, kidney ailments, diabetes, eczema (internally), stomach ailments, constipation, and appetite stimulant.	[35]

<sup>a</sup>Crop type -Legume (L), Herb (H), Cereal (C), Shrub (S), Leafy vegetable (LV), Tree (T).  
<sup>b</sup>Plant part—Root (R), Shoot (Sh), Seed (Sd), Stem (St), Flower (Fr), Pod (Pd), Leaves (Lv), Bark (B).

**Table 2.**

Potential medicinal benefits of a few selected underutilized medicinal plants of South Africa.



Common name	Scientific name	Crop type <sup>a</sup>	Plant part used <sup>b</sup>	Human nutrition	Pharmaceutical and nutraceutical properties	Reference
Jute mallow	<i>Corchorus carinata</i> C. <i>olitorius</i> L.	LV	Lv, Sd	High in beta-carotene, folate, calcium, protein, B vitamins, iron, vitamins C and E, lipids, carbohydrate, and dietary fiber.	The leaves may have antibacterial, anticancer, and anti-inflammatory properties which may prevent the common cold, asthma, acne, arthritis, cure gonorrhea, pain, fever, and tumors. The Lycopene on the leaves has an antioxidant that protects cells from oxidative damage, which elevates disease risk.	[35–39]
Leafy Amaranthus	<i>Amaranthus</i> spp.	LV	LV	The leafy vegetable is rich in fiber, protein, calories, protein, carbohydrates, fat, manganese, magnesium, phosphorus, iron, selenium, and copper.	Treat diarrhea, ulcers, swollen mouth, and throat.	[22, 32, 40]
Bambara groundnut	<i>Vigna subterranea</i> (L.) Verdc.	Legume	Sd	Source of moisture, protein, carbohydrate, energy, crude fiber, calcium, potassium, magnesium, sodium, phosphate, iron, zinc, copper, ascorbic acid, β-carotene, lysine, methionine, and thiamine.	N/A	[41–43]
Purslane	<i>Portulaca oleracea</i>	LV	Lv	It is rich in β-carotene, folic acid, vitamin C, and essential fatty acids.	Heal headache, stomach ache, painful urination, enteritis, mastitis, lack of milk flow in nursing mothers.	[44, 45]

<sup>a</sup>Crop type - Legume (L), Herb (H), Cereal (C), Shrub (S), Leafy vegetable (LV), Tree (T).  
<sup>b</sup>Plant part - Root (R), Shoot (Sh), Seed (Sd), Stem (St), Flower (Fr), Pod (Pd), Leaves (Lv), Bark (B).

**Table 3.**  
Potential nutritional and medicinal benefits of a few selected underutilized leafy vegetables of South Africa.



breeders from the private and public sectors [48]. This rendered them less competitive in the market as compared to the exotic or commercial cultivars.

In 2017, the African Nutrition Society reported that the food pricing system in Africa delivers food at a cost that makes nutritious food unaffordable to the majority of the population, particularly the rural communities. Consequently, a resultant high disease burden associated with child malnutrition, micronutrient deficiencies, high body mass, and dietary risk factors was later reported in a study [49]. All these challenges were associated with the fact that many African families cannot afford the expensive nutritional exotic crops and therefore rely on low-cost underutilized vegetables. As a result, the preference for normal vegetables shifted extensively away from exotics and toward the growing underutilized crop market [50].

Currently, underutilized vegetable crops are receiving a lot of attention from plant breeders, researchers, farmers, and other stakeholders including government, nutritionists, and consumers due to their recognized potential contribution toward nutritional quality and climate adaptability [40]. Apart from their commercial, medicinal, and cultural value, these crops are also considered important for sustainable food production as they reduce the impact of production systems on the environment, as many of these crops are hardy, adapted to specific marginal soil and climatic conditions, and can be grown with minimal external inputs [51, 52]. The majority of the underutilized vegetable crops are regarded as of high nutritional value in relation to global vegetables like tomato and cabbage [53]. Underutilized legume crops such as mung bean have the potential to contribute significantly as sources of essential vitamins, micronutrients, protein, and other phytonutrients toward strategies aimed at attaining nutritional security [47]. Similarly, Jew's mallow is a very nutritious vegetable that is high in beta-carotene, folate, calcium, protein, B vitamins, iron, vitamins C and E, lipids, carbohydrates, and dietary fiber in its leaves [36]. Moreover, it provides 70% and 25% of the recommended daily amount value of vitamins C and A, respectively [54]. About 87 g of cooked Jew's mallow contains about 0.021 g of tryptophan, 0.113 g of threonine, 0.152 g of isoleucine, 0.266 g of leucine, 0.151 g of lysine, 0.044 g of methionine, 94 micrograms of vitamin K, 2.73 milligrams of iron, 0.496 milligrams of vitamin B6, 225 micrograms of vitamin A, 28.7 milligrams of vitamin C, and 0.222 milligrams of copper [54]. Jew's mallow is more nutritious in contrast to cabbage and spinach [55]. According to Zeghichi et al. [56], Jew's mallow is a better source of vitamins C and E, glutathione, carotenoids, minerals, and fatty acids than most other cultivated vegetables. In addition, it can be easily integrated into children's diets as it is reputed to taste much better in many culinary dishes than spinach [56]. A larger number of the rural populations in Africa depend on underutilized leafy vegetable crops such as Jew's mallow for nutrition [57]. Most of the underutilized crops serve as an essential source of vitamins, micronutrients, and protein, thus, a valuable component to attain nutritional security. Vegetables in general are of considerable commercial value and therefore an important source of household income, particularly the small-scale farmer who rely greatly on the cultivation of underutilized crops for most of their nutritional needs.

Moreover, the increased health consciousness and dietary shifts towards healthier foods in society contribute towards the growing popularity, production, and marketing of functional food crops such as amaranth (*Amaranthus tricolor* L.), cancer bush (*Sutherlandia frutescens* L.), honeybush tea (*Cyclopia vent*), mint (*Mentha* spp), and ginger (*Siphonochilus aethiopicus* (Schweinf.) B.L. Burtt) [47]. All these crops are dual-purpose crops functioning as food and herbal medicinal crops or plant-based dietary

compounds for therapeutic, nutraceutical, and pharmaceutical benefits [35]. The majority of these crop species have the potential to be distributed at a global scale but are restricted to a more local production and consumption system. Underutilized crops constitute an important part of the local diet of communities providing valuable nutritional components, which is often lacking in staple crops [47]. Hence, a wider use of neglected and undervalued crops, either intercropped with main staples in cereal-based systems or as stand-alone crops, would provide multiple options to build temporal and spatial heterogeneity into the cropping systems and, as a result, enhance the resilience of crops/farms to biotic and abiotic stress factors and ultimately leading to a more sustainable supply of diverse and nutritious food as well as providing for medicinal needs.

### 3. Overview of a few selected underutilized medicinal and leafy vegetable plants of South Africa and their potential uses

Underutilized plants are found in numerous agricultural ecosystems and often survive in marginal areas or fragile environments. Underutilized plant species are essential to the livelihoods of millions of people worldwide, due to their numerous



**Figure 1.**  
*A few selected underutilized crops of Southern Africa (a) Sutherlandia frutescens; (b) Amaranthus sp.; (c) Corchorus olitorius, and (d) Vigna subterranea (L.) Verdc.*

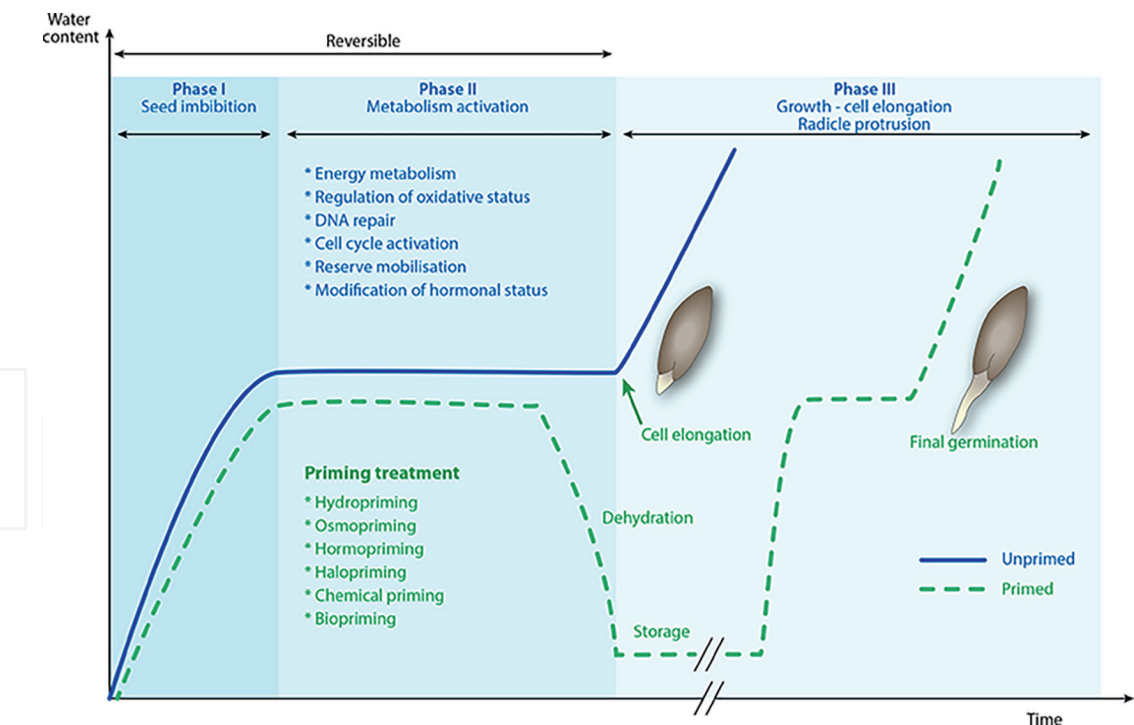


nutrition and medicinal advantages contributing significantly to poverty elimination through employment opportunities and income generation, contribute to sustainable livelihood through household food security as they add nutritional value to diets, and also are convenient food source for low-income people. Okigbo and Anyaegbu [58] emphasized that, for these plants to be called underutilized species and prioritized for selection, they must be proven able to best address challenges of food security, poverty elimination, and environmental sustainability as mentioned above. Moreover, underutilized species should be proven able to be cultivated either in the past or currently cultivated less than comparable plants. A summary of published information related to the uses of a selected underutilized medicinal and leafy vegetable plants of South Africa (see **Figure 1** and **Tables 2** and **3**) is given below.

## 4. Dormancy challenges associated with unlocking the potential of underutilized plants

### 4.1 Seed dormancy in relation to germination

Seeds play an important role in plant propagation and species maintenance within an ecosystem. The germination of seeds serves as the foundational step thereof, emphasizing the need to investigate the physiological facets of seed germination



**Figure 2.** Seed hydration and germination process in primed and unprimed seeds. The three distinct phases: (1) Phase I: the passive imbibition process related to rapid water uptake by the hard coat seed through hydration. Phase II is associated with an increase in embryo respiration after the establishment of metabolic activities. The increase of enzymes synthesis results in hormone release from the embryo. Lastly, Phase III demonstrates the completion of germination related to visible embryo growth processes and radicle protrusion (root and plumule) that will develop into shoot [62, 63]. Both I and III stages are associated with water uptake and increasing water content while phase II has stable water content. With primed seeds, it is common that before the end of Phase II, the seeds may dry up again and germination becomes reversible. The seed may remain alive again during storage and able to subsequently re-initiate germination under favorable conditions.

[59, 60]. Seed germination is regulated by the precise balance between endogenous (phytohormones and endosperm decay) and exogenous factors (environmental factors such as temperature and light) [61]. The transition from dormancy to germination as shown in **Figure 2** may occur as a result of the dry seed coming into contact with water and absorb water by imbibition and finally radicle emergence [62]. This encounter activates the internal metabolic process, involving the careful equilibrium phytohormones [64], in the presence of optimum light and temperature to overcome the seed dormancy [65]. Any imbalance that may occur between both factors will result in failure of seed to complete germination which is also perceived as dormancy. To understand dormancy or improve seed germination potential in plants, it requires a deeper and sequential understanding of the environmental stimuli around the seed and the interaction of intrinsic factors with extrinsic factors.

Seed dormancy is a natural process that delays seeds from germinating even when conditions are suitable for it. Several scholars define it as an innate constraint on germination under conditions that would otherwise promote germination in non-dormant seeds [66–68]. In simpler terms, dormancy must not only be associated with or defined as the absence of germination but rather the environmental conditions and characteristics of the seed that determine the conditions required for germination. When dormancy is considered in this way, any environmental cues that alter the conditions required for germination are by definition altering dormancy [69]. Other scholars define dormancy as “an innate state of arrested growth that occurs across all life forms” [69, 70]. According to Amen [71], dormancy is an internally controlled process (by enzymes, chemical inhibitors/promoters), and externally induced (by factors such as water, light, or temperature) temporal inhibition of development that is associated with reduced metabolic activity. Seed dormancy is a physiological phenomenon in wild and crop plants, more common in wild plants than crop plants [72].

During the dormancy period, seeds remain in an inactive/dormant state, often protected by mechanisms that prevent early germination. Dormancy allows seeds to germinate only when conditions become favorable. This is an adaptive feature that optimizes the distribution of seed germination over an extended period through varying degrees of dormancy [73] and bet-hedge against unpredictable variable environments (such as water content, temperature, light exposure, oxygen availability, and genetic attributes (plant hormones abscisic acid and gibberellins)) as shown in **Figure 1** [69, 74, 75]. This varied germination timing plays a pivotal role in ensuring species’ survival, especially in demanding environmental circumstances [76]. By controlling the timing of germination, dormancy can strongly affect plant survival and adaptation [77]. Although, dormancy is the major determinant of species diversification by allowing colonization of new and different sites, however, this can only be possible under appropriate seasonal conditions with dormant seeds. Contrarily, non-dormant seeds that lack germination inhibitors, thus are better able to explore new and different environments because their germination is independent of specific dormancy-breaking cues that might be absent in that new environment [78]. This promotes diversification by fostering divergence and allopatric speciation [78].

Seed dormancy may be viewed as an important ecological trait ensuring survival for wild species, however, it remains an unfavorable trait in agriculture (crop species), as the main objective is to promote rapid seed germination and growth [79]. There are situations in crop production where seed dormancy can offer significant advantages, particularly during the seed development stage [79]. This advantage often benefits the production of cereal crops, which possess dormancy mechanisms that restrict germination while grains are still attached to the parent plant’s ear. There it

acts as a safeguarding mechanism for the plant which prevents germination, particularly during the rainfall period during harvest (also known as preharvest sprouting) to avoid agricultural losses [79]. Moreover, dormancy contributes a significant challenge for agriculture especially when it concerns issues of weed problems. Weed seeds equally maintain their inherent dormancy mechanisms as they mature and persist in the soil for many years, until the right conditions for germination arise. This may pose a threat to crop cultivation, as these seeds can rapidly multiply when favorable conditions finally occur.

## **4.2 Classification of dormancies**

Seed dormancy classification is important in identifying the correct type of method to use to overcome any specific kind of dormancy [65]. Misidentifying or misinterpreting the dormancy of the seed may lead to failure to overcome the dormancy. Hence, the need to always direct methods of breaking dormancy towards the specific kind of dormancy. Owing to that fact, several researchers have elucidated some of the different classification systems of dormancy [80–82].

### *4.2.1 Classification based on barrier factors*

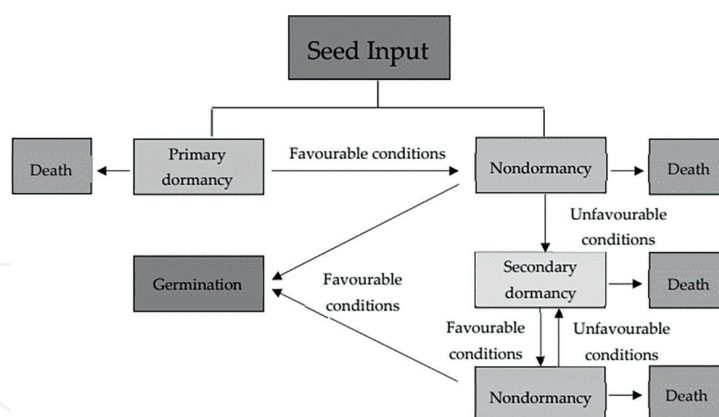
This kind of classification categorizes dormancy in terms of barrier factors that exist within the seed. It is the earliest dormancy class discovered by Nikolaeva [82]. The barrier factors may exist inside the seed (endogenous dormancy) or outside the seed (exogenous dormancy). Exogenous dormancy is caused by conditions outside seed embryo that can prevent the seed from germination. While endogenous dormancy includes characteristics of the seed embryo that prevent the seed to germination [83]. Endogenous dormancy can be a result of an incomplete embryo development after ripening period or chemical inhibitors inside the seed. In the case of underdeveloped embryo, the seeds may require enough time to develop to their normal size [83]. The endogenous dormancy comprises the physiological, morphological, and morphophysiological characteristics of the seed embryo which may prevent germination. Within this classification, there is combinational dormancy which is activated by the combination of both exogenous and endogenous dormancy which exist in complementary fashion.

### *4.2.2 Classification based on time of induction*

Seed dormancy is further categorized or grouped by Hilhorst [81] into primary and secondary dormancies.

#### *4.2.2.1 Primary seed dormancy*

It occurs when freshly and newly harvested seed from the mother plant is dispersed already in a dormant state [83]. Seed may be exposed to favorable conditions yet fail to complete germination, see **Figure 3** below. Primary dormancy occurs during the seed maturation phase due to the accumulation of abscisic acid (ABA). The abscisic acids prevent the loosening of the embryo cell wall which impedes water uptake and inhibits endosperm rupture instead of testa rupture. The induction of primary level of seed dormancy is regulated by several factors: genetic and non-genetic regions [83]. These factors may cause physiological variation in the seeds which manifests in different seed



**Figure 3.**  
 A general model of the changes that happen in mature seed after being released from mother plant [84].

morphological sizes, weight, and color. Seeds with physiological variation experience the transitional period of conditional dormancy before becoming fully non-dormancy (**Figure 3**). At first, seeds gain the ability to germinate under a narrow range of environmental conditions, which increases with the loss of dormancy until they become completely non-dormant and germinate under a wide range of conditions. If non-dormant seeds are unable to germinate, because of changes in the environment, they re-enter conditional dormancy but can germinate under a full range of conditions. As time passes, the range of conditions within which germination is possible narrows to the extent that germination is not possible under any condition and the seed acquires secondary dormancy [84]. The primary dormancy is further categorized into induction seed dormancy and genetic dormancy [85].

#### 4.2.2.2 Induction (coat-imposed) dormancy

Induction seed dormancy occurs when seeds fail to germinate due to some physical properties of the seed coats that inhibit germination [86]. Induction seed dormancy may also be what is called physical dormancy (PY) and is largely regulated by external factors (such as water, light, and temperature) regulating this kind of dormancy [87]. Hence, these three factors, water, gases, and mechanical resistance, are considered in relation to induction dormancy [88]. Physical seed dormancy is associated with some histological properties of the seed coat, such as dense epidermal palisade cells and the presence of numerous chemical compounds such as lignin, callose, lipids, phenolic deposits, cutin, wax, and suberin, in any layer of the seed coat [89]. The water-impermeable layers of palisade cells in the seed coat limit water transport, causing seed coat dormancy [90, 91].

#### 4.2.2.3 Genetic dormancy

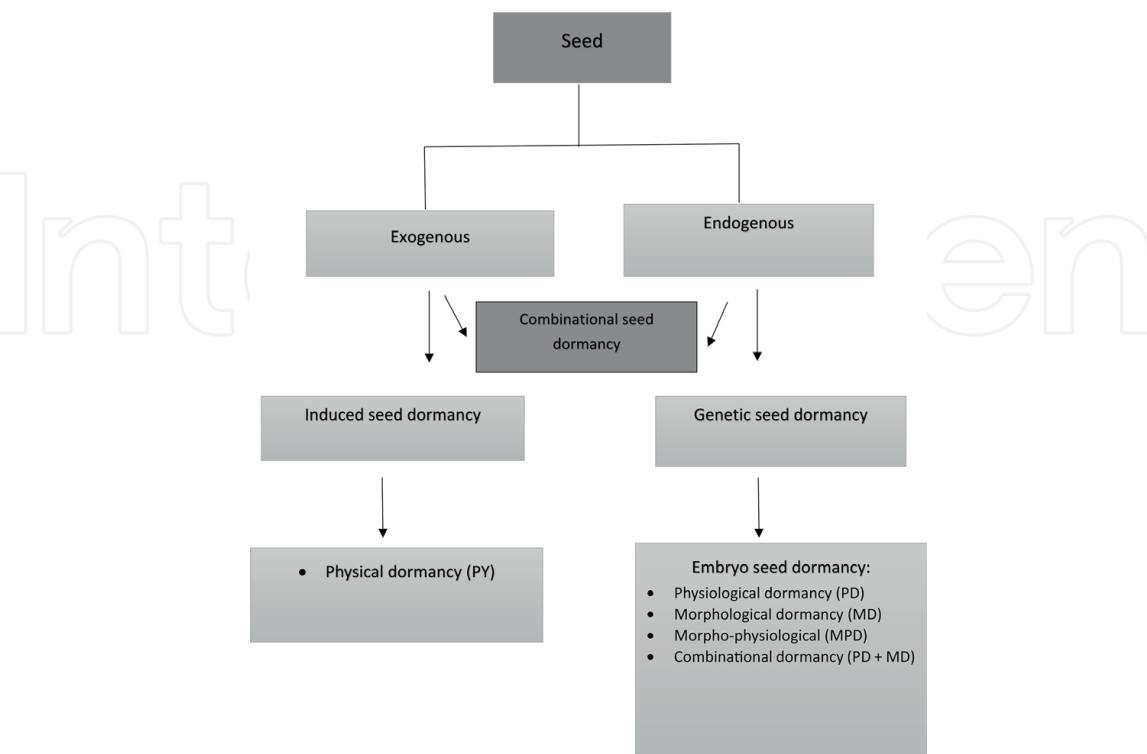
This is a kind of dormancy that is entirely regulated by the intrinsic factors of the seed such as embryos maturity and response to growth regulators [87]. Genetic dormancy is underpinned by three kinds of dormancies which include morphological dormancy (MD), morphophysiological dormancy (MPD), and physiological (PD).

Morphological dormant (MD) seeds have small, underdeveloped embryos that do not have a mechanism of physiological dormancy; hence, they do not require a dormancy-breaking intervention, rather sufficient time to further develop to full size to sprout [69, 80, 92].



Morphophysiological dormant seeds are also evidence of immature or underdeveloped embryos; however, they possess a component of physiological dormancy [80], as there may be hormone imbalance or the embryo's inability to push through the hard endocarp [93]. Such seeds therefore need pre-sowing treatment for dormancy breaking [80]. The time required for embryo growth or radicle protrusion to occur in seeds with morpho physiological dormancy is much longer compared to seeds with morphological dormancy [80].

Physiological dormancy (PD) is the most abundant form of dormancy found in seeds, gymnosperms, and all kinds of angiosperm clades. Due to a number of inhibitors, germination, growth-promoting enzymes and hormones can be inhibited as a result prevent complete germination of the seed. Any imbalance between inhibitors such as abscisic and promoters such as gibberellic acid may influence germination [90, 91, 94]. This suggests that if the two acids are not balanced; then, the balance or ratio needs to be tipped in the favor of those that will allow germination to proceed. Sufficient levels of abscisic inhibitors may counteract growth-promoting enzymes such as gibberellins since the two enzymes have opposite functions. These two enzymes present in seed endosperm, cotyledons, and sometimes on the outer coverings of the seed or fruit. Most of these chemicals are water soluble and can easily be leached from the seed which may help in shifting the balance towards the growth-promoting enzymes allowing germination [87]. Some of these chemicals must be degraded into other forms or reduced concentration. Inhibitors that are found in the seed embryonic axis are mostly controlled by temperature, sometimes light. Temperature may also favor the production of growth-promoting hormones and enzymes in the embryonic axis. Cool temperatures generally shift the balance of promoters and inhibitors towards promoting germination [95].



**Figure 4.**  
*An outlines the primary seed dormancy mechanisms, adopted from [83, 85].*



Seeds with combinational dormancy comprised both physical dormancy and physiological dormancy [80].

#### *4.2.2.4 Secondary dormancy*

This is also called temporary or real dormancy, entirely associated with environmental conditions where seeds are planted such as light, temperature, and water; thus, when appropriate conditions are provided, the seeds will start germinating (**Figure 4**) [96].

### **4.3 Factors responsible for physical seed dormancy**

#### *4.3.1 Water impermeability of seed coat*

The inability of seed coat to allow water penetration, which may be known as seed coat impermeability to water imbibition may be influenced by environmental and genetic factors. The interaction of environmental conditions such as climate or soil during seed development are contributing factors toward seed impermeability [87]. Seeds with impenetrable coats or hard-coated seeds may be a result of cuticle layer strong epidermal layer/cells surrounding the seed [87]. These cells render the seed impermeable to water as a result hindering germination. For instance, legumes constitute large reserves of lignin, cutin, or suberin. In some seeds, seed coat impermeability is due to large buildup of hilum, strophiole which restricts the movement of water through the seed coat.

#### *4.3.2 Seed coat impermeability to gas exchange*

Oxygen is one of the major atmospheric gases also present in soil pores spaces and is required by seeds for the metabolism process. If seeds are deprived of it either due to seeds being buried too deep into the soil or in waterlogged soils, the seed may be starved of this gas [97]. Seedlings use oxygen as the main energy source during aerobic respiration until they have grown leaves. Seed internal membrane impermeability (due to harden-seed coat) may hinder sufficient gas exchange, and such may be prevented when the seed coat is worn out enough to allow gases exchange ( $\text{CO}_2$  and  $\text{O}_2$ ) and water penetration from the environment.

#### *4.3.3 Mechanical resistance of the seed coat*

This may be associated with the development of physical limitations on the seed coat during embryo development. Although the seed may be absorbing enough water, it might not be enough to cause seed cracking and germination. Inhibitors on the seed coat may be a cause of such resistance and such is common in plantain, raspberry and cherry, and legume seeds [80, 98, 99].

### **4.4 Factors responsible for endogenous seed dormancy**

#### *4.4.1 Germination inhibitors*

Many species' seeds fail to germinate even when the embryos are completely developed when the seed is ripe, even though the environmental conditions are

excellent. In such seeds, dormancy is caused by the physiological state of the embryo [62]. The embryos of such seeds will not grow when they initially mature, even if the seed covers are removed. Abscissic acid (ABA) is one of the most commonly detected inhibitors of germination.

#### *4.4.2 Dormant embryo*

Even when the embryos are fully grown when the seed is ripe, many species' seeds fail to germinate, even when the environmental conditions are ideal. The physiological state of the embryo causes dormancy in such seeds [62]. Even if the seed coverings are removed, the embryos of such seeds will not grow when they first mature. During the period of dormancy, some physiological changes called after-ripening occur in the embryo before the seed is capable of germination.

### **4.5 Seed priming and breaking of dormancy**

Seed priming using pre-sowing treatments is one of the approaches recommended for dormancy-breaking and enhancing germination [100]. As shown in **Table 4**, the different pre-sowing treatments use different modes of action to disrupt dormancy in plants. The majority of the pre-sowing treatments soften the water-impermeable seeds (or fruit) coat in high-order plants and enhance plant growth factors including germination rate and uniformity, as well as contributing to increased yields and plant resistance [124].

Although dormancy is an evolutionary mechanism that enables a species' long-term survival by allowing it to persist in the face of adversity [80, 91]. The ability to break dormancy is however crucial to getting seeds to germinate when necessary [91]. The purpose of breaking dormancy is to provide moisture to stimulate the seed's metabolism in repairing damages before commencing embryo development and root emergence [124].

Mechanisms of breaking dormancy are divided into seed coat treatments, also known as seed scarification techniques, and embryo treatments [87]. The embryo treatments are used to break genetic dormancy while the seed coat treatments are used to break physical dormancy which is associated with the physical properties of the seed coats.

Seed scarification techniques are used to overcome the hard, impermeable seed coat and include mechanical and chemical scarification, freeze-thaw, and cold-water soaking [87, 90, 125]. Mechanical scarification can be performed by rubbing the seed between pieces of sandpaper, abrasive, or sand, or by shaking the seed vigorously [87]. This is done to create a small hole in the seed (or fruit) forming an opening (or water gap) which will allow water to move and reach the embryo for embryo growth [126–128]. Mechanical scarifying of seeds is the most effective technique for dormancy-breaking although, it is time-consuming mostly if a large quantity of seeds requires scarification. With mechanical scarification, there are machines that allow the seeds to roll or blow seeds against abrasive surfaces (i.e. splinters or sandpaper inside containers) [128]. However, these machines do not work well for thick-coated seeds such as *Acacia* species, except on small and thin-coated seeds such as *Trifolium subterraneum* [128]. Sandpaper is used for scarification and is effective depending on the genus or species [129].

Seed priming method	Mode of action	Reference
Mechanical scarification	<ul style="list-style-type: none"> <li>• Weakening/remove tissues covering the embryo surface.</li> <li>• Opens the micropyle.</li> </ul>	[101, 102]
Acid scarification	<ul style="list-style-type: none"> <li>• Burns/weakens the seed coat and epidermal layers.</li> </ul>	[102, 103]
Hot treatment	<ul style="list-style-type: none"> <li>• Weakening of seed coat by dissolving the lignin and pectins present in epidermal layers.</li> </ul>	[103]
Hydropriming	<ul style="list-style-type: none"> <li>• Activation of enzymes and mobilization of reserves in the aleurone layer.</li> <li>• Softening of hard seed coats and leaching out of chemical inhibitors (mainly ABA).</li> </ul>	[102, 104–109]
Bio-priming	<ul style="list-style-type: none"> <li>• Activation of early phases of germination.</li> <li>• Weakening of seed coat layers during the soaking (seed hydration) phase.</li> <li>• Protects seeds against the soil and seed-borne pathogens by applying antagonistic microorganism during priming.</li> </ul>	[63, 107–110]
Gibberellic acid (GA3)	<ul style="list-style-type: none"> <li>• Activates DNA in the aleurone cells.</li> <li>• GA counteracts the effect of ABA by promoting the embryo growth potential.</li> <li>• Weakening of tissues covering the embryo.</li> <li>• GA3 enhances cell enlargement and cell division in embryo.</li> <li>• Chemical activator and growth hormone.</li> <li>• stimulate the synthesis and production of the hydrolases enzymes resulting in the germination of seeds</li> </ul>	[15, 102, 106–109, 111, 112]
Absciscic acid (ABA)	<ul style="list-style-type: none"> <li>• Prevents loosening of the embryo cell wall which impedes water uptake.</li> <li>• Inhibit endosperm rupture instead of testa rupture.</li> </ul>	[109, 113]
Indole-3-acetic acid (IAA)	<ul style="list-style-type: none"> <li>• One of the prime auxins in plants, that regulate cell division, enhance photosynthetic activities, and activate the translocation of carbohydrates that enhance root initiation.</li> </ul>	[106]
Halo-priming	<ul style="list-style-type: none"> <li>• Activation of early phases of germination.</li> </ul>	[63, 107–109]
Embryo rescue	<ul style="list-style-type: none"> <li>• Break immature embryo using warm stratification.</li> <li>• Eliminate seed germination inhibitors.</li> </ul>	[114]
Solid matrix priming	<ul style="list-style-type: none"> <li>• The use of solid medium allows seeds to hydrate slowly and simulates natural imbibition process occurring in the soil.</li> </ul>	[107–110, 115]
Osmo-priming (PEG, sugar, mannitol and sorbitol, NaNO3, MgCl2, NaCl, and KNO3)	<ul style="list-style-type: none"> <li>• Allow pregermination metabolic activities.</li> <li>• Through a delayed water entry to seed reduces the ROS accumulation and thus protects the cell from oxidative injury.</li> </ul>	[107, 109, 116]

Seed priming method	Mode of action	Reference
Priming with plant extract (such as phenolic compounds, terpenoids, flavonoids, saponins, alkaloids, and steroids)	<ul style="list-style-type: none"><li>• Saponins can enhance nutrient absorption as they are readily soluble in water.</li><li>• Alkaloids, saponins, and phenolic compounds present in the leaves of various plants are involved in the production of antioxidant activities and protect the plants against pathogens.</li></ul>	[106, 117]
Nanoparticles (calcium-phosphate, SiO <sub>2</sub> , ZnO, and Ag)	<ul style="list-style-type: none"><li>• Allows for greater penetration of seed coat that improves nutrient and water uptake efficiency of the seed.</li></ul>	[109, 118, 119]
Seed priming through physical agents (magnetic field, UV radiation, gamma radiation, X-rays, and microwaves)	<ul style="list-style-type: none"><li>• Magnetic field improves germination rate, vigor, and seedling biomass as well as tolerance to various environmental stresses by means of reduction in reactive oxygen species (ROS) with increasing activities of antioxidant enzymes.</li><li>• Rays interact with cellular components directly and improve the germination at lower doses.</li><li>• Ultrasound priming induces mechanical pressure on seed coat that increases the seed's porosity known as acoustic cavitation and activation of enzymatic and other biological reactions due to greater water uptake in the seed.</li></ul>	[106, 120–123]

**Table 4.**  
Mode of action of seed priming methods and promotion of germination.

Freeze-thaw scarification is a method of breaking the seed coat by exposing seeds to extreme cold (very low temperatures). Freeze-thaw scarification decreases hard-coated seed by creating microscopic scars on the hard seed coat and leaving the seed coat soft, which improves germination [125]. Chemical scarification involves the use of acids such as hydrochloric acid or sulfuric acid to burn the seed coating of the seed by immersing seeds in acids for a couple of minutes or seconds [130]. Hot water scarification involves the immersion of seeds in boiling water to soften their outer covering, the effectiveness of heat or hot water scarification varies with the type of device used, treatment time, and temperatures [125, 130]. However, it is necessary to identify sufficient scarification, as excessive scarification can result in the damaging of the embryo [91]. Seeds with non-deep physiological dormancy can germinate after undergoing chemical or mechanical scarification [80]. Several studies conducted on *Cassia occidentalis*, *C. obtusifolia*, *Indigofera astragalina*, *I. tinctoria*, *I. senegalensis*, *Tephrosia purpurea* and *Sesbania pachycarpa* [131], *Parkia biglobosa* (Jacq. Benth) [132], *Astragalus hamosus* and *Medicago orbicularis* [127], *Tylosema esculentum* (Buech) L. Schreib [133], *Senna alata* (L.) Roxb. [130], and *Senna alata* [134] have shown that when seeds were immersed in concentrated sulfuric acid, it resulted in improved final germination percentage of the dormant seed.

Hydropriming techniques may include cold water soaking and heat treatment using dry and wet heat. The dry and wet priming methods are both grouped together under heat scarification where two heating devices, which include the oven and hot water baths, are used to soften the hard seed coat [125]. The kind of heating device used, heating temperature and time, determines the effectiveness of each heat treatment. Wet heat involves the immersion of seeds that are water-impermeable in hot water so that they become permeable [126]. According to Baskin and Baskin [126],



this method involves placing the seeds in cloth bag and dipped in water baths for the required period of time. The seeds are allowed to cool for a few minutes after the water bath. This method was proven effective in softening the seed coat and enhancing germination of *Sena alata* (L.) Roxb resulting in 77.7% [130]. Dry heat is the most common technique used to render seeds (of species that are water-impermeable) permeable to water by placing them in an oven at a definite temperature [130]. These techniques are effective for physical dormancy-breaking in a number of species [126].

Embryo treatments include chemicals (such as GA3 and KNO3), high temperature, and stratification treatments [125]. Stratification is the process of incubating seeds at a low temperature (also called pre-chilling) over a moist surface before transferring them to a temperature that will allow them to germinate [135]. According to Kimura and Islam [125], the force that forms scars on seed coat using this procedure is determined by the shape, size, and moisture content of the seeds, and also the duration and intensity of the treatment [125].

Bio-priming, also called the biological seed treatment, is an advanced technique of preventing stunted plant growth as a result of reduced quality of seeds physiology through the integration of biological agents (inoculation of seeds with beneficial microorganisms to protect seed) [136] or combination [137]. The treatment is applied on the seed surface, and the seed is allowed to dry. Biological seed treatment as explained in **Table 4** provides an ecological advantage to seeds by controlling several seed or soil-borne pathogens which also provide an alternative chemical treatment [136]. According to Rafi and Dawar [136], seed bio-priming enhances the initial step in the development of plants by increasing seed tolerance to different stress (seed or soil-borne pathogens), thus improving seed germination, and *Trichoderma* is the most widely used species.

#### 4.6 Work documented on the recommended seed priming methods for breaking dormancy of some underutilized crops

Seed priming is a physiological technique that involves seed hydration and drying to enhance the metabolic process before germination in order to quicken germination, seedling growth, and crop yield under normal, as well as different biotic and abiotic stress conditions [108]. Seed priming has emerged as an effective seed treatment tool for many crops especially underutilized crops; however, treating conditions and methods of priming tend to differ with plant species (see **Table 4**) as explained below. Each of these methods can be tailored to the specific requirements of the seed species being primed as previously discussed, and different species may have different mechanisms of dormancy. Understanding the biology of the seed and dormancy mechanism, the mode of action (see **Table 4**) of the priming method is key for choosing the most effective priming method. Numerous work has been done and documented on seed priming of some underutilized medicinal and leafy vegetable plants in order to improve the final yield (see **Table 5**). Although in species such as *Athrixia phylicoides* DC. and *Siphonochilus aethiopicus* (Schweinf.) B. L. Burt (see **Table 5**), there is no work done.

#### 4.7 Biochemical and molecular factors regulating seed germination in plants

Dormancy release and seed germination are controlled by interconnected molecular processes regulated by different types of hormones such as abscisic acid (ABA), gibberellins (GA), ethylene, and auxin that interact with each other [94]. Furthermore, abscisic acid and gibberellins act antagonistically to each other, whereby ABA promotes induction and maintenance of dormancy during imbibition while GA promotes germination

Species name	Priming method	References
<i>Sutherlandia frutescens</i> L.	Scarification (mechanical and acid)	[11, 16]
<i>Athrixia phyllicoides</i> DC.	Temperature (15, 20, and 25°C) treatments under constant light exposure	[138]
<i>Momordica charantia</i> (L.)	Hydropriming, halopriming (NaCl and 48 hours of ZnONP)	[106, 110, 139]
<i>Siphonochilus aethiopicus</i> (Schweinf.) B. L. Burtt	—	—
<i>Cyclopia</i> (Vent.) spp.	Scarification (H2SO4, mechanical), hot water treatment	[140]
<i>Ceratonia siliqua</i> L.	Scarification (mechanical and H2SO4), Hot water treatment, soaking in distilled water (24 h)	[141–143]
<i>Portulaca oleracea</i>	Hot water treatment, hydropriming for several hours, 100% relative humidity for several hours	[143, 144]
<i>Amaranthus</i> spp.	Osmo-priming, hydropriming	[145, 146]
<i>Vigna subterranea</i> (L.)	Osmo-priming	[147]
<i>Moringa oleifera</i>	Hydropriming	[148–150]
<i>Corchorus olitorius</i>	Hot water treatment	[14, 151]

**Table 5.**  
List of plants and recommended priming method.

Phytohormone	Control of seed germination	Reference
Absciscic acid (ABA) and gibberellins (GAs)	<ul style="list-style-type: none"><li>• ABA and GAs balance plays a significant role in controlling seed dormancy.</li><li>• ABA significantly inhibits seed germination, and a high ABA and GA ratio normally hinders germination in dormant seeds.</li><li>• A decrease in ABA is mostly important for initiating germination and GA levels increased.</li><li>• High levels of ABA in seeds inhibit germination by increasing the expression of dormancy-related enzymes such as NCED (9-cis-epoxycarotenoid dioxygenase) and gene DOG1 (delay of germination1) gene</li><li>• And reducing growth-related GA-responsive genes such as GA3ox1 and GA3ox2</li></ul>	[60, 152, 153]
Ethylene	<ul style="list-style-type: none"><li>• Promotes seed germination in plants, is produced right after seed imbibition, and increases as germination continues.</li><li>• Production can be increased by nitric oxide, hydrogen cyanide, low temperatures, and GA treatments, encouraging seed germination.</li><li>• Arabidopsis ethylene-responsive factor ERF12 can bind to the promoter of the important dormancy gene DELAY OF GERMINATION 1 (DOG1) and recruit the transcriptional co-repressor TOPLESS (TPL), which decreases DOG1 expression and increases seed germination.</li></ul>	[154]

(**Table 6**) [156–158]. Ethylene is also a promoter of seed germination, having receptors such as ethylene response factor 1 (ETR1) that reduce dormancy phenotype and enhance germination [159]. Ethylene continues to be produced as germination proceeds and can be increased by nitric oxide, hydrogen cyanide, low temperatures, and GA treatments, promoting seed germination (**Table 6**) [154]. However, auxin functions negatively and positively in seed germination depending on its amount, whereby high levels of auxins promote seed dormancy by activating AB13 through auxin-responsive transcription factors (ARF) 10 and ARF16 being released [160]. Additionally, low levels result in ARF 10 and ARF16 being oppressed by AXR2/3 and failure to activate the expression of AB13 and maintain dormancy (**Table 6**) [65].

4.7.1 *Phytohormone that controls dormancy and germination.*

Phytohormone	Control of seed germination	Reference
Auxins	<ul style="list-style-type: none"><li>• Auxins modulate ABA positively and GA biosynthesis and signaling pathways negatively, promoting dormancy. However, auxins can also break dormancy by interacting with GA which promotes germination and is crucial for the development of the root system during germination.</li><li>• While low levels of auxins result in ARF10 and ARF16 being oppressed by AXR2/3 and failure to activate the expression of AB13 and maintain dormancy.</li><li>• High levels result in auxin-responsive transcription factors ARF10 and 16 being released to active AB13 transcription and maintain seed dormancy.</li></ul>	[65, 155]

**Table 6.**  
*Phytohormone that controls dormancy and germination.*

4.7.2 *Endosperm decay hinder embryo growth*

Endosperm performs as a mechanical barrier to seed germination in various angio-sperm clades in which a decrease in the mechanical resistance of the endosperm layer covering the radicle tip appears to be a prerequisite for radicle protrusion during seed germination [69]. Moreover, through bidirectional communication, the endosperm can affect the embryo’s initial growth or even completely prevent seed germination [161], whereby endosperm weakening can be enhanced by GA hormone and inhibited ABA (**Table 7**) [164, 165].

4.7.3 *Light regulation of seed germination and dormancy*

Seed germination and dormancy are not only controlled by plant hormones which are internal signals but also depend on external environmental elements such as light and temperature [101]. Moreover, seeds can be categorized based on their response to light during germination, whereby the controlling effect of light on seed germination depends on the light spectrum (**Table 8**) [168]. There are two types of light-sensing systems which include blue-light (photo regulation) and red-light (phytochrome regulation) sensitive systems, in which blue light promotes dormancy [169]. In



Endosperm decay impact on embryo growth	Reference
<ul style="list-style-type: none"><li>• Endosperm break down during seed germination releasing nutrients for the growing embryo.</li><li>• Slow endosperm decay can limit nutrient availability, slowing down embryo growth.</li><li>• Fast endosperm decay can lead to an overabundance of nutrients, causing an imbalance that hinders embryo growth.</li></ul>	[162, 163]

**Table 7.**  
*Endosperm decay hinders embryo growth.*

Light regulation of seed germination and dormancy	Reference
<ul style="list-style-type: none"><li>• The spectrum of light influences how seed germination is regulated.</li><li>• Blue light inhibits the germination of seeds and stimulates ABA.</li><li>• Red light, 600-760 nm stimulates GA biosynthesis, restricting ABA production and active seed germination.</li><li>• Far-red light, 760-800 nm can inhibit seed germination.</li></ul>	[61, 166]
<ul style="list-style-type: none"><li>• Plants can be categorized based on their response to light during germination.</li><li>• Those that require light to germinate.</li><li>• Require darkness to germinate.</li><li>• Plans that have a large percentage of seed neutral photoblastic.</li></ul>	[167]

**Table 8.**  
*Light regulation of seed germination and dormancy.*

contrast, red light promotes seed germination and far-red light inhibits seed germination (Table 8) [166]. Furthermore, temperature elevation or lowered may impede different physiological and molecular mechanisms, hence delaying the germination of seeds causing dormancy to be disrupted while high temperatures disrupt dormancy, which causes germination (Table 9) [60]. Low temperatures delay germination by increasing ABA synthesis and lowering water absorption, protein breakdown, glucose metabolism, and energy production (Table 8) [170].

4.7.4 Temperature regulation of seed germination and dormancy

Role in regulating seed germination	Reference
<ul style="list-style-type: none"><li>• Determines germination time by influencing germination directly and regulating dormancy.</li><li>• High or low temperatures can cause a delay in the germination of seeds due to the obstruction of various molecular and physiological processes.</li><li>• Low temperatures delay germination by increasing ABA synthesis and decreasing water absorption, protein breakdown, carbohydrate metabolism, and energy production.</li><li>• High-temperature conditions disrupt dormancy, leading to germination.</li><li>• For optimal germination, most seeds require temperatures between 15 and 30°C. For instance, <i>Vigna subterranea</i> (L.) requires an optimum temperature from 30 to 35°C for germination.</li></ul>	[170, 171]

**Table 9.**  
*Temperature regulation of seed germination and dormancy.*

## 5. Future prospectus in the production of underutilized medicinal and leafy vegetables

Steps towards the understanding of mechanisms of seed dormancy, identification of genes, hormones, and metabolites involved, and the role of the environment have modernized ways of addressing challenges of seed dormancy in a range of crops. Molecular biotechnology is one modern approach that has revolutionized research in biological science, resulting in the development of superior crop material [172–174].

Gene editing and genome engineering as tools have offered great advances in the study of seed dormancy [174]. In recent years, the use of CRISPR/Cas9 in gene editing has gained extensive use in plant and animal physiology [175]. Research and manipulation of seed dormancy genes such as delay of germination 1 (DOG1), seed dormancy 4 (SDR4), and mother of FT and TFL 1 (MFT) in medicinal plants and indigenous vegetables could greatly improve seed germination [176]. The applicability of the technique has been tested previously on a number of crops, including grasses, wheat, and barley [175–177]. Glison et al. [176] extensively reported on the application of genetic editing and genome engineering in the seed dormancy of grasses. The potential of marker-trait associations (MTAs) and marker-assisted selection of genes for engineering in breeding for seed dormancy in wheat was reviewed by Kulwal [177], while [175] reduced seed dormancy in rice (*Oryza sativa* L.) by knockout viviparous-1 (OsVP1) gene responsible for seed dormancy. In barley, the genetic editing of QTL for seed dormancy 1 (Qsd1) and Qsd2 genes affected seed germination of the plant [178]. Induced mutation of the Qsd1 homeoalleles was responsible for the regulation of seed germination in wheat [179].

Unlike genetic editing and genome engineering, epigenesis regulation is one modern technique exploited in the understanding and regulation of seed dormancy, that involves altering the gene expression and associated proteins without changing their sequence [180, 181]. The leading mechanisms in epigenesis include DNA methylation, modifications to chromatin, loss of imprinting, and non-coding RNA [180]. An impressive work done by Luján-Soto and Dinkova [182] in the use of epigenesis modifications in seed dormancy, highlighted the potential of the technology in detail. Work done by Sato et al. [183] on *Arabidopsis* demonstrated the applicability of epigenesis modification, in stimulating and inhibiting seed germination. On the other hand, [174] demonstrated that histone deacetylase HDA19 and histone methyltransferase SUVH5 both worked together in the regulation of seed dormancy in *Arabidopsis*. Recently, [184] reported also the histone modifications, acetylation, and methylation, moderating the seed dormancy of *Arabidopsis thaliana*. Secondary seed dormancy depth and germination in *Capsella bursa-pastoris* were reported to be regulated also by histone methylation [185]. Using epigenetic modification, [186] demonstrated the potential for influencing seed dormancy in *Paris polyphylla*.

Recent advances in understanding the role of environmental factors from seed development to seed dispersal have also opened a door in addressing the challenge of seed dormancy [187, 188]. Focus previously has been on the effects of temperature, light, and moisture as environmental effects, but advances in the field of metabolomics and hormonal signaling on seed dormancy and germination have recently received much attention [160, 189].

The potential of this technology in the improvement of seed dormancy and germination in medicinal and indigenous vegetables could not be overestimated. The exploitation of these modern and advanced research tools and techniques on

seed dormancy regulating physiological factors could potentially be applied to the improvement and commercialization of medicinal and indigenous vegetables.

**6. Conclusion**

Seed dormancy is a survival trait for wild plants, but a great hindrance to the domestication of important medicinal and indigenous vegetables as it affects the crop germination rates and crop stand, resulting in reduced yield. Medicinal and indigenous vegetables have been identified as crops with potential in addressing challenges of food security and malnutrition in poor rural communities if domesticated and commercialized. This book chapter makes it clear that advances in gene editing, genome engineering, and epigenesis modification present a big opportunity in overcoming seed dormancy of these wild plants.

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**Conflict of interest**

The authors declare no conflict of interest.

**Acronyms and abbreviations**


AUC	African Union Commission
ARF	Auxin responsive transcription factors
DOG 1	delay of germination 1
ERF	ethylene response factor 1
OsVP1	knockout viviparous 1
MTAs	Marker trait associations

**Author details**

Thobile Perseverance Mkhwanazi\*, Gugu Cynthia Maseko  
and Zakheleni Palane Dube  
University of Mpumalanga, Mbombela, South Africa

\*Address all correspondence to: mkhwanazithobile5@gmail.com

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