

Review

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Posted Date: 17 March 2026

doi: 10.20944/preprints202603.1204.v1

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Review

# Advances and Deficits of Conventional and Novel Seed Enhancement Technologies

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## Abstract

Global population growth, climatic extremes, and rising resource pressures necessitate innovative agricultural methods to boost food, feed, fibre and fuel production sustainably. Seed enhancement technologies (SETs), such as seed coating and priming, have emerged as effective strategies to improve seed viability and vigour, seedling establishment and overall crop yield. Conventional seed treatments, including film coating, encrusting, pelleting, and various seed priming techniques, offer advantages such as improved seed handling, uniform germination, and promotion of early growth. However, they also have significant drawbacks, such as the harmful effects of re-drying seeds after treatment, uneven distribution of active ingredients, environmental pollution, reduced seed longevity and decreased soil microbial health. To tackle these issues, new non-traditional SETs are being investigated, including nanotechnology and novel biodegradable coatings, which help to lessen the negative effects of traditional SETs. These innovative methods demonstrate great promise in enhancing seed performance, minimising environmental impact, and ensuring cost-effective scalability across diverse agricultural settings. This review critically examines both conventional and novel SETs, discusses their pros and cons, and outlines strategic research and industry directions to enhance agricultural sustainability and productivity in light of global food and resource security challenges.

**Keywords:** seed enhancement technologies; seed coating; seed priming; nanotechnology

## 1. Introduction

The global population is projected to reach 9.7 billion by 2050, necessitating a 25-70% increase in agricultural productivity, which presents a formidable challenge [1]. Concomitantly, global upheavals such as the US-China trade conflict, wars, such as in the Middle East and Ukraine, and the global COVID-19 pandemic have resulted in volatile prices for on-farm resources such as energy, water and agrichemicals [2], slowing the Global Agricultural Productivity (GAP) Index, measured by total factor productivity (TFP), from 1.95% during 2001-10 to 0.76% during 2014-2023 [3]. Simultaneously, rapid shifts in consumption patterns from globalisation and economic growth are contributing to water pollution, soil degradation, and the depletion of crucial resources. Furthermore, anthropogenic greenhouse gas emissions impact the global climate, resulting in unpredictable weather patterns and increased frequency of extreme events that challenge the resilience of agricultural and eco- systems [4,5].

The silver lining is that such global upheavals and increasing demand for food, feed, fibre and fuel are pushing industries and researchers to develop more eco-friendly and cost-effective products and techniques, thus stimulating a new agri-technological revolution [6,7]. One highly promising area where drastic improvements are being made is for conventional seed enhancement technologies

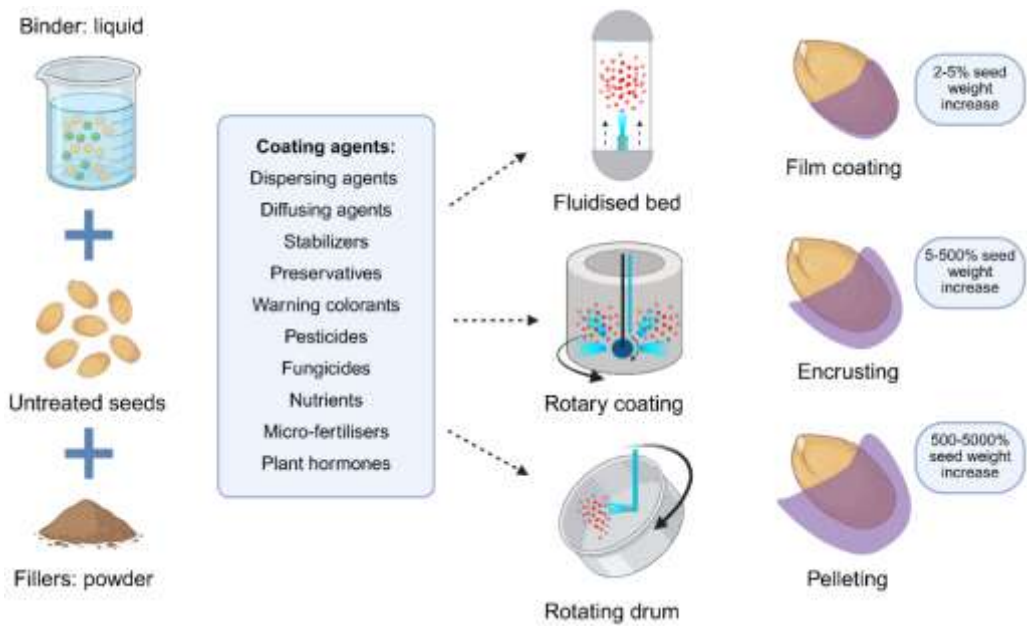
(SETs), which include seed coating and priming [8,9]. SETs have been developed to improve seed lot quality, which in turn can enhance seedling emergence, survival, crop productivity, and effectively administer chemicals [10,11] and biological treatments [12].

A quality seed lot has high seed viability and vigour, as well as genetic purity and immunity from disease [13]. Seed viability is defined as the ability of a seed to germinate and produce a normal seedling under favourable conditions, while vigour encompasses planting value (emergence-ability, -rate and -uniformity, seedling growth) across environments, including under unfavourable conditions. Vigour also includes seed lot storage potential and performance after storage [13]. Therefore, while viability is crucial for achieving high crop yields [14], if a seed lot has low vigour, in-field biotic and abiotic stressors can drastically reduce crop productivity and yield. Biotic stressors can include pests, weeds, and pathogens, while abiotic stressors can encompass temperature extremes, drought, poor soil characteristics, pollution, etc [15–17]. SETs are therefore designed to maximise both seed viability and vigour and minimise disease, thereby enhancing seed quality, planting value and crop yield [9].

To thoroughly review this topic, we first compare conventional seed coating and priming technologies that are currently utilised for crops and critically analyse the advantages and disadvantages of each technology. Then we focus on emerging or alternative technologies that aim to overcome specific disadvantages of conventional technologies. The following section defines and analyses the first conventional SET: seed coatings.

2. Conventional Seed Coating

Seed coating technologies, such as pelleting, encrusting and film-coating (Figure 1), are used to improve seed planting practice, for example, by changing seed shape, weight, and surface characteristics to make seeds better suited for specific planting conditions, to fit into machinery and to increase soil-seed contact [18–20]. Increasingly, seed coatings are also used to deliver nutrients [21,22], bio-stimulants [12], crop protection agents, such as systemic insecticides [23], fungicides [24], and phytohormones [25]. Coating advances in literature also promise improved plant stress tolerance [26].



**Figure 1. Conventional and commercial seed coating methods.** Untreated seeds are mixed with coating agents (liquid binders, powder fillers, additives, etc.) inside commercial coating equipment (fluidised bed, rotary coater, rotating drum, etc.) to film coat, encrust or pellet the seed [18,27,28].

The origins of seed coating date back to c. 23-79 AD when the Roman naturalist, Pliny the Elder, coated vegetable seeds with goat dung pellets to assist emergence [29] and many iterations have followed, such as wheat flour paste pellets improving cotton seed quality in 1866 [30]. Prior to today's techniques, dry powder coating mixed seeds with dry powders in a planter-box prior to sowing, however this led to poor loading, lack of uniformity, and dust-off problems [18,31]. The most common commercially used techniques today, film coating, encrusting and pelleting (Figure 1), were developed in the 1980s to replace dry powder coating. The total gross value of seed coatings was US\$ 2.38 billion in 2025 and is expected to reach US\$ 3.52 billion by 2030 (CAGR of 8.2%) [32]. During conventional seed coating, the seed is coated in one or more layers of materials, and coatings are purported to accelerate germination and enhance seed viability and vigour compared with untreated seeds, especially where stressful conditions and/or pathogens constrain growth [33]. Forecasts are that polymers as additives and cereals and grains as crops will hold the largest market shares [32].

2.1. Disadvantages Across Conventional Seed Coating Techniques

As summarised in Table 1, there are some universal disadvantages across seed coating techniques. Coatings can have substantial negative impacts on the seed microbiome, especially the depletion of gram-negative bacteria. This is significant because early microbial colonisers of germinating seedlings can substantially influence plant development and health, with seed endophytes increasing resilience against pathogens [34]. Also, the uneven distribution of coating agents can severely impact the performance of actives, which are, as a consequence, applied at too low or too high a dose [18]. Coating thickness variations can also significantly influence germination. For example, zinc-coated chickpea seeds displayed a negative correlation between a higher concentration of coating agent and seedling growth [35], while germination of cucumber seeds treated with a polymer coating with and without pesticides was significantly reduced compared to non-treated seeds [36]. Coatings can also restrict water and/or oxygen uptake. For example, coatings on barley, rye, and wheat seeds resulted in near anoxic conditions within the developing embryonic tissues, as well as a lower rate of imbibition and imbibition capacity compared to uncoated seeds [37]. Also, dosages of actives such as fungicides and insecticides are high enough in coatings to pose environmental risks [38], and the release of dust by abrasion of coated seeds during handling/planting remains a matter of concern [39,40]. Indeed, increasingly utilised neonicotinoid insecticides within seed coatings continue to cause bee mortality and environmental pollution through dust release.

Table 1. A summary of the disadvantages of conventional seed coating techniques.

| Techniques        | Disadvantages                                                                                                                                                                                          | References |
|-------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------|
| All seed coatings | Seed coating materials depleted the seed microbiome, especially gram-negative bacteria.                                                                                                                | [34]       |
|                   | Degradation of microplastics in seed coating materials might negatively affect soil health, especially for small and irregularly shaped seeds.                                                         | [40]       |
|                   | Uneven distribution of coating agents impacts performance, delivery of actives & can impede germination & growth.                                                                                      | [18]       |
|                   | The coating agent can restrict water uptake, causing a delay in entering phase II of germination & can result in temporal membrane damage.                                                             | [35,36]    |
|                   | Dosages of actives, such as fungicides and insecticides, are high enough to pose substantial environmental risk & harm, such as to wild bees.                                                          | [38,41]    |
|                   | Bio-priming is a better technique for certain applications than seed coating, such as for wild plant restoration. Seed coating reduced germination for wild plant restoration and was not recommended. | [42,43]    |
|                   | Storage complexities and limited shelf life of seeds (discussed in depth in Section 4 and Table 3).                                                                                                    | [32]       |



|              |                                                                                                                                                                                       |         |
|--------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------|
| Film-coating | Effectiveness depends on the polymer type and dosage.                                                                                                                                 | [44]    |
|              | Irregularly shaped seeds are hard to process.                                                                                                                                         | [45]    |
|              | Release of dust by abrasion of film-coated seeds during handling/planting remains a matter of concern, e.g. neonicotinoid insecticides cause bee mortality & environmental pollution. | [39,40] |
|              | To minimise abrasion losses from film-coated seeds, seeds can require extra processing, e.g. removing the outer wax layer on maize seed pericarp prior to applying coat formulations. | [39]    |
|              | Detached coating film fragments from commercial polymer mixtures persist in soil for longer than biodegradable plastic formulations (i.e. <48 d vs. <32 d).                           | [40]    |
| Encrusting   | Encrusting requires copious amounts of water to ensure an even covering layer forms, hence drying equipment is needed to re-dry freshly encrusted seed back for storage.              | [46]    |
|              | Thicker seed covering makes seeds take longer to germinate than film-coating.                                                                                                         | [37]    |
| Pelleting    | Due to the thick coating, one must carefully select coating materials that do not prevent or delay seed germination.                                                                  | [28]    |
|              | Pelleting agents must have the correct particle size distribution, porosity, water holding capacity, water imbibition ability and be non-toxic.                                       | [47]    |
|              | Requires optimised processing time & handling equipment to ensure seeds germinate without any restriction.                                                                            | [31]    |

For example, when an insecticide containing the neonicotinoid clothianidin and the non-systemic pyrethroid  $\beta$ -cyfluthrin was coated on *Brassica napus* seeds, reductions in density, colony growth, and reproduction of wild bees under field conditions were observed [41]. For ecological management specifically, bio-priming is recommended as a better technique than seed coating [42], and indeed, seed coating has reduced wild plant germination and was not recommended for ecological restoration [43,48]. Also, seed longevity is limited by the seed coating [32], which is discussed in depth in Section 4. Sections below individually review film-coating, encrusting and pelleting.

2.2. Film-Coating

Film-coating utilises a binder (often a polymer) to adhere active compounds, such as fungicides, insecticides and stimulants, to the seed via a thin coating layer that increases seed weight by 2-5% (Figure 1), hence has little impact on seed shape, size, or weight [20]. The technique was repurposed from pharmaceutical applications and is now the most widely used coating technique. In fact, it is used for most seed coating purposes except for seeds that are very small in size or are irregularly shaped [40].

The advantages of film-coating are that seeds have high flowability for sowing, dust is controlled relative to dry powder coating, seed colour can be enhanced, and seedlings more easily emerge through the thinner coating compared to encrusting or pelleting [31]. Compared with crop spraying/broadcast application, film coating is more sustainable in protecting seeds/seedlings due to lower amounts of active ingredients needed [18], can significantly reduce dust/spray formation, and can reduce pesticide residues in soil [44]. Film-coating is also known for its broad versatility, being suitable for a wide range of crop seeds and capable of delivering multiple compounds simultaneously [18]. Indeed, rice seed film-coated with 1000 mg L<sup>-1</sup> GA<sub>3</sub> improved seed vigour, seedling growth, and yield [49] while barley seeds film-coated with free and immobilised alkaline phosphatase gained a better phosphorous uptake [50]. Film-coating can also be used for pest management, as demonstrated for cotton seeds film-coated with various concentrations of amino polysaccharides, which effectively protected cotton from pests, as well as increased seed germination and plant growth rates [51].

Modern film-coating techniques achieve high recovery rates, minimising waste of coating materials and ensuring cost-effectiveness. It is reported that recovery rates for film-coating techniques can often exceed 90% (i.e. >90% of coating materials applied to seeds successfully adhere) [28,31,46].

#### Disadvantages of Film-Coating

As summarised in Table 1, film-coating effectiveness depends on the polymer type and dosage used [44]. Many seeds that have irregular shapes, are waxy, or are small, such as lettuce and wild plant species, cannot be film-coated and require encrusting or pelleting and/or extra processing [18,45]. Indeed, film-coating of corn seed using aqueous slurries sprayed on seeds in rotary drums negatively impacted the uniformity of the coat due to low adhesiveness to the external wax layer and shape irregularities in corn kernels. Thus, to minimise abrasion losses, seeds required extra processing, including the removal of the outer wax layer of the seed prior to applying coat formulations [39]. Also, the release of dust by abrasion of film-coated seeds during handling/planting remains a matter of concern [39,40]. The detached coating film fragment degradation rate is variable and depends on the composition of the coating. The lowest degradation rate (<48 days) was observed in fragments detached from seeds coated with a commercial polymer mixture, while fragments from a biodegradable formulation degraded completely within 32 days [40].

#### 2.3. Encrusting

Encrusting increases seed weight by 5 to 500% (Figure 1) [18]. Being 'lighter' than pelleting, it is also called 'mini pelleting'. Encrusting leads to a smooth and homogenised seed surface, which promotes ease of handling [52]. Advantages of encrusting include the ability to improve seed quality. For example, seeds encrusted with salicylic acid assisted grass seed establishment for ecological restoration [53]. Another study indicated that sunflower seeds treated directly with pesticides had a negative impact on seed germination, while seeds encrusted with pesticides did not exhibit such negative germination effects [54]. Indeed, encrusting can improve seed germination, seedling growth, and pest control. For example, seed encrusting helped to fill irregularities that naturally occur on the rough surface of onion seeds and assisted in the ease of handling [55], while increasing certain binders, such as soybean flour, can further increase the integrity and compressive strength and lengthen the time for coatings to disintegrate [12].

#### Disadvantages of Seed Encrusting

As summarised in Table 1, encrusting requires copious quantities of water to ensure the formation of an even layer of covering. Therefore, drying equipment is needed to re-dry freshly encrusted seed back to its original moisture for storage [18]. Also, the thicker covering layer makes coated seeds take longer to germinate than film-coating, although the thickness of the layer can be modified by the amount of binding agent added [56].

#### 2.4. Pelleting

Seed pelleting increases the weight and size of seeds by 500 to 5000% (Figure 1), thus seeds are uniform and smooth, and the original seed shape is no longer visible [57]. Pelleting is especially useful for large-scale automated planting devices, where high-value small-sized crop seeds are modified, such as for lettuce [58], carrot [59], and tomato [60]. Also, the more accurate application of protective additives via this technology (relative to film coating/encrusting) has resulted in a rapid global increase in use, and there are now numerous companies and researchers testing combinations of materials. For example, soybean seed pelleted with foliar nutrition under irrigated conditions improved growth and yield [61]; fly ash seed pelleting in rice under aerobic conditions resulted in better crop growth and field productivity [62]. Similarly, tomato [63] and broccoli [64] seed pelleting has significantly enhanced germination rate and seedling emergence compared with uncoated seed. Pelleting techniques can also assist in seed security by protecting varieties; for example, seeds were

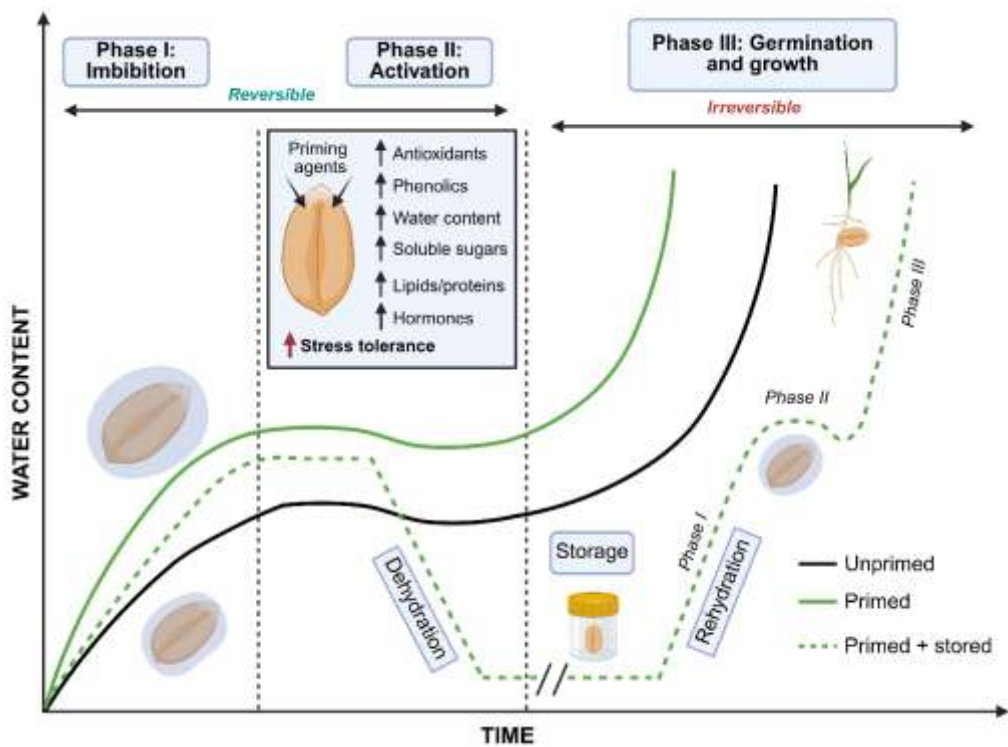
pelleted with magnetic powder and a fluorescent compound to act as a marker for tobacco growers [65].

Disadvantages of Seed Pelleting

Disadvantages of pelleting are summarised in Table 1. Due to the thick seed covering of a pellet, a critical objective is to select coating materials that do not prevent or delay seed germination [28]. This requires a careful choice of pelleting agents, such as fillers and binding agents, with the correct particle size distribution, porosity, water holding capacity, water imbibition ability, and non-toxicity [47]. Successful pelleting also requires optimised processing time and appropriate handling equipment to make sure seeds germinate without any restriction from excessively thick pellet coatings [31].

3. Conventional Seed Priming

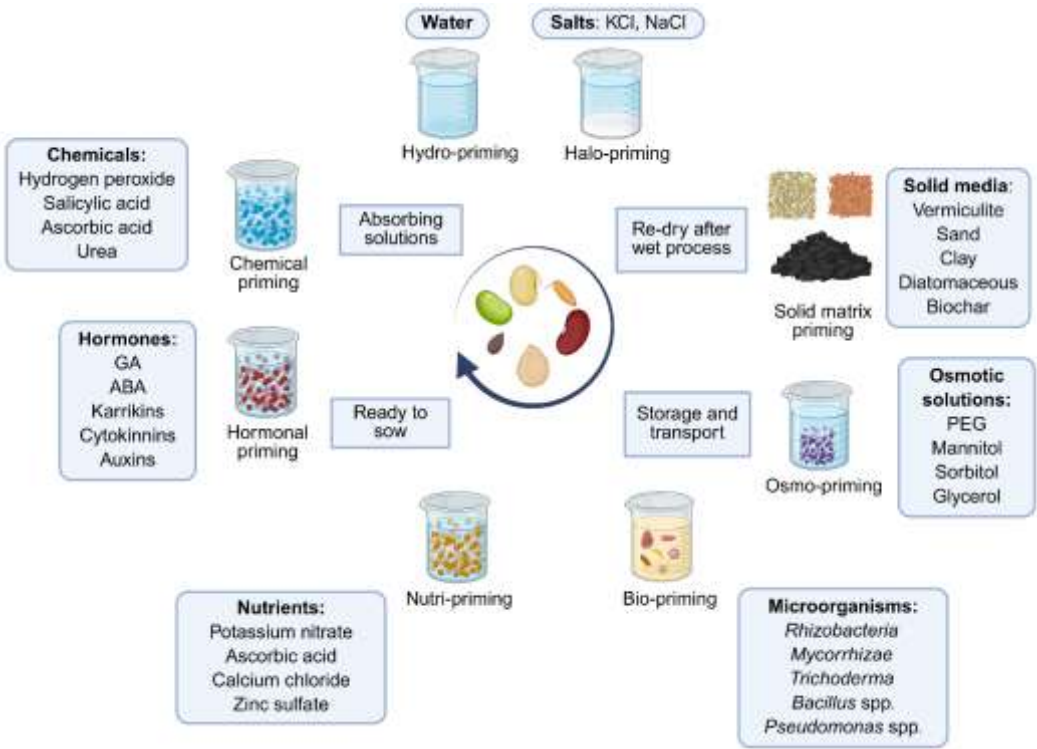
Conventional seed priming (CSP) is a pre-germination treatment that involves the controlled hydration and dehydration of seeds before planting, aiming to activate metabolic processes without allowing the seeds to germinate (Figure 2) [66]. In its most basic form, priming with water (named hydro-priming) reduces risk to the grower by accelerating germination and growth, as seeds do not need to spend time in the field absorbing water but are already pre-hydrated and substantially closer to emergence when sown [67]. Priming agents used today can increase seed quality and provide better tolerance against in-field stress through internal changes such as increased antioxidants and phenolics, higher internal water and greater lipid content (Figure 2) and can enhance structural and metabolic repair to accelerate and synchronise seedling germination and establishment, enhance vigour, deliver active compounds to seeds, assist field outcomes, expand germination temperature ranges and assist crops to gain tolerance to abiotic and biotic stressors (Supplementary Table 1) [68,69].



**Figure 2.** The phases of seed germination, showing seed water uptake and seedling growth for primed, primed and dried and unprimed seeds. Seed priming involves controlled hydration of seeds using various solutions at the Phase 1 and 2 stages of germination, followed by surface drying (solid green line) or re-drying to original moisture levels before Phase 3 (green dotted line). Both can result in potentially faster, more uniform germination

and improved stress tolerance in-field [70]. By contrast, standard germination of unprimed seeds (black line) relies on direct water uptake from the media/soil, which results in a slower germination process during phase 3 and a more variable germination rate. Figure modified from [9,71].

Although today there are many different types of seed priming (Figure 3, including hydro-, halo-, solid matrix, osmo-, bio-, nutri-, hormonal and chemical priming), priming has been utilised for centuries. For example, in ancient Greece, soaking seeds in water, diluted manure, milk with honey and other solutions was known to increase seed germination and seedling emergence (e.g. Democritus: c. 460-370 BC, Theophrastus: c. 371-287 BC) [29].



**Figure 3.** Different types of seed priming techniques, which include hydro-priming, halo-priming, solid matrix priming, osmo-priming, bio-priming, nutri-priming, hormonal priming, and chemical priming. Conventional seed priming involves soaking seeds in solutions with specific ingredients and then re-drying them to their original moisture levels for storage until sowing [66]. The different priming techniques include: Hydro-priming: Soaking seeds in water [72]; Halo-priming: Soaking seeds in salt solutions [73]; Solid matrix priming: Mixing seeds with a wet solid water carrier [57]; Osmo-priming: Soaking seeds in aerated osmotic solutions with different water potentials [74]; Bio-priming: Soaking seeds in solutions containing beneficial/antagonistic microorganisms [75]; Nutri-priming: Soaking seeds in nutritional solutions [76]; Hormonal Priming: Soaking seeds in plant growth regulator solutions [77]; Chemical Priming: Soaking seeds in beneficial chemical solutions [78].

3.1. Disadvantages of Conventional Seed Priming Techniques

As summarised in Table 2, there are some critical limitations to priming. Firstly, the re-drying process after priming imparts negative impacts on seed quality and longevity, especially after a certain duration of storage [79,80]. Indeed, primed seeds of most crops/species are known to have a reduced storage longevity if they are not used immediately or soon after drying [81,82]. Sugars, including sucrose and raffinose family oligosaccharides, play a key role in desiccation tolerance and seed longevity by maintaining membrane integrity and protein structures. Since these sugars are consumed during priming and re-drying does not allow their re-accumulation, seeds rapidly deteriorate in storage [83]. Additionally, priming alters proteins involved in the structure and



integrity of DNA, thereby increasing its susceptibility to damage during storage [84]. In their extensive review of priming effects on seed longevity and quality, [85] described the ‘relationship between priming and longevity’ as ‘largely enigmatic’. Indeed, priming reduced seed longevity in 56 of the 69 studies reviewed, with a further 13 studies showing no effect, while only 22 studies showed improved longevity post-priming. The reduced storage longevity of primed seeds requires careful management of the priming process and subsequent drying and storage conditions [86]. Variation in longevity of seeds post-priming is influenced by environmental factors, such as storage temperature and seed moisture content, genetic factors, and seed quality prior to priming [87]. Fast re-drying is particularly damaging to seed quality and usually reduces longevity [85].

The efficacy of seed priming can vary among different crop species, genotypes, and environmental conditions, making it crucial to tailor priming protocols to specific crops and growing conditions [88]. Indeed, the duration and timing of priming are crop and variety specific, and an unsuitable priming duration can lead to the loss of seed tolerance to desiccation [89]. Soaking duration depends on the radical protrusion time of each crop, variety or species, hence it must be optimised [70]. The selection of priming materials, solution dosages, duration, and priming environment all need to be validated carefully before commercialisation. Also, the temperature, humidity and air composition during storage can lead to uncontrolled influences on primed seed quality and performance, therefore, it must be controlled [90].

**Table 2.** A summary of the disadvantages of conventional seed priming techniques.

| Techniques       | Disadvantages                                                                                                                                                                                                                                                                                                                            | References |
|------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------|
| All seed priming | Re-drying after priming has shown to have a negative impact on seed longevity, seed quality and vigour, especially after a crop-specific duration [79,80,82,90] of storage.                                                                                                                                                              |            |
|                  | “The relationship between priming and longevity remains largely enigmatic”. In a review of effects on seed longevity after priming across broad genera, priming reduced seed longevity in most cases: 56 studies showed a decrease in seed longevity, 22 showed an increase, and 13 showed no effect. Contradictory effects were common. | [85]       |
|                  | Priming low vigour seed-lots tends to positively affect seed longevity, while high vigour seed-lots are negatively affected. Also, priming seeds with deeper dormancy can have positive effects on seed longevity.                                                                                                                       | [85]       |
|                  | A rapid dehydration is commonly applied at the end of priming by subjecting the seeds to low (30–50%) relative humidity or high temperature. Fast drying is hypothesised to cause damage to the seed and to reduce longevity.                                                                                                            | [85]       |
|                  | Poorly optimised temperature, humidity and air composition during storage can negatively affect primed seed quality and crop performance.                                                                                                                                                                                                | [90]       |
|                  | Duration & timing of priming is variety-specific.                                                                                                                                                                                                                                                                                        | [89]       |
|                  | Priming protocols must be tailored to specific crops & growing conditions & efficacy can vary among crops, genotypes, & environments.                                                                                                                                                                                                    | [88]       |
|                  | An unsuitable priming duration can result in the loss of seed desiccation tolerance.                                                                                                                                                                                                                                                     | [89]       |
|                  | Seeds can be inoculated by harmful pathogens.                                                                                                                                                                                                                                                                                            | [91]       |
|                  | Priming material selection, solution dosages, priming duration, and post-priming environment must be optimised before commercial use.                                                                                                                                                                                                    | [91]       |
|                  | Effective priming solution concentrations in laboratory tests may not be effective in field conditions.                                                                                                                                                                                                                                  | [92]       |
|                  | Priming has practical challenges, e.g. specialised equipment is needed, procedures are labour-intensive, and large-scale field application is complicated.                                                                                                                                                                               | [84]       |

|                      |                                                                                                                                                                                                                                                                            |           |
|----------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------|
|                      | Prolonged hydration has a deleterious effect on germination after seed storage.                                                                                                                                                                                            | [85]      |
|                      | High priming temperature has a deleterious effect on germination after seed storage. Seeds primed at lower temperatures are less prone to membranes, enzymes, and other cell components being damaged.                                                                     | [85]      |
|                      | Priming conditions and duration of priming must be optimised to avoid negative impacts on seeds.                                                                                                                                                                           | [93,94]   |
|                      | Uncontrolled water imbibition can cause an accumulation of reactive oxygen species & oxidative injury to seeds.                                                                                                                                                            | [89]      |
| Hydro-priming        | Osmo-priming is a technically & cost-effectively better option. Hydro-priming results in slower germination, seed imbibition damage is more likely & seed performance is poorer under unfavourable environmental conditions.                                               | [95]      |
|                      | Seed aeration issues can occur.                                                                                                                                                                                                                                            | [96]      |
|                      | Rapid hydration may be especially damaging to seeds with thin coats, making them prone to nutrient leakage and seed damage.                                                                                                                                                | [97]      |
|                      | Priming durations and water potentials (concentrations) are crop species and cultivar-specific.                                                                                                                                                                            | [98]      |
| Halo-priming         | Can lead to seed damage and reduced seed germination if inappropriate concentrations and priming durations are used. Can cause critical nutrient imbalances within the seed/seedling.                                                                                      | [99]      |
|                      | May elicit seed toxicity or perturb the pH milieu, compromising seed viability and germination efficiency.                                                                                                                                                                 | [100]     |
|                      | Solutions/concentrations must be strictly selected & tested to avoid disturbing the internal osmotic balance and nutrition balance                                                                                                                                         | [74]      |
| Osmo-priming         | Concentrated solutions can induce excessive solute uptake, perturbing osmotic equilibrium, resulting in cellular dehydration                                                                                                                                               | [96]      |
|                      | Solutions that contain salt can lead to seedling toxicity, nutrient imbalances, etc.                                                                                                                                                                                       | [96]      |
|                      | The cost of osmotic agents is high when using large amounts, such as PEG                                                                                                                                                                                                   | [96]      |
| Solid matrix priming | The solid medium must have specific physicochemical properties, such as high water-holding capacity, low matric potential, solubility, non-toxicity to seeds, ability to provide sufficient oxygen to seeds while priming, low bulk density, and easy to remove from seeds | [101]     |
|                      | Priming duration, matrix material & water concentrations must be optimised                                                                                                                                                                                                 | [102]     |
| Bio-priming          | Efficiency, environmental impact in-field and fate of introduced microorganisms in the soil ecosystem are not fully understood                                                                                                                                             | [103]     |
|                      | The concentration of micronutrients and priming duration must be optimised to cultivar-specific levels                                                                                                                                                                     | [22,104]  |
| Nutri-priming        | High concentrations of nutrition priming agents can result in seed toxicity, disruption of osmotic equilibrium and alteration of the pH environment, reducing emergence and seedling viability                                                                             | [22]      |
| Chemical priming     | Treatment duration, concentration and choice of compounds must be perfected as improper application methods can inflict damage upon seeds                                                                                                                                  | [78]      |
|                      | Pesticides that are not precisely applied can disrupt soil integrity and adversely impact ecosystems                                                                                                                                                                       | [78]      |
| Hormonal priming     | Complicated crosstalk between external PGRs and internal phytohormones can lead to negative impacts on seed quality                                                                                                                                                        | [105,106] |
|                      | Redrying previously wet seeds can make seeds substantially less sensitive/responsive to plant growth regulators or hormones                                                                                                                                                | [107,108] |

Due to treatment and crop variety differences, there are still many limitations and inconveniences for commercial utilization

[89]

The long-term outcomes of seed priming techniques exhibit instability, with some conflicting data regarding the yield potential of primed seeds. For example, it was observed in sugar beet that despite a faster germination rate under glasshouse conditions with priming, there was no disparity in yield between primed and non-primed seeds in a two-year field study [109]. Additionally, priming formulations effective in laboratory tests may not prove equally effective in field conditions. For example, lentil seeds primed with GA<sub>3</sub> in pot trials were taller compared to untreated seeds, while there was no significant impact on plant height or yield under field conditions [92]. Also, the adoption of seed priming on a commercial scale remains limited due to factors such as a lack of studies conducted in agricultural settings and discrepancies between controlled environments (laboratory, glasshouse studies) and field investigations [109]. Thus, evaluating the performance of seed-primed plants in the field until maturity is crucial to understanding yield impact.

Practical challenges, such as the need for specialised equipment and labour-intensive procedures, also limit widespread adoption [84]. Also, seeds can be inoculated by harmful pathogens during priming, resulting in poor production outcomes [91]. Consequently, future research should focus on avoiding re-drying damage to seeds and replicating laboratory findings in real-world environments to provide more accurate insights. The diversity of seed priming techniques, illustrated in Figure 3, are detailed below.

3.2. Hydro-Priming

Hydro-priming is a simple and cost-effective method relative to other priming techniques because it entails simply soaking seeds in water, typically for 7-48 h, depending on the species/crop/variety, and redrying to a certain moisture level or weight prior to storage or sowing [72]. When performed well, hydro-priming can improve seed germination, seedling emergence, vigour indices and crop yield [110]. For example, hydro-priming can help seeds to germinate earlier and produce more seedlings with a higher vigour, which ultimately improves crop productivity. Furthermore, it is reported that hydro-priming can assist seedling survival under extreme conditions, such as heat and drought, by improving seed water uptake and hydration. For example, hydro-primed *Piptadenia moniliformis* Benth. had better seedling vigour under salinity stress [111] while chickpea showed faster seedling growth due to faster carbohydrate metabolism (rapid hydrolysis of transitory starch) under water deficit stress following hydro-priming [112].

Disadvantages of Hydro-Priming

One clear disadvantage of hydro-priming (Table 2) is uncontrolled seed water imbibition, which often causes an accumulation of reactive oxygen species with resultant oxidative injury within the seeds [89]. Additionally, seeds with thin coats may be prone to nutrient leakage and seed damage from rapid hydration [77]. Also, the priming conditions and duration of priming must be correct. For example, rice (*Oryza sativa* L.) seeds primed with water for 12 to 48 hours gained higher seed vigour, while a priming time over 60 hours did not [113]. Similarly, sorghum seeds primed with water for 12 and 24 hours significantly increased germination percentage and speed, while priming for 36 hours showed no difference compared to the control [94]. For Australian wild plant species, hydro-priming either reduced or did not affect seed germination speed or synchronicity [114].

3.3. Osmo- and Halo-Priming

Osmo-priming is one of the most common priming methods and has been patented and used commercially since the 1970s [79]. It involves the soaking of seeds for specific times in aerated osmotic solutions with specific water potentials (instead of water), followed by re-drying to their original moisture and weight [74]. Commonly used agents are salt solutions, organic solutions such as

polyethylene glycol (PEG) and sugars. Osmo-priming can benefit seed germination, seedling emergence and can assist crops in coping with climatic extremes [57]. For example, aged soybean seeds primed with PEG-6000 displayed a higher seedling vigour [115], wheat and barley showed a higher germination rate [116] and tomato seeds primed with seaweed extracts resulted in a higher yield under salt-stressed conditions [117]. Compared to hydro-priming, osmo-priming is a technically and cost-effectively better option for growers and seed companies due to faster germination, better water-imbibition-injury protection and better seed performance under unfavourable environmental conditions [95]. This is because osmo-priming can control water potential and the imbibition process by adding PEG, salts or sugars to help slow water uptake, thus reducing internal seed damage [89]. Osmotic solutions that lower water potential more than pure water include PEG, mannitol, sorbitol, glycerol, and salt solutions [118]. If applied within a certain timeframe during germination, orthodox seed desiccation tolerance can be re-established by priming with agents such as PEG [119].

'Halo-priming' (Figure 3) is osmo-priming using salts such as sodium chloride (NaCl), potassium chloride (KCl), calcium chloride (CaCl<sub>2</sub>), potassium nitrate (KNO<sub>3</sub>), sodium nitrate (NaNO<sub>3</sub>) etc. [73]. For example, wheat seeds primed with CaCl<sub>2</sub> showed improved pest resistance and better seed quality [120] while rice seed priming with 1-5% KCl solution resulted in improved seedling emergence and a taller crop [121].

#### Disadvantages of Osmo-and Halo-Priming

Disadvantages of osmo- and halo-priming are that solutions and concentrations must be strictly selected and tested to avoid disturbing the internal osmotic and nutritional balance [74]. For example, solutions containing salts have the propensity to modulate the nutritional milieu surrounding the seed, potentially causing imbalances in critical nutrients essential for germination and seedling development. Furthermore, elevated concentrations of certain priming solutions may elicit seed toxicity or perturb the pH milieu, thereby compromising seed viability and germination [89]. For instance, exposure of pea seeds to PEG-6000 negatively affected germination and seedling growth [122]. While the cost of osmotic agents, especially PEG, was a significant issue [96], this can now be overcome by the discovery of alternative agents, such as D-mannitol [123].

#### 3.4. Solid Matrix Priming

Solid matrix priming (SMP) or conditioning (Figure 3) was developed to avoid the disadvantages of hydro-, halo-, and osmo-priming, such as aeration issues with hydropriming and the cost of osmotic agents [96]. The process mixes seeds with a wet solid water carrier for stimulation, and after a certain duration (before radicle emergence), the primed seeds are separated from the solid medium and redried to their original moisture content [124].

The advantages of SMP compared to hydro-, halo-, and osmo-priming are that SMP allows seeds to hydrate slowly and similarly to soil conditions, which results in better seed quality [125]. Vermiculite, sand, clay, diatomaceous earth, water-absorbing polymers, biochar and charcoal have been used commercially as the matrix medium [101]. For example, broccoli and cauliflower seeds that were primed on wet vermiculite showed higher seed germination and seedling growth under salt stress conditions compared to unprimed seeds [126]. SMP can also contribute to stress tolerance, such as mung bean priming with normal or nano-sized chitosan under salinity stress [127]. It has been utilised for native species, such as cool-season grasses in dryland ecosystems [128].

#### Disadvantages of Solid Matrix Priming

Disadvantages of SMP are that the solid medium requires specific chemical and physical features, including high water-holding capacity, low matric potential, non-toxicity to seeds, ability to provide sufficient oxygen to seeds during priming, low bulk density, and it must be easy to remove from the seeds [101]. Priming duration, material selection and water concentrations are three major



factors that influence SMP performance [89]. For example, soybean seeds primed with SMP for 1-2 days showed a higher germination, however, germination of seeds primed for over 2 days was significantly decreased [102].

### 3.5. Biological Priming (Bio-Priming)

Biological priming or 'bio-priming' (Figure 3) integrates seed priming with biological management by inoculating seeds with beneficial/antagonistic microorganisms during priming [75]. Advantages of bio-priming are that it can overcome the threat of harmful pathogen inoculation during priming [91], increase seed germination and provide protection against soil and seed-borne pathogens, hence increasing seed/plant quality and yield. For example, watermelon and melon seeds bio-primed with *Pseudomonas fluorescens* and *Bacillus amyloliquefaciens* showed reduced bacterial fruit blotch incidence [129], and pea seed bio-primed with *Trichoderma asperellum* showed plant growth promotion [130]. Bio-priming proved to be an effective biological control method for faba bean [75] and sugar beet [131] pathogens and nutritional solutions with beneficial microbes increased water and nutrient uptake of cabbage [132,133]. Compared with seed coating techniques, such as pelleting and film-coating, bio-priming has been suggested as a better technique for ecological management [42].

#### Disadvantages of Bio-Priming

Disadvantages of bio-priming are that the efficacy and environmental impact of bio-priming in the field, particularly the fate of microorganisms introduced to soil ecosystems, are not fully understood. There is a need for further research to assess the long-term effects on soil microbiota as well as interactions between introduced and soil-borne microorganisms. Biochar has been proposed as a promising novel bio-priming agent, but it can have both beneficial and negative impacts on soil, microbes, and plant health [103,134].

### 3.6. Nutri-Priming

Nutri-priming involves the priming of seeds with micro- and/or macro-nutrient solutions (Figure 3) and has resulted in positive nutritional and biochemical changes within the seed and seedling [76]. For example, seed priming with zinc [135], boron [136], magnesium, copper [137], molybdenum [138] and phosphorus [139] have resulted in better seed germination and early seedling growth, as well as improved tolerance to environmental stressors [140].

#### Disadvantages of Nutri-Priming

Disadvantages are that seeds must be primed with a specific concentration of micro-nutrients for a cultivar-specific duration to enhance the nutrient content, as well as assist with water imbibition efficiency [104]. If not carefully managed, agents can result in seed toxicity, disruption of osmotic equilibrium and alteration of the pH environment, which can negatively affect seed viability and germination efficiency [22].

### 3.7. Hormonal Priming

Hormonal priming involves priming with hormones and/or plant growth regulators (Figure 3) such as abscisic acid [77], auxins [141], gibberellins (GA<sub>3</sub>) [142], paclobutrazol [143], polyamines [144], salicylic acid (SA) [145], karrikinolide (KAR<sub>1</sub>), etc [107,146]. These treatments have enhanced seed germination, early seedling growth, root and shoot development and improved environmental tolerance and yield [140]. Indeed, priming with plant growth regulators has become an important research topic because it has the potential to advance sustainable agriculture, particularly by assisting crop tolerance to abiotic stress [147].

#### Disadvantages of Hormonal Priming

There are still many limitations for commercial utilisation of hormonal priming due to the positive effects that generally disappear within two weeks [84,148,149], crop variety inconsistencies [77] and complicated crosstalk between external plant growth regulators/hormones with internal phytohormones, which can lead to negative impacts on seed/crop quality [105,106]. Additionally, re-drying the seed after wetting can result in seeds that are substantially less sensitive or not responsive to the plant growth regulator/hormone [107,108].

3.8. Chemical Priming

Chemical priming uses chemical solutions to improve seed/plant performance (Figure 3). Solutions can utilise natural or synthetic compounds such as agrichemicals [150], urea [151] and others. Advantages are that some crops can gain better seedling vigour and stress tolerance [152,153], for example, treating mung bean seeds with sodium molybdate dihydrate at 0.02% and 0.04% for 5 hours resulted in increased yield [154], priming seeds with  $\beta$ -amino butyric acid enhanced drought and salt tolerance of green gram [155] and ascorbic acid assisted stress tolerance in wheat by modifying internal protein metabolism and storage [156].

Disadvantages of Chemical Priming

Disadvantages of chemical priming are that the selection of chemical agents demands meticulous attention to detail regarding treatment duration, concentration, and choice of compound(s). Improper application methods can inflict damage upon seeds, resulting in diminished germination and compromised seedling development. Furthermore, chemicals such as pesticides and insecticides have the potential to disrupt soil integrity and adversely impact the surrounding ecosystem, thereby posing threats to human and environmental health. Hence, judicious selection and precise application of these agents are imperative to mitigate potentially adverse effects [78].

4. Disadvantages of Conventional Seed Coating and Priming Technologies

As summarised in Table 3, all conventional seed priming and coating techniques have clear disadvantages. One significant disadvantage that impacts long-term crop performance is that both seed priming and coating apply actives directly to seeds via a solution, followed by seed re-drying [107]. Yet, the re-drying of previously wet seeds has numerous potentially critical issues, including that plant benefits from actives are short-lived, generally disappearing within two weeks [84,148,149]; re-dried seeds can become substantially less sensitive/responsive to hormones and plant growth regulators [107,108]; seed quality can be compromised by storage [32], especially for high-quality seed lots [82,84,85,157]; and dehydration may alter seed coat properties, such as by damaging the mucilage layer, producing secondary dormancy, or causing fatal injury to the embryo if at a critical development stage [85,108,158].

Thus, given that conventional priming and coating techniques can damage seed/seedling quality rather than provide protection, the following sections review novel and non-conventional technologies that have introduced exciting potential advancements in the realm of SETs.

Table 3. Summary of the disadvantages of all conventional seed enhancement techniques.

| Techniques                                                           | Disadvantages                                                                                                                                                 | References   |
|----------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------|
| Seeds are dried back to their initial water content (re-dried) after | Redrying the seed after wetting results in short-lived plant benefits from actives, whereby effects generally disappear within two weeks                      | [84,148,149] |
|                                                                      | Redrying the seed after wetting can result in seeds that are substantially less sensitive/responsive to plant growth regulators/hormones (e.g. karrikinolide) | [107,108]    |
|                                                                      | Redrying the seed after wetting can severely compromise storage longevity, especially for high-quality seed lots                                              | [82,157]     |

|                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |              |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------|
| seed coating Redrying the seed after wetting may alter seed coat properties, damage the and priming mucilage layer, produce secondary dormancy, or cause fatal injury to the embryo if at a critical development stage                                                                                                                                                                                                                                                                                                          | [108,158]    |
| Fast drying (subjecting seeds to 30–50% relative humidity or high temperature) causes damage to seeds & reduces longevity. Likely resynthesis of late embryogenesis abundant (LEA) proteins degraded during imbibition may not be possible during conventional fast-drying methods. Controlled moisture content reduction (MCR) before subsequent fast drying has very small gains. Slow drying is better, but seed longevity is still compromised.                                                                             | [85]         |
| Suggested immediate sowing after priming and avoiding re-drying for wheat, faba bean & chickpea. Seed priming with surface drying resulted in beneficial starch metabolism, which resulted in uniform & early emergence & a vigorous seedling; this was reduced by re-drying. Surface-drying post-priming was more effective than re-drying: lower EC of seed leachates, reduced emergence time, better synchronised emergence, improved final emergence, seedling size and weight, possibly due to improved starch metabolism. | [69,159,160] |
| Maize productivity was not improved by re-drying after priming. By contrast, surface drying after priming improved seedling emergence and growth of the maize crop.                                                                                                                                                                                                                                                                                                                                                             | [149]        |

5. Non-Traditional Seed Technologies: Sowing Without Redrying

All conventional SETs use re-drying of previously wet seeds, which can have negative effects on seed quality and longevity. Hence, this section reviews techniques that aim to maximise the beneficial impacts of SETs without the deleterious effects of re-drying.

Studies across broad crops, such as wheat, faba bean, chickpea [69,159,160], maize [149] and lettuce [107] have demonstrated that sowing wet or surface-dried seeds after priming is more beneficial than re-drying seeds post-priming. Relative to re-dried seeds, surface-dried or wet seeds show improved starch metabolism, which can lower seed leachates and can reduce seedling emergence times and enhance uniformity, increase seedling vigour and result in larger and heavier seedlings. For example, seed surface drying post-priming improved crop performance more than re-drying to original weight for: lentil, *Lens culinaris* Medik., under drought and well-watered conditions, which increased seedling weight, chlorophyll, sugar content and anti-oxidant activity; [161] for faba bean, *Vicia faba* L., under drought stress which reduced lipid peroxidation and regulated  $\alpha$ -amylase activity and soluble sugars [160]; and for chickpea and wheat, which improved  $\alpha$ -amylase activity and increased total soluble sugars [69,159].

Other authors have shown that avoiding re-drying after wetting results in longer-lived benefits to the crop/plant from actives [84]. For example, while priming followed by re-drying and surface drying both improved early maize seedling emergence rate and uniformity, only surface-dried seeds resulted in long-term effects on crop productivity, while re-dried seeds showed no long-term benefits [149]. Similarly, [107] demonstrated that the emerging plant growth regulator, karrikinolide (KAR<sub>1</sub>), benefited lettuce growth when seeds were sown wet immediately post-priming, while its effects on seedling growth were diminished by re-drying. Additionally, re-drying harmed seed longevity, whereby storage for 1-2 months reduced germination by 30-50% without KAR<sub>1</sub> and 10-20% with KAR<sub>1</sub> [108]. Similarly, diminished KAR<sub>1</sub> effects were noted for *Brassica tournefortii* seeds that were hydrated and re-dried.

Ref. [67] ascertained that sowing wet or surface-dried seeds may be especially beneficial for resource-poor growers, such as in Africa or Asia, where rapid emergence determines crop establishment success. Indeed, commercial SETs tend to be inaccessible to such growers because seeds are usually farm-saved or from local/informal sources [162]. Also, commercial SETs are usually

cost-prohibitive, complicated to use and require specialised equipment. Hence, [67] advocated on-farm overnight hydro-priming, followed by immediate wet sowing or surface air drying as a low-cost technique, increasing yields by 5-36% across studies. If sowing was delayed by poor weather, surface-dried seeds could be stored for several days without viability loss or dried for one day to increase storability to one month.

For upscaling, a unique hydro-priming system was developed by [163] named ‘drum priming’, which uses a horizontal rotating drum connected to a boiler producing vapour. Seeds are contained by the drum, and water vapour is released to enable seed hydration until a predetermined water content is reached, usually over one day. The volume of water and time required for seed hydration are strictly controlled to avoid radicle emergence. Hydrated seeds can be kept in the rotating drum for two weeks before being directly planted into soil/media [140].

*Disadvantages of Sowing Without Redrying*

The disadvantages of sowing seeds wet or surface-dried after priming are summarised in Table 4. [83] noted that direct seeding of primed seed is generally unfeasible in resource-rich countries because wet seeds bridge within seeding machinery, resulting in a halt in seed flow and planting inefficiencies. Also, if poor weather conditions delay sowing, potentially catastrophic seed quality loss can occur. [164] observed that moist seeds pose handling and pathogen complications, and inadequate drying can result in mould growth, heating issues, and mite infestation. For example, for rapeseed with 10.6% moisture content at 25 °C, clumping was observed after 11 days, fungal colonies after 21 days, and germination declined after 40 days. Recommendations were that seeds not be maintained above 10% moisture for more than 1-2 weeks prior to drying or sowing.

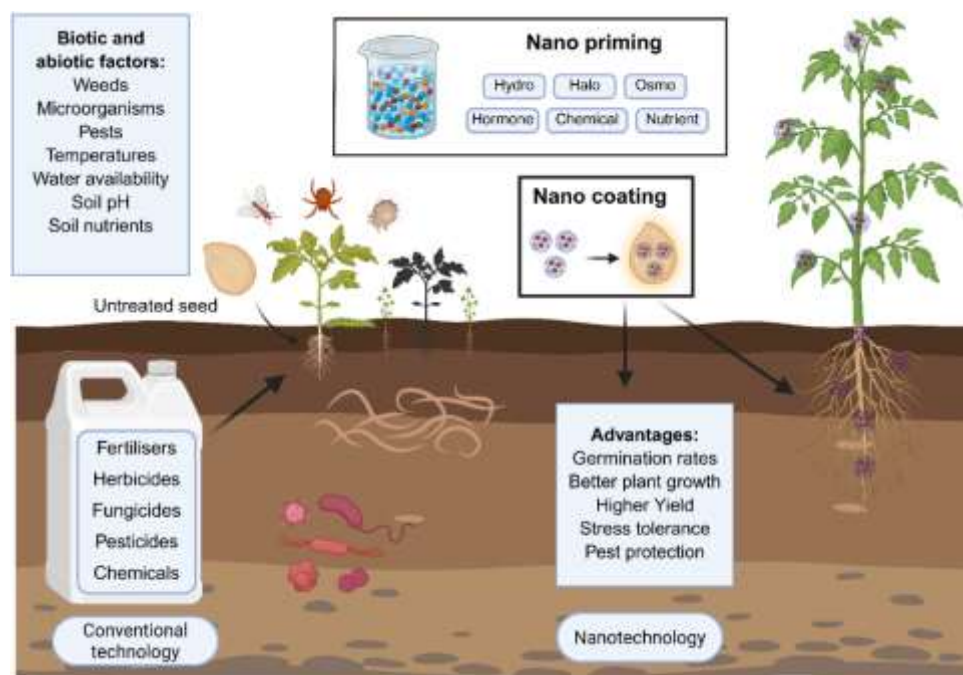
**Table 4.** A summary of the disadvantages of seed enhancement techniques that sow seeds wet or surface-dried after priming.

| Technique                                         | Disadvantages                                                                                                                                                                                                                                                                                              | References |
|---------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------|
| Seeds are surface-dried or sown wet after priming | Surface drying caused a greater decline in seed vigour after ageing compared with dried-back seeds                                                                                                                                                                                                         | [85]       |
|                                                   | Sowing wet seeds can result in bridging within hoppers/seeder                                                                                                                                                                                                                                              | [83]       |
|                                                   | Sowing wet or surface-dried seeds can be risky, for example, if rain delays the seeding date. Surface-dried seeds can be stored in a dry place for only several days without viability loss.                                                                                                               | [67,83]    |
|                                                   | Priming and sowing wet seeds on-farm is unaffordable for a small farm in resource-rich countries                                                                                                                                                                                                           | [83]       |
|                                                   | Moist seeds pose handling and pathogen complications. Recommends that seeds are not maintained at >10% moisture for >1-2 weeks                                                                                                                                                                             | [164]      |
|                                                   | For resource-poor growers, safe limits for seed soaking should ideally be calculated for each crop variety so the seed/seedling is not damaged by excessive soaking that results in total crop failure. However, ‘overnight soaking’ followed by surface drying is the technique employed by most growers. | [67]       |

**6. Novel Nanotechnologies for Seed Enhancement**

Nanotechnologies utilise particles and structures with nano-scale dimensions (1-100 nm) that endow them with an elevated surface-to-volume ratio and surface energy, promising better penetration of actives into the plant, heightened active solubility, instant reactivity, and substantially more precise delivery [165]. Such technologies have been utilised as novel priming and seed coating materials (Figure 4) and are detailed below.





**Figure 4. Nanotechnology versus conventional technology in agriculture.** Crops growing in natural environments face various biotic and abiotic threats. Conventional commercial agricultural practices use large quantities of chemical products, such as fertilisers, insecticides, fungicides, and pesticides, which impose a significant burden on the environment. By contrast, nanotechnology, such as nano-coating and nano-priming, presents a potentially exciting future for agriculture by more precisely and effectively delivering substances to crops in smaller amounts, better providing effective pathogen and pest protection, reducing environmental damage, and promoting sustainable development [165].

### 6.1. Nanopriming

Nanopriming fuses nanotechnology with priming, by treating seeds with nanoparticles (NPs) in suspensions or solutions with a view to enhance seedling vigour and establishment uniformity, biotic and abiotic stress resilience and more efficient nutrient uptake [166]. As for conventional priming, nanopriming occurs prior to germination and involves seed redrying upon completion. NPs can be absorbed by the seed or remain on the seed surface during and/or after priming [167].

NPs theoretically introduce a sophisticated level of control, enabling high-precision active delivery which promises to variously control gene expression and metabolic processes, enhance antioxidant activity and promote enzymatic defence systems in plants [168–170]. The NPs used in agriculture are categorised as inorganic or organic [171,172]. The most common inorganic NPs include metal and metal oxide-based, carbon-based, silicon-based, and magnetic inorganic NPs, some of which have already been commercialised [172]. Organic NPs are created from organic molecules, such as lipids, proteins, and polymers such as poly(lactic-co-glycolic) acid (PLGA), polyethylene glycol (PEG), and polylactic acid (PLA).

Inorganic NPs have been shown to enhance many plant processes. For instance, wheat seeds primed with 80 nm-sized iron oxide NPs at 200 and 400 ppm for 12 hours exhibited improved germination and shoot length. Additionally, there was a substantial increase in iron content in the grain compared to plants from untreated seeds [173]. Wheat treated with 20–40 ppm 15–30 nm-sized Cu NPs displayed improved stress resistance [174], and canola seeds primed with 75 ppm calcium oxide NPs demonstrated improved germination, biomass, antioxidant defence and yield under drought stress conditions [175]. Inorganic NPs have also improved antimicrobial activity, such as for rice seeds treated with silver and gold NPs at 200 ppm showed significantly greater pathogen inhibition of the radicle (73% and 61%, respectively) [176].

Nonetheless, inorganic NPs can pose potential plant toxicity, environmental and human health safety issues [177]. By contrast, organic NPs or nanomaterials (NMs), including chitosan and other natural polymeric materials, offer a potentially better alternative with equally high precision but lower toxicity, better biocompatibility with living organisms, biodegradability and eco-friendliness. For example, priming with chitosan NPs has been shown to improve wheat seed germination and seedling growth at a lower concentration ( $5 \mu\text{g mL}^{-1}$ ) compared to chitosan-treated seeds ( $50 \mu\text{g mL}^{-1}$ ) [178].

#### Disadvantages of Nanopriming

Disadvantages of nanopriming are that modulating parameters such as the size, shape, and surface chemistry of NPs will influence their adsorption and interaction with the seed surface, thus requiring precise tailoring [179]. For example, common bean seeds primed with 25 nm-sized CuO NPs showed better root development compared to 40 nm-sized NPs [180]. Additionally, some NPs may induce phytotoxicity and hinder seedling development, as evidenced by the inhibitory impact of ZnO NPs on the root length of corn and cucumber seedlings [181].

Also, the process of redrying nanoprimed seeds to their initial moisture may alter the effects of NPs, making nanoprimed seeds potentially less stable and viability losses more permanent and irreversible, even more than with conventional priming. This is especially true if redrying is rapid. Hence, extra treatments at additional cost may be required, resulting in higher expenses for seed companies and growers. The worst-case scenario is that germination potential may never be recovered [171].

The effects of NPs are contingent upon their physical and chemical characteristics, including size, zeta potential, and concentration, resulting in varying biological impacts on seeds and plants [182,183]. Thus, NPs can exhibit inhibitory effects on seed germination and can cause seedling phytotoxicity [184]. Notably, smaller-sized NPs can easily traverse biological barriers and consequently may exhibit more toxic effects on seeds and seedlings, leading to inhibited germination and growth, as observed in common beans, whereby 25 nm and 40 nm copper oxide NPs at  $1 \text{ mg L}^{-1}$  and  $10 \text{ mg L}^{-1}$  increased root development, yet decreased root development at  $1000 \text{ mg L}^{-1}$  [180].

Additionally, there are potential ecological risks associated with the entry of NPs into ecosystems via soil and water, affecting soil microbiota, aquatic organisms, and plants. Residues of NPs in plant tissues during crop growth may impact crop quality and food safety, whereby human exposure to NPs may occur through the consumption of affected crops or contact with contaminated soil and water, posing potential health risks, such as inflammation [177]. For example, Ag<sup>+</sup> concentrations in silver beet and spinach leaves treated with citrate-coated silver NPs can reach  $5 - 10 \text{ mg kg}^{-1}$ , which can pose a risk to human health [185].

#### 6.2. Nanocoating

Nanocoating entails the application of nanomaterial coating onto seed surfaces which can serve as a protective barrier, helping to shield seeds from environmental stressors such as pests, disease and harsh weather conditions, and/or facilitate controlled release of nutrients and agrichemicals [186]. The typical procedure involves dispersing the NPs (ranging from *c.* 1-100 nm in size) in a carrier solution or suspension, followed by application onto seeds using specialised equipment that ensures uniform coverage of the seed surface and redrying [187]. The specific technique selected depends on the requirements for the coating and the seed type and can include spray coating, dip coating, or vacuum deposition [27]. The primary benefit of nanocoating compared to conventional seed coating is delivery efficiency. Due to their small size and high surface area-to-volume ratio, NPs can provide enhanced protection and nutrient delivery compared to larger particles, as well as reduced quantities of agrichemicals as compared to conventional seed coatings, which hence contribute to reduced environmental load [172].

In fertiliser management, nanocoating enables the controlled release of nutrients, reducing the environmental impact of excess fertiliser application. Nanocoated fertilisers can enhance nutrient uptake by plants, promoting efficient resource utilisation and minimising nutrient runoff, which is a common issue in conventional agriculture. For instance, zinc is an important nutrient for crops that can be effectively delivered to maize, soybean and pigeon pea via a ZnO nano-powder coating (<100 nm) [21].

Additionally, nanocoatings can be designed to encapsulate pesticides and herbicides, allowing for targeted and controlled release. This targeted delivery reduces the need for excessive chemical inputs, minimising the environmental footprint associated with traditional pest and weed management. For example, it was reported that neem oil encapsulated in zein NPs as a nanopesticide was effective against *Bemisia tabaci* and *Tetranychus urticae* and showed no phytotoxicity to *Phaseolus vulgaris*, thus showing potential for the enhanced control of agricultural pests [188].

Nanofibers produced by electrospinning have emerged as innovative seed coatings. These fibers can effectively embed micronutrients, pesticides, or plant hormones, forming uniform and functional seed coatings that can significantly improve seed germination and early seedling development. For instance, a biodegradable organic wet electrospinning technology that facilitates the precise delivery of Cu<sup>2+</sup> to tomato and lettuce seeds at minimal doses improved seed germination and seedling growth. This approach outperformed conventional seed coating methods [189].

Biodegradable wet seed coatings based on cellulose nanofibers have also shown promise for agriculture. For example, a coating was tested on tomato and lettuce seeds in glasshouse conditions, resulting in more rapid germination and increased seedling biomass (12-29%) using only one quarter of the agrichemical when compared to conventional film-coating [189].

Disadvantages of Nanocoating

As summarised in Table 5, nanocoating has similar limitations to nanopriming, including toxicity issues, environmental and health safety concerns, and re-drying post-nanocoating, which harms seed quality and longevity [187,190]. Further, organic NMs used in coating may not be as stable in the environment compared to inorganic NPs, making them susceptible to degradation from factors such as light, humidity, pH, and temperature changes, which can affect their long-term effectiveness [191]. For example, the release rate of active compounds from chitosan NPs depended upon the pH of the medium [192]. Additionally, there are concerns that organic NMs may interact with other biological components in plants or soil, leading to uncertainty about their biological activity and effects on soils and ecosystems [193].

One critical flaw is that NPs/NMs are applied via conventional seed coating or priming methods [165], and thus, the application process is still a wet application followed by seed re-drying. Specific applications include seed dip coating, priming, dressing in a slurry, and/or with a binder [8,27] or via electrospinning of a polymer solution onto seeds [189]. Additionally, apprehensions surround the safe use of NMs in agriculture, such as effects on the macro- and micro-environments of seeds, exposure levels, and potential long-term environmental and human health impacts. These must be understood prior to large-scale commercial applications [172].

**Table 5.** A summary of the disadvantages of nanotechnologies for seed enhancement.

| Nanotechnologies | Disadvantages                                                                                                                                         | References |
|------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------|------------|
| All              | The application process is still a wet application followed by seed re-drying, thus will impact seed quality, longevity, and effectiveness of actives | [165]      |
|                  | Apprehensions surround safe use in agriculture: exposure levels, potential environmental and human health impacts are unknown                         | [172]      |
|                  | Some NPs inhibit seed germination & cause seedling phytotoxicity                                                                                      | [184]      |

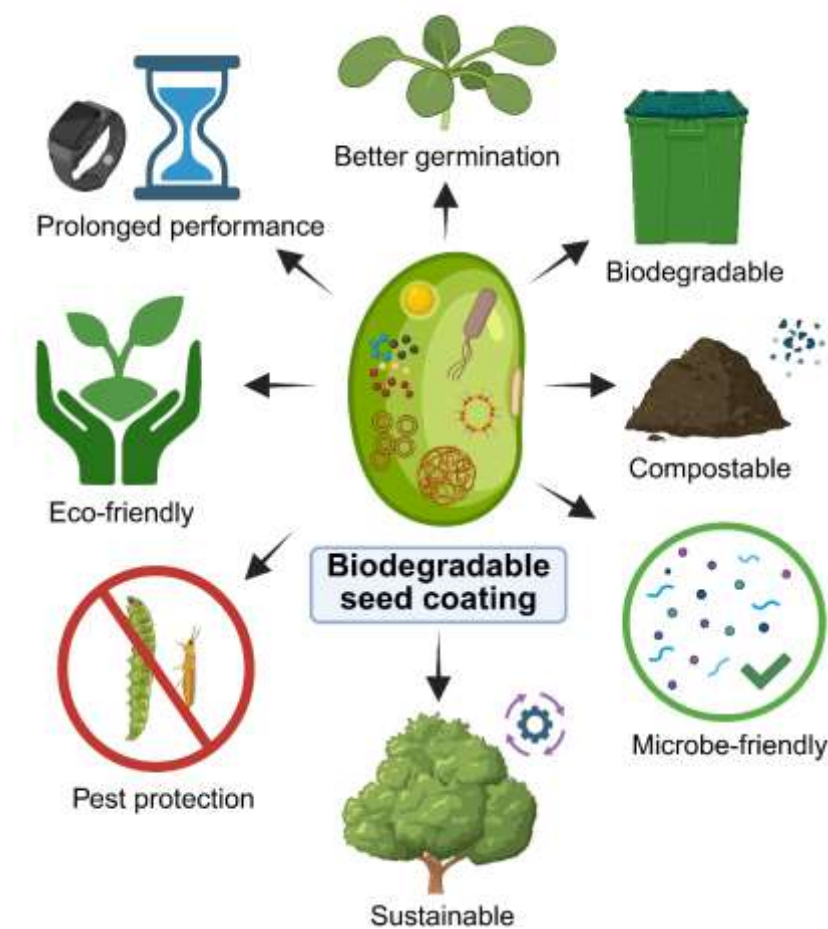
|                                                     |                                                                                                                                                                     |           |
|-----------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------|
| Inorganic nanoparticles (NPs)                       | Variation in biological impacts due to physicochemical characteristics such as size, zeta potential, concentration, etc.                                            | [182,183] |
|                                                     | May exhibit toxic effects on seeds & seedlings &/or inhibit germination/growth due to small nanoparticle size traversing biological barriers & surface charge.      | [194]     |
| Nanopriming                                         | Effects are variable and are contingent on a myriad of factors such as NP size, concentration & chemical properties                                                 | [172]     |
|                                                     | Certain NPs may induce phytotoxicity and hinder seedling development                                                                                                | [181]     |
|                                                     | A comprehensive understanding of potential risks is essential to guide the responsible integration of nanopriming into mainstream agricultural practices            | [195]     |
|                                                     | Parameters such as the size, shape, and surface chemistry of NPs must be precisely tailored for maximum efficiency                                                  | [180]     |
|                                                     | Re-drying nanoprimered seeds may alter the effects of nanopriming, and make seeds less stable, and viability losses may be permanent and non-reversible             | [171]     |
|                                                     | Human exposure to NPs may occur through the consumption of treated crops or contact with contaminated soil and water, posing potential health risks                 | [177]     |
| Nanocoating                                         | Nanocoating typically disperses NPs in a carrier solution or suspension, followed by the application onto the seeds and subsequent re-drying and storage, or sowing | [196]     |
|                                                     | Nanocoating can have toxicity issues, environmental and health safety concerns, and re-drying post-nanocoating can harm seed quality and/or longevity               | [187,190] |
| Organic nanomaterials (NMs) and nanoparticles (NPs) | May not be as stable as inorganic NMs, thus susceptible to degradation from factors such as light, humidity, pH, and temperature changes                            | [191]     |
|                                                     | Release rates of active compounds may change with the environment (such as pH)                                                                                      | [192]     |
|                                                     | Uncertainty about NM biological activity could result in potentially unexpected/harmful effects on soils and ecosystems                                             | [193]     |

7. Novel Biodegradable Seed Coatings

Novel biodegradable coating materials are being trialed to allow coating technologies to better fit into sustainable agricultural systems. Positive characteristics of such coatings are shown in Figure 5 and can include longer active performance, higher germination, better biodegradability of materials, greater microbial health and use of sustainably-sourced materials [187].

Hydrogel-based coatings are protective layers made from hydrophilic networks that can retain large amounts of water, with a view to improving seed germination and seedling growth by maintaining moisture around the seeds and delivering actives in a controlled manner [197]. For instance, it was reported that the combination of a polymeric hydrogel consisting of carboxymethyl chitosan, sodium alginate, and calcium chloride, and endophytic plant growth-promoting rhizobacteria increased the yields of *Brassica napus* by 30% within acidic environments [198].





**Figure 5. Novel biodegradable seed coatings.** New biodegradable coating technologies promise to achieve sustainable agriculture [187].

Polysaccharide-based seed coatings are protective layers made from natural carbohydrate polymers. Such coatings can enhance seed germination and seedling growth by improving water retention, providing a source of nutrients, and delivering bioactive compounds. Examples include coatings made from materials like chitosan, alginate, and starch [199].

Microbial seed coatings apply beneficial microorganisms to the surface of seeds. Such coatings can improve plant growth and health by promoting nutrient uptake, enhancing disease resistance, and stimulating growth. Examples include coatings with bacteria such as *Rhizobium*, *Bacillus*, and *Pseudomonas*, or fungi like *Trichoderma* and mycorrhizae [187,200].

Trehalose seed coatings involve the application of a layer of trehalose to the seed (a natural disaccharide sugar), which can enhance seed viability and stress tolerance by protecting seeds from dehydration, improving germination rates, and enhancing seedling vigour [26,201].

*Disadvantages of Novel Biodegradable Seed Coatings*

Novel biodegradable coatings present diverse and conflicting outcomes, as summarised in Table 6, emphasising the intricate nature of such technologies. For example, it was reported that wheat, cabbage, basil, and radish seeds coated with sodium alginate hydrogels achieved a dryable seed coating stable for 90 days but resulted in a significant reduction in seed germination in vitro and in vivo [202]. Similarly, a composite coat consisting of alginate reduced seed germination percentage and speed in beans by acting as a physical barrier that hindered seed water absorption [203]. Microbial seed coatings can have a short-term or null impact depending on growing conditions. Some studies report no positive effects on crop productivity, nodulation, and biological nitrogen fixation, even causing a delay in germination [187,200]. For instance, coating sweet pepper seeds with a



mixture of plant beneficial microbes (PBMs) resulted in negative impacts on seed germination and plant height. Similar undesirable effects were observed for lettuce seeds coated with the same mixture of PBM [204].

Trehalose seed coatings can inhibit seedling growth under high temperature stress, as was observed for wheat [205]. Furthermore, long-term effectiveness may be a problem as trehalose can be degraded by plants [193].

**Table 6.** A summary of the disadvantages of seed coatings that use biodegradable materials.

| Biodegradable coating types | Disadvantages                                                                                                                                                         | References |
|-----------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------|
| Hydrogel-based coatings     | Outcomes are conflicting, e.g., a sodium alginate hydrogel achieved a dryable seed coating stable for 90 days, but seed germination was reduced                       | [202]      |
|                             | Can reduce germination percentage & speed                                                                                                                             | [203]      |
| Microbial seed coatings     | Effects can be of short-term, neutral, or there can be a reduction in beneficial effects, e.g., for crop productivity, nodulation, biological nitrogen fixation, etc. | [187,204]  |
| Trehalose seed coatings     | Can reduce seedling growth under high temperature stress                                                                                                              | [205]      |
|                             | Degradable by plants, short life                                                                                                                                      | [193]      |

In summary, more recently developed biodegradable seed coatings need further research to overcome deficits. The choice of coating agents and achieving uniform coating thickness and distribution remains a challenge, impacting germination and seedling establishment outcomes. Even with optimal coating, seeds face deterioration over time due to the need for redrying after coating. These collective challenges underscore the need to address weaknesses in all seed coating techniques for agriculture. Additionally, environmental considerations, especially regarding coating material use, require careful evaluation to address issues like leaching and potential harm to non-target organisms [19].

8. Conclusions and Future Directions

Modern seed enhancement technologies (SETs) are redefining the interface between plant biology and agricultural engineering, offering a new paradigm for improving germination, early seedling vigour, and resilience to biotic and abiotic stressors. This review has examined the current state of SETs, including conventional seed coating, seed priming, nano-enabled delivery systems, and integration of novel biodegradable seed coatings with an emphasis on mechanistic insights, agronomic value, and translational barriers. These SETs provide a modular platform for delivering bioactives, such as plant growth regulators, beneficial microbes, chemicals, and nutrients, directly to the seed microenvironment. By fine-tuning the timing, location, and dosage of these agents, seed enhancements can substantially optimise seed-soil interactions.

Nevertheless, current applications remain constrained by several critical limitations. Firstly, conventional methods involve the re-drying of seeds after treatment, which can lead to several issues. For instance, plant benefits from actives are typically short-lived, often disappearing within two weeks. Additionally, the re-drying process can compromise seed quality and longevity, especially for high-quality seed lots. Re-dried seeds can become less sensitive to plant growth regulators, and dehydration may alter seed coat properties, damage the mucilage layer, induce secondary dormancy, or cause fatal injury to the embryo. Secondly, biological inconsistency leads to variable performance under field conditions due to factors such as soil complexity, microbial competition, and environmental unpredictability. Formulation constraints are the third limitation. For example, many biologically active compounds, such as peptides and live inoculants, exhibit limited stability under industrial-scale processing and storage. Incomplete mechanistic understanding, especially the

interactions among carrier materials, bioactives, and plant-microbe signalling networks, remains underexplored, limiting the design of seed enhancement strategies. Lastly, a lack of harmonised global standards hinders commercialisation and cross-border deployment, particularly for nano-based interventions.

To overcome current bottlenecks and deliver scalable, field-relevant solutions, several interlinked strategies should be pursued (Figure 6), including material innovation, a better understanding of microbial ecology and integration of digital agriculture and plant omics. A major step forward would be the development of technologies that bypass or reduce the need for post-application seed re-drying, which presents a promising path to improve the viability of sensitive compounds, such as live microbes or peptides, and expand adoption in regions with limited processing infrastructure. Parallel progress is needed in designing microbe-friendly matrices, which can protect inoculated beneficial microbes during processing and storage while supporting effective rhizosphere colonisation under field conditions.



**Figure 6. Future perspectives of seed enhancement.** Conceptual illustration of future directions in seed enhancement technologies, highlighting seven interlinked strategies. These include smart bioresponsive carriers that release actives in response to environmental cues; microbe-compatible matrices that support microbial survival and colonisation; omics-informed systems that tailor treatments using genomic and microbiome data; field-validated deployment models ensuring consistent performance across environments; integration with digital agriculture for real-time monitoring and adaptive management; ongoing ecological and ethical evaluation to ensure biosafety and equitable access; and novel delivery platforms designed to eliminate or reduce the need for post-treatment seed drying. Together, these approaches converge to enable resilient, scalable, and sustainable seed-based technologies.

Advancements in omics-guided seed systems further promise enhancement strategies to be tailored to specific crop genotypes and local microbiomes. By integrating transcriptomic, metabolomic, and microbial community data, seed treatments can be increasingly personalised for targeted physiological outcomes. In parallel, rigorous field validation frameworks incorporating multi-environment trials and modelling will be essential to ensure reproducibility and to ensure climate resilience across diverse agroecosystems.

As seed enhancement technologies become more sophisticated, their integration with digital agriculture platforms will facilitate real-time tracking of germination, emergence, and early vigour, enabling dynamic input management. Equally important is the ongoing commitment to ecological and ethical evaluation, ensuring that new materials and strategies are safe, socially responsible, and accessible to large and small-holder farming systems.

In summary, these interconnected directions signal a transition from passive seed protection to dynamic, responsive, and ecosystem-aware enhancement systems. Achieving this vision will require interdisciplinary collaboration and coordinated innovation across materials science, plant biology, agronomy, and agricultural data systems. Seed enhancement is no longer a singular technique but a convergent platform at the nexus of biotechnology, materials engineering, and agronomic innovation. Its future lies in creating intelligent, adaptive, and ecologically responsible solutions that support food system transformation under climate and resource constraints. By linking molecular precision with field-level scalability, seed enhancement technologies promise to play a foundational role in building resilient, high-performing, and sustainable agricultural systems globally.

**Author Contributions:** Conceptualisation, A.B., J.K.; writing—original draft preparation, A.B., Y.W., and J.K.; writing—review and editing, A.B., J.K.; Supervision, A.B., B.F., and J.K.; Project administration, J.K., B.F.; Funding acquisition, J.K.

**Funding:** This work was supported by the Australian Institute for Bioengineering and Nanotechnology and the School of Agriculture and Food Sciences at The University of Queensland.

**Acknowledgments:** We would like to acknowledge The University of Queensland for providing a license of the software BioRender and the Adobe suite that have been utilised for drafting figures in this publication. We would also like to express our gratitude to the Chinese Scholarship Council, The University of Queensland Joint Scholarship, and The University of Queensland top-up Scholarship for supporting the author who drafted this work during his PhD.

**Conflicts of Interest:** The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

|                  |                             |
|------------------|-----------------------------|
| CSP              | Conventional Seed Priming   |
| GA <sub>3</sub>  | Gibberellic Acid            |
| KAR <sub>1</sub> | Karrikinolide               |
| NM               | Nanomaterials               |
| NP               | Nanoparticles               |
| PEG              | Polyethylene Glycol         |
| PBM              | Plant Beneficial Microbes   |
| SET              | Seed Enhancement Technology |
| SMP              | Solid Matrix Priming        |

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