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REVIEW

Recent innovative seed treatment methods in the management of seedborne pathogens

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Abstract

Seed is a critically important basic input of agriculture, because sowing healthy seeds is essential to food production. Using high quality seed enables less use of synthetic pesticides in the field. Seedborne pathogens can reduce yield quantity and quality of the crops produced. Seed treatments protect plant seedlings from pathogen attacks at emergence and at the early growth stages, contributing to healthy crop plants and good yield. However, there is increased concern about the application of synthetic pesticides to seeds, while alternatives are becoming increasingly addressed in seedborne pathogen research. A series of strategies based on synthetic fungicides, natural compounds, biocontrol agents (BCAs), and physical means has been developed to reduce seed contamination by pathogens. The volume of research on seed treatment has increased considerably in the past decade, along with the search for green technologies to control seedborne diseases. This review focuses on recent research results dealing with protocols that are effective in the management of seedborne pathogens. Moreover, the review illustrated an innovative system for routine seed health testing and need-based cereal seed treatment implemented in Norway.

Keywords Healthy seed · Seed health testing · Seed treatment · Inoculum threshold

1 Introduction

The United Nations (2019) expects that the global population may possibly reach 9.7 billion by 2050. Global agriculture will face major challenges to improve its production by at least 50% to ensure global food security in sustainable ways (Searchinger et al., 2019). Seeds play a crucial role in promoting food security: almost 90% of the world's food crops are grown from seeds (Dongyu, 2021). Therefore, sowing healthy, high quality seeds is essential to secure crop yields and food production (Moumni et al., 2020; Kumar & Gupta, 2020). Many pathogens, including fungi, bacteria, viruses and nematodes, which are responsible for important diseases in several crops, occur on and in seeds (Agarwal & Sinclair, 1996; ISTA Reference Pest List, 2022; ISTA, 2022a, b, c).

The association between seed and pathogen is an important means for pathogen dispersal on a large scale. Seed association is one common strategy for pathogen survival (Denancé & Grimault, 2022). Important seedborne pathogens include, among many examples, the fungus *Urocystis tritici* that can cause more than 50% yield reduction in wheat (Tao et al., 2014), the bacterium *Xanthomonas campestris* pv. *campestris*, responsible for yield losses that can reach 50 to 60% in *Brassica* spp. (Singh et al., 2018), and *Stagonosporopsis cucurbitacearum*, which has caused 15 to 50% yield losses of cucurbit production under warm and humid environments (Keinath et al., 1995). Knowledge of the transmission and localisation of pathogens in seeds is required to reduce seedborne inoculum (Maruthachalam et al., 2013; Zhang et al., 2018). The use of seed certified disease-free or seeds that are certified to have contamination levels below a given threshold is often recommended as a primary management strategy (Murolo et al., 2022). Seed health testing is therefore a fundamental step in the management of crop diseases (Kulkarni, 2019; Mancini et al., 2016). New and efficient technologies, such as polymerase chain reaction and high throughput sequencing, are increasingly being used to allow rapid and efficient testing of large numbers of samples (Hiddink et al., 2022).

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Eliminating or reducing seedborne inoculum is one key way to prevent plant disease epidemics (Van der Plank, 1963). This is mainly done by seed treatment methods, using chemical and biological agents and physical treatments applied to seed. This contributes to healthy seedlings and the establishment of healthy crops.

The use of chemical pesticides is a very common practice worldwide, due to their efficacy. To limit the negative impacts of pesticides on the environment and human health, along with preventing pathogens from adaptation to pesticides, strategies based on Integrated Pest Management (IPM; Raffa & Chiampo, 2021; Romanazzi et al., 2022) have been developed. These strategies are mandatory in the European Union (Directive 2009/128/EC) since 2014. IPM-based seed health strategies provide environmentally sound and economically feasible alternatives for seedborne disease management. Some of these IPM-based seed health strategies are now available to farmers or will be in the near future (Thomas-Sharma et al., 2017; Gupta & Kumar, 2020).

A systematic literature search from 2013 to 2022 was carried out, using the database of Scopus (https://www.scopus.com) with the keywords ‘seed treatment’. Publications were retained in the present review if the two words “seed” and “treatment” occurred in ‘Article title, Abstract, and Keywords’. The number of studies on application of seed treatment has increased considerably in past decade, demonstrating the increased interest of the scientific community in the subject (Fig. 1).

Seed treatments reduce the environmental impact of the production process by decreasing the need for application of pesticides (especially fungicides) later in the season (Brodal, 1995). Several seed treatments can be used according to the precise location of the pathogen on or in the seed (Fig. 2).

The objective of this review is to provide a survey of recent innovative seed treatment methods in the management of seedborne pathogens. An example of innovation for sustainable management of seedborne pathogens in Norway is reported as an illustration.

2 Fungicide seed treatments

Chemical seed treatment consists of the application of pesticides (fungicides, insecticides, bactericides, nematicides and rodenticides) to control pests and seedborne diseases or to stimulate the germination or plant growth (Andersson & Djurle, 2020). Considering the fungal pathogens, there are three classes of seed treatment fungicides. The first group includes fungicides that act by contact, which are only effective to control fungal spores localized on the seed coat and protect seeds and seedlings from soilborne pathogens. The second group includes fungicides which are locally systemic and target both surface and internally seedborne pathogens. The third group of fungicides is fully systemic, and in the xylem, they become mobile. Systemic fungicides can also be effective against soilborne pathogens, protecting seedlings after germination (Ayesha et al., 2021). Unlike the first group, these fungicides can present less risk to crops, animals and the environment because they may be degraded by soil microorganisms, which decreases their accumulation in the soil. These benefits include improved seed germination, seedling emergence and prevention of seed transmission of seedborne pathogens (da Silva et al., 2017). The delay between seed treatment and sowing needs to be low in order to avoid negative effects on seed germination and/or seedling emergence and to reduce phytotoxicity (EPPO, 2014). Nowadays, seed

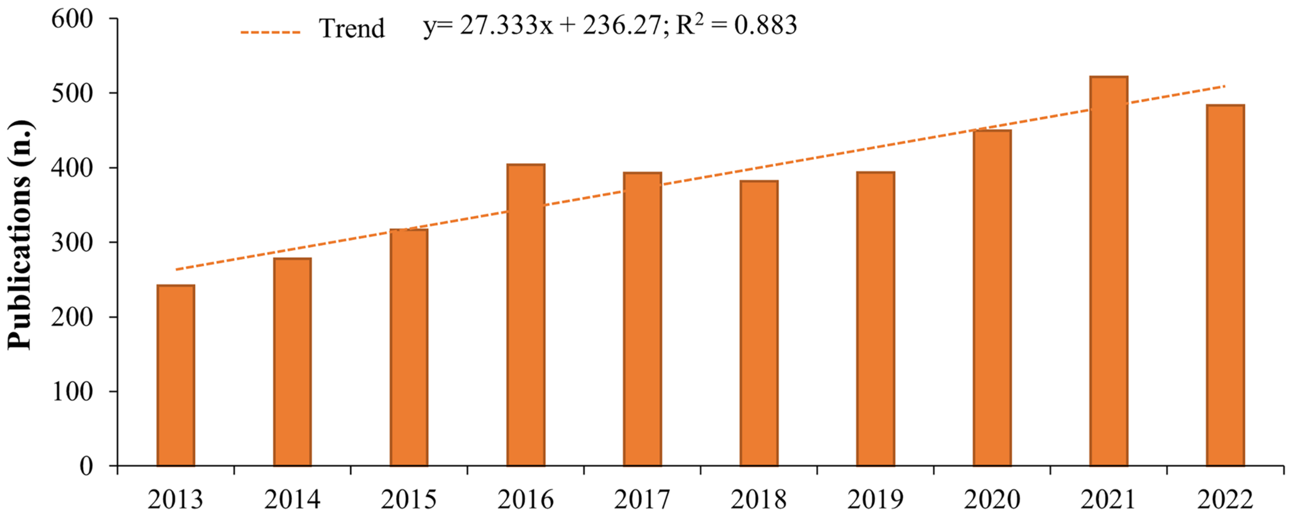

Fig. 1 Number of publications available on Scopus through searches with keywords ‘Seed treatment’ in ‘Article title, Abstract, and Keywords’ published over the last 10 years (Source: Scopus, accessed on 25 July 2023; https://www.scopus.com)

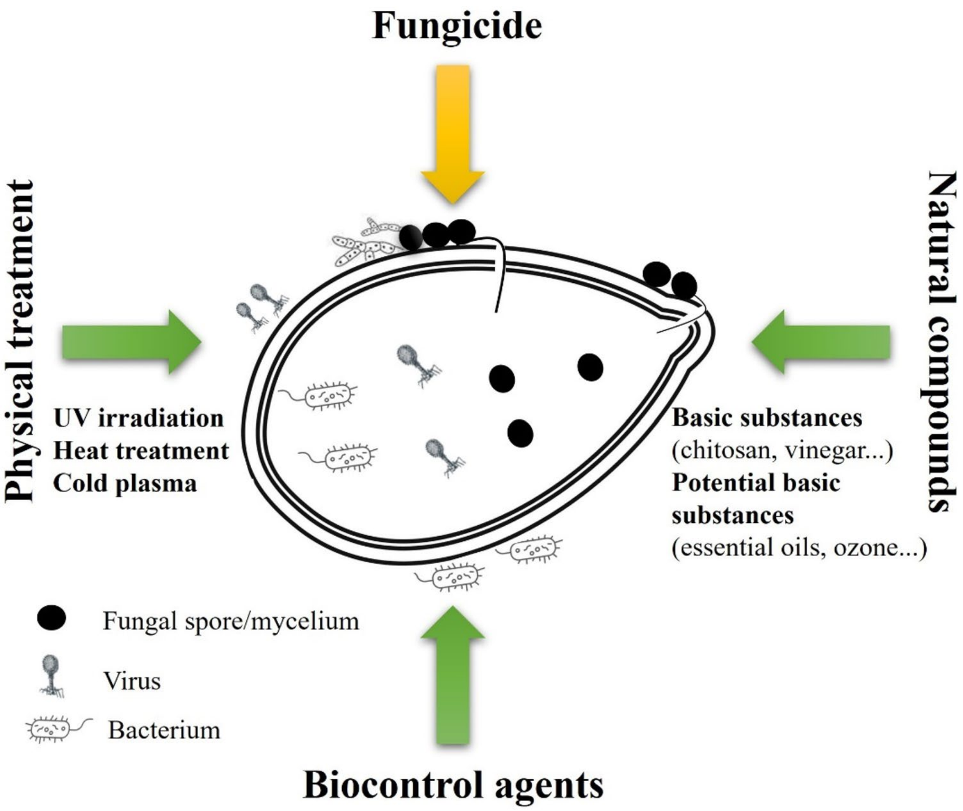

Fig. 2 Main seed treatments applied to control seedborne fungi, bacteria, and viruses

treatment with fungicides is very common and is practiced worldwide. Although fungicidal seed treatments carry important benefits, they also pose certain environmental risks, phytotoxicity risks and the possible selection of resistant pathogen populations. Seed treated with a fungicide can be a source of water and soil contamination.

Iprodione, benomyl, mancozeb and thiram are fungicides widely used in seed treatment. However, in some areas of the world (e.g. in the EU), changes in legislation have led to the banning of these fungicides, which were used for seed treatment (https://www.pan-europe.info/sites/paneurope.info/files/public/resources/reports/Report_Banned%20pesticides%20still%20widely%20used%202023.pdf). Up to 90% of applied pesticides do not reach the target species, due to the development of resistant pathogens and pests. The search for alternative products for crop protection is a strategy to promote more sustainable agricultural systems. Therefore, methods alternative to fungicide treatment to manage seedborne pathogen populations are of great interest to the scientific community to ensure safe agricultural production and reduce environmental pollution, and on these potential innovations this review will be focused.

3 Natural compounds

3.1 Basic substances

Basic substances are products that are used as a food, food ingredient or drink (foodstuffs). They are relatively novel compounds that can be used in plant protection without neurotoxic or immune-toxic effects (Marchand et al., 2021). Basic substances are still poorly known by phytosanitary consultants, researchers, growers, consumers, and are not placed on the market as plant protection products. Twenty-four basic substances are currently approved in the EU, and five of them, chitosan hydrochloride, chitosan, vinegar, mustard seed powder, and hydrogen peroxide, are used for seed treatment (Romanazzi et al., 2022).

3.1.1 Chitosan

Chitosan is a naturally occurring compound which is derived from crab-shell chitin. It is a biopolymer with antiviral, antibacterial, and antifungal properties (Riseh et al., 2022; Romanazzi et al., 2018). Chitosan hydrochloride was approved by the European Union as one of the first basic substances for plant protection, including seed treatment for cereals, potatoes, and sugar beet, and a second chitosan formulation was approved in 2022. This natural compound has been explored for many agricultural uses and it helps to reinforce host plant defences (Rajestary et al., 2021; Siddaiah et al., 2018). In addition, chitosan was reported to improve seed germination and plant growth under normal conditions and also, to combat oxidative and salt stress (Alkahtani et al., 2020; Sadeghipour, 2021). Chitosan activity has shown activity against several species of seedborne pathogens (Table 1). Treating pearl millet with chitosan under field conditions reduced infection of *Magnaporthe grisea* (Bhardwaj et al., 2022), and on seeds of *Triticum spelta*, reduced the severity of *Fusarium culmorum* (Buzón-Durán et al., 2020). Under greenhouse conditions, groundnut seed treatment with chitosan and chitosan–polyethylene glycol blend containing *Trichoderma harzianum* led to a decrease of *Aspergillus niger* infections (Prasad et al., 2020). Treatment of pepper seeds with chitosan enhanced the activities of chitinase and glucanase, resulting in increased seed germination (Samarah et al., 2020). The multiple properties of chitosan, including the coating effects, allow the possibility of combination with other compounds with antimicrobial activity, producing a slow release (Romanazzi & Moumni, 2022).

3.1.2 Other basic substances

Basic substances such as vinegar, mustard seed powder, and hydrogen peroxide were approved by the EU between 2015 and 2017 (Romanazzi et al., 2022). These basic substances were applied as seed treatments on several crops (Table 1). Vinegar was applied in seeds of wheat (*Triticum vulgare*), common wheat (*Triticum aestivum*), durum wheat (*Triticum durum*) and spelt (*Triticum spelta*) to control *Tilletia caries* and *Tilletia foetida* (Romanazzi et al., 2022). Vinegar seed treatment promoted the early seedling development of various plants, such as rice (Zhang et al., 2022), wheat (Wang et al., 2019), as well as pepper and tomato (Luo et al., 2019). Hydrogen peroxide enabled the control of *Xanthomonas campestris* pv. *vitians* on lettuce seed (Pernezny et al., 2002; Romanazzi et al., 2022). This treatment on pine seed (*Pinus radiata*) reduced the amount of *Fusarium circinatum* on seedlings (Berbegal et al., 2015).

3.1.3 Potential basic substances

Potential basic substances are those which are used as ‘foodstuffs’, but are not yet approved, such as essential oils and ozone (https://ec.europa.eu/food/plant/pesticides/eu-pesticides-database/start/screen/active substances). Essential oils are obtained from various plant parts, such as flowers, buds, seeds, leaves, bark, wood, roots and fruits (Orzali et al., 2020). Essential oils contain a wide range of volatile molecules, which possess several biological activities including antibacterial, fungicidal, and nematicidal (Moumni et al., 2021a; Raveau et al., 2020). The chemical compounds produced vary with the plants from which they are obtained, growing conditions and extraction methods, because even minor chemical compounds present in the essential oil can have a strong antimicrobial efficiency (Gonçalves et al., 2021). Various studies have reported antifungal activities in vitro and in vivo against seedborne pathogens (Table 2). These products have biodegradable properties, and do not have residual effects on fresh produce (Xylia et al., 2019). Essential oils can be used as a natural seed treatment to control fungal pathogens which cause superficial infections, but for pathogens localized within the seeds, products able to penetrate the seeds are needed (Gullino et al., 2014). Ozone applications for agriculture and food processing have increased in recent years, as ozone has been declared a GRAS (Generally Recognized As Safe) substance that is approved in some countries for its use in organic foods (McHugh, 2015). Ozone was applied for microbial decontamination and improving seed quality. Several factors affect the effectiveness of ozone, such as concentration, duration of treatment, and texture of the seed coat (Sivaranjani et al., 2021; Waskow et al., 2021). Some studies have indicated that a 15 min ozone treatment at 700 ppm increased seed germination of barley seeds by 12.3% (Dong et al., 2022). The ozone gas was used to control various microorganisms (Table 3). This treatment can decontaminate seeds of wheat, pea, and barley from several fungi such as *Alternaria* spp., *Aspergillus* spp., *Fusarium* spp., and *Penicillium* spp. (Ciccarese et al., 2007). Pepper seeds infected with a low concentration of pepper mild mottle virus (PMMoV) were treated with 20 ppm ozone for 14 h, leading to inactivation of the seedborne virus, without affecting germination. At high virus concentrations, however, this treatment was insufficient to prevent infection (Stommel et al., 2021).

4 Physical seed treatment

4.1 Heat treatment

Heat treatments are applied with hot water, hot air, and electron treatments. At the end of the nineteenth century, hot water treatment was applied to control seedborne fungi of cereals, and this method is now receiving new importance for organic farming (Bänziger et al., 2022). Several studies have reported the effectiveness of hot water treatments against seedborne pathogens (Table 3), and it has been applied successfully applied on a large scale (Koch & Roberts, 2014). Hot water treatments are classical physical methods of plant protection and are reported to reduce the incidence of seedborne fungi, enhance germination and

Table 1 Effectiveness of treatment with chitosan and other basic substances against seedborne pathogens

Basic substance	Target pathogen	Crops	Reduction of pathogen on seeds/ plant (%)	Seed germination/ seedling emergence *vs*. control (%)	References
Chitosan	*Rhizoctonia solani*[b]	Green bean (*Phaseolus vulgaris*)	54.4	-[d]	El-Mohamedy et al. (2017)
	Fusarium solani[b]		52.6		
		Fenugreek (*Trigonella foenum-graecum*)	87.5	96.0[e]	Ghule et al. (2021)
	Magnaporthe grisea[a]	Pearl millet (*Pennisetum glaucum*)	4.7–26.9[c]	-	Bhardwaj et al. (2022)
	Fusarium culmorum[b]	Spelt (*Triticum spelta*)	50.0	89.5[f]	Buzón-Durán et al. (2020)
	Aspergillus niger[b]	Groundnut (*Arachis hypogaea*)	51.8[c]	96.6[e]	Prasad et al. (2020)
	Macrophomina phaseolina[b]	Safflower (*Carthamus tinctorius*)	15.7[c]	83.3[e]	
	Phytophthora capsici[b]	Cucumber (*Cucumis sativus*)	85.0[c]	100[f]	Zohara et al. (2019)
	Acidovorax citrulli[b]	Watermelon (*Citrullus lanatus*)	32.9[c]	-	Li et al. (2013)
	Fusarium graminearum[b]	Durum wheat (*Triticum durum*)	33.3–42.1[c]	92.0[e]	Orzali et al. (2014)
Vinegar	*Colletotrichum lupini*[a]	White lupin (*Lupinus albus*)	16.9[c]	> 90.0[e]	Alkemade et al. (2022)
Mustard seed powder	*Tilletia caries*[a]	Wheat (*Triticum* spp.)	82.0–94.0	-	Koch et al. (2006)
	Pyrenophora graminea[a]	Barley (*Hordeum vulgare*)	78.0	-	
	Colletotrichum lindemuthianum[a]	Bean (*Phaseolus vulgaris*)	91.9	94.0[e,g]	Tinivella et al. (2009)
	Ascochyta spp.[a]	Pea (*Pisum sativum*)	10.5	90.7[e,g]	
Mustard meal (wet method)	*Fusarium culmorum*[b]	Wheat (*Triticum aestivum*)	66.7–100 66.0–78.0[c]	94.6–98.6[e] 63.0–78.0[h]	Kowalska et al. (2021)
Hydrogen peroxide	*Xanthomonas campestris* pv. *campestris*[a]	Cabbage (*Brassica oleracea*)	100	95.3[e]	Sanna et al. (2022)
Hydrogen peroxide stabilized with silver ions	*Alternaria radicina*[a]	Carrot (*Daucus carota*)	43.2	60.3[e]	Górski et al. (2020)
Hydrogen peroxide	*Fusarium circinatum*[b]	Pine (*Pinus radiata*)	98.2[c]	69.9[g,h]	Berbegal et al. (2015)
Gaseous chlorine dioxide	*Fusarium* spp.	Rice (*Oryza sativa*)	42.0–95.0	Slightly reduced germination	Jeon et al. (2014)

[a] Natural contamination

[b] Artificially inoculated

[c] Inhibition of pathogen on seedling or plant

[d] Data not available

[e] Rate of seed germination equal to the control

[f] Increased seed germination

[g] Seedling emergence

[h] Reduce of seedling emergence

seedling emergence, when conducted under specific conditions with a precise temperature according to each crop and pathogen (Alkemade et al., 2022; Mancini & Romanazzi, 2014). Temperature and the seed immersion time depend on the texture of the seed coat and target pathogen. Under greenhouse conditions, *Brassica napus* seed treatment with

Table 2 Examples of in vivo activities of essential oils against seedborne pathogens and their impact on seed germination and seedling emergence

Antimicrobial compound(s) (relative amount (%))	Source plant	Target pathogen	Crops	Reduction of pathogen on seeds (%)	Germination/ seedling emergence *vs.* control (%)	References
Eugenol (76.2%); caryophyllene (19.9%)	*Ocimum gratissimum*	*Colletotrichum lindemuthianum*[b]	Bean (*Phaseolus vulgaris*)	73.9	94.5[d]	Silva et al. (2022)
Eugenol (92.7%); α-farnesene (6.1%)	*Syzygium aromaticum*			65.5	98.5[d]	
Eugenol				76.3	86.0[d]	
-[a]	*Eucalyptus grandis*	*Fusarium oxysporum*[c]	Tomato (*Solanum lycopersicum*)	73.0	-	Yousafi et al. (2022)
-	*Cuminum cyminum*			53.1	-	
-	*Citrus sinensis*			84.3	-	
Carvacrol (67.6%); o-cymene (11.6%)	*Origanum vulgare*	*Fusarium oxysporum* f. sp. *lycopersici*[c]		52.0	24.4[5d,e]	Gonçalves et al. (2021)
Carvacrol				54.0	27.4[d,e]	
Eugenol (87.3%); β-caryophyllene (9.3%)	*Eugenia caryophyllus*	*Cladosporium* sp.[b]	Lettuce (*Lactuca sativa*)	86.0	82.0[f]	Waureck et al. (2022)
		Alternaria sp.		70.0		
Geraniol (48.7%); neral (42.2%)	*Cymbopogon citratus*	*Cladosporium* sp.[b]		98.0	38.0[f]	
		Alternaria sp.[b]		85.0		
1.8-cineole (39.6%); camphor (27.7%); limonene (22.0%)	*Rosmarinus officinalis*	*Cladosporium* sp.[b]		33.0	76.0[f]	
		Alternaria sp.[b]		7.5		
Bornyl acetate (57.5%); α-pinene (15.6%)	*Abies alba*	*Alternaria alternata*[b]	Onion (*Allium cepa*)	10.4	80.0[d]	Dorna et al. (2021)
		Botrytis allii[b]		80.5		
		Botrytis cinerea[b]		76.9		
		Cladosporium spp.[b]		28.5		
		Fusarium spp.[b]		84.2		
α-pinene (35.5%); β-pinene (18.6%)	*Pinus sylvestris*	*Alternaria alternata*[b]		16.3	70.7[d]	
		Botrytis allii[b]		55.5		
		Botrytis cinerea[b]		88.4		
		Cladosporium spp.[b]		7.1		
		Fusarium spp.[b]		84.2		
Thymol (34.2%); p-cymene (26.2%)	*Thymus vulgaris*	*Alternaria alternata*[b]		10.4	76.0[d]	
		Botrytis allii[b]		80.5		
		Botrytis cinerea[b]		100		
		Cladosporium spp.[b]		35.7		
		Fusarium spp.[b]		94.7		
p-cymene (25.9%); carvacrol (20.7%)	*Thymus vulgaris*	*Pseudomonas syringae*[c]	Soybeans (*Glycine max*)	29.7	84.0[d]	Sotelo et al. (2021)
		P. savastanoi pv *glycinea*[c]		24.0		

Table 2 (continued)

Antimicrobial compound(s) (relative amount (%))	Source plant	Target pathogen	Crops	Reduction of pathogen on seeds (%)	Germination/seedling emergence *vs.* control (%)	References
D-limonene (31.6%); d-carvone (44.8%)	*Nigella sativa*	*Plasmopara halstedii*[c]	Sunflower (*Helianthus annuus*)	70.1	-	Er et al. (2021)
Octadec-9-enoic acid (70.5%); l-(+)-Ascorbic acid 2,6-dihexadecanoate (9.5%)	*Sambucus nigra*			87.3	-	
Camphor (20.6%); l-fenchone (14.3%)	*Hypericum perforatum*			90.5	-	
Linoleic acid (61.8%); palmitic acid (12.1%)	*Allium sativum*			90.0	-	
Triacetin (21.9%); 2-butanone, 4-(4-hydroxyphenyl-) (8.5%)	*Vitis vinifera*			91.2	-	
Benzyl Alcohol (43.0%); bornyl acetate (31.3%)	*Zingiber officinale*			90.2	-	
α-citral (51.6%); β-citral (26.0%)	*Cymbopogon citratus*	*Stagonosporopsis cucurbitacearum*[b]	Squash (*Cucurbita maxima*)	72.0	86.0[d]	Moumni et al. (2021b)
		Alternaria alternata[b]		88.1		
Eucalyptol (63.5%); β-selinene (4.1%)	*Lavandula dentata*	*S. cucurbitacearum*[b]		67.7	86.0[d]	
		A. alternata[b]		89.2		
Linalool (33.7%); camphor (9.3%)	*L. hybrida*	*S. cucurbitacearum*[b]		73.2	85.0[d]	
		A. alternata[b]		75.2		
Terpinen-4-ol (41.1%); γ-terpinene (16.0%)	*M. alternifolia*	*S. cucurbitacearum*[b]		75.7	85.0[d]	
		A. alternata[b]		81.7		
Eucalyptol (47.9%); α-terpinyl acetate (10.2%)	*Laurus nobilis*	*S. cucurbitacearum*[b]		66.2	86.0[d]	
		A. alternata[b]		89.2		
Terpinen-4-ol (50.1%); p-cymene (17.8%)	*O. majorana*	*S. cucurbitacearum*[b]		84.4	85.0[d]	
		A. alternata[b]		87.0		

[a] Data not available

[b] Natural contamination

[c] Artificially inoculated

[d] Rate of seed germination equal to the control

[e] Seedling emergence

[f] Reduce of seed germination

hot water (50 °C for 30 min) showed good effect against *Xanthomonas campestris* pv. *campestris* and led to increased seedling emergence (Mandiriza et al., 2018).

4.2 Ultraviolet irradiation

Several studies have investigated the effect of ultraviolet (UV) irradiation to control seedborne pathogens (Table 3). UV irradiation is divided according to the wavelength into long—UV-A (315–390 nm), medium—UV-B (280–315 nm), and short—UV-C (100–280 nm) (Falconí & Yánez–Mendizábal, 2022). Pre-sowing treatment of lupin seeds with UV-B (2.83 kJ m^{-2}) combined with thermal radiation (76 °C for 45 min) reduced the percentage of seeds infected with *Colletotrichum acutatum* by 80% (Falconí & Yánez–Mendizábal, 2019). UV-C improved the germination

Table 3 Seed treatment with physical means recommended for the eradication of seedborne pathogens

Treatment	Temperature (°C)/ time (min) and doses/ time (min) combination	Target pathogen	Crops	Reduction of pathogen on seeds/ seedlings (%)	Seed germination/ seedling emergence *vs.* control (%)	References
Hot water	50 for 15	*Ralstonia solanacearum*[a]	Eggplant (*Solanum melongena*)	55.2[c]	-[d]	Nahar et al. (2019)
		Phomopsis vexans[a]		65.2[c]	-	
	55 for 15	*Colletotrichum kahawae* subsp. *cigarro*[b]	Eucalyptus (*Eucalyptus nitens*)	55.6[c]	85.0[e]	Mangwende et al. (2020)
	55 for 10	*Colletotrichum lupini*[a]	White lupin (*Lupinus albus*)	15.0[c]	> 90.0[e]	Alkemade et al. (2022)
	55 for 15	*Alternaria brassicicola*[b]	Kale (*Brassica oleracea* var. *acephala*)	99.1	85.6[e]	Cardoso et al. (2020)
	45 for 120	*Microdochium* spp.[a]	Winter wheat (*Triticum aestivum* subsp. *aestivum*)	78.3–96.1	> 55[f]	Bänziger et al. (2022)
	45 for 120 or 180	*Ustilago nuda*[b]	Winter wheat	65.0–99.0		Bänziger et al. (2022)
	54 for 15	*Alternaria alternata*[a]	Coriander (*Coriandrum sativum*)	69.5	75.0[f,g]	Mangwende et al. (2019)
	50 for 15	*Pyricularia oryzae*[b]	Rice blast (*Pyricularia oryzae*)	65.6	87.0[e]	Hashim et al. (2019)
	50 for 30	*Xanthomonas campestris* pv. *campestris*[b]	Rape (*Brassica napus*)	89.4	84.0[f]	Mandiriza et al. (2018)
	55 for 10	*Alternaria radicina*[b]	Carrot (*Daucus carota* subsp. *sativus*)	33.0[c]	65.0[e]	Lopez-Reyes et al. (2016b)
Dry air	65 for 10	*Fusarium oxysporum* f. sp. *basilici*[b]	Basil (*Ocimum basilicum*)	47.3[c]	75.0[e]	Lopez-Reyes et al. (2016a)
	65 for 480	*Colletotrichum acutatum*[a]	Andean lupin (*Lupinus mutabilis* Sweet)	66.2[c]	66.3[f,g]	Falconí and Yánez–Mendizábal (2016)
Aerated steam (ThermoSeed)		*Bipolaris sorokiniana*	Barley (*Hordeum vulgare*)	26.0–78.0	92.3–93.5[e]	Liatukas et al. (2019)
UV-C	57.6 kJ m^{-2} for 480	*Colletotrichum acutatum*[a]	Andean lupin (*Lupinus mutabilis*)	72.2–85.0[c]	56.0–53.3[f,g]	Falconí and Yánez–Mendizábal (2018)
	4 kJ m^{-2}	*Botrytis cinerea*[b]	Tomato (*Solanum lycopersicum*)	10.3[c]	87.3[h]	Scott et al. (2019)
Ozone	60 mg L^{-1} for 300 min	*Aspergillus* spp. *Fusarium* spp.[b]	Wheat grains (*Triticum aestivum*)	~ 54.3	-	Trombete et al. (2017)
	60 mg L^{-1} for 480 min	*Aspergillus* spp.[b]	Maize (*Zea mays*)	99.7	-	Porto et al. (2019)
		Fusarium spp.[b]		99.9		
	2.14 mg L^{-1} for 50 h	*Aspergillus* spp.[a]		78.5	-	Brito et al. (2018)
		Penicillium spp.[a]		98.0		
Cold plasma	Gas injection in vacuum chamber for 20 min	*Aspergillus* spp.[b] *Penicillium* spp.[b]	Legumes and cereals	99.0 both species	No damage to germination rate	Selcuk et al. (2008)
		Fusarium circinatum[b]	Pine (*Pinus radiata*)	14.0–100	2.6%-7.0[h]	Šerá et al. (2019)
			Ginseng (*Panax ginseng*)		Positive effects	Lee et al. (2021)
			Buckwheat (*Fagopyrum esculentum*)	> 50.0	Reduced germination	Mravlje et al. (2021b)

[a] Natural contamination

[b] Artificially inoculated

[c] Inhibition of pathogen on seedling or plants at heading

[d] Data not available

[e] Rate of seed germination equal to the control

[f] Increased seed germination

[g] Seedling emergence

[h] Reduce of seed germination

rate by 24% and increased the concentration of bioactive molecules in *Phaseolus vulgaris* seed coat (Guajardo-Flore et al., 2014). On the other hand, seed treatment using UV can reduce germination and decrease root length (Bokhari et al., 2013). UV seed treatment should be done at a precise dose to better control pathogens and limit the negative impact on seed germination (Shaukat et al., 2013).

4.3 Cold plasma

Plasma is an ionized gas, achieved using thermal energy, electric current or electromagnetic radiation. During the past two decades, the use of cold plasma technologies, a form of non-thermal processing, has developed as an effective method for surface decontamination and elimination of fungi on seed surfaces, as shown by numerous studies and reviewed by Mravlje et al. (2021a). Some examples include the reduction of fungal contamination on seeds of cereals and legumes (Selcuk et al., 2008), ginseng (Lee et al., 2021) and buckwheat (Mravlje et al., 2021b). However, some challenges concerning germination damage have been observed, as in pine (Šerá et al., 2019), wheat (Zahoranova et al., 2016) and maize (Zahoranova et al., 2018). Future research would need to explore possibilities for shorter exposure times and avoid detrimental effects on germination.

5 Biocontrol agents (BCAs)

The use of BCAs has notably increased over the past years, with a list of BCA-based methods reaching the market, including application as seed treatment (Bisen et al., 2020). Several microorganisms including fungi and bacteria provide an environmentally sound alternative to protect plants and seeds against many diseases. The search for new BCAs with potent biocontrol efficacy against seedborne pathogens will be necessary for economical agricultural production (Dethoup et al., 2018). The endophytic *Bacillus thuringiensis* can promote the growth of wheat plants and control *Urocystis tritici* in wheat seeds. *Trichoderma* spp. have been widely studied as potential BCAs to control many plant pathogens, stimulate plant growth, and enhance plant defence responses. Other BCAs used for seed coating include plant-growth-promoting rhizobacteria (PGPR), which have been screened, characterized, identified, and used as seed treatment against numerous diseases (Fariman et al., 2022). Several studies have shown that BCAs and PGPRs were effective antagonists against a wide range of pathogens (Table 4). PGPR used for seed treatment such as *Achromobacter xylosoxidans*, *Stenotrophomonas maltophilia*, and *Alcaligenes faecalis* have been reported to be effective. It remains important to understand the mechanisms underpinning the activity of these microorganisms, to ensure their greater efficacy (Singh et al., 2016).

Wheat seed treatment with lactic acid bacteria can contribute to effective management of seedborne fungi such as *Fusarium* spp., *Bipolaris sorokiniana* and *Alternaria* spp., although a decrease of seed germination was reported following application (Suproniene et al., 2015).

6 Need-based cereal seed treatment – an example of innovation for sustainable management of seedborne pathogens in Norway

Surveys conducted in many countries over many years have shown frequent occurrences of seedborne pathogens in small grain cereal seeds, such as *Pyrenophora* spp. in barley and oats, *Parastagonospora nodorum* in wheat, and *Fusarium* spp., *Microdochium* spp. and *Bipolaris sorokiniana* in seeds of all cereal species (e.g. Brodal et al., 2009, 2016; Carmona et al., 2004; Clear et al., 2000a, b; Cristani, 1992; Cunfer, 1978; Gilbert et al., 2003; Ioos et al., 2004). The seedborne inoculum of these pathogens was controlled since the 1930s/1940s by the routine and extensive use of organo-mercury seed treatments. Organo-mercury treatment was relatively inexpensive and easily applied and was used for many decades. Because of its extreme toxicity, the EU banned the use of organo-mercury fungicides in 1979, although some countries continued its use until the beginning of 1990s. Another reason to stop using mercury seed treatments was the development of resistance against the mercury-based compounds, in e.g. *Pyrenophora avenae* in oats in Scotland (Noble et al., 1966) and *Pyrenophora graminea* in barley in Norway (Magnus, 1981). In the 1980s, several new fungicides for seed treatment (e.g., imazalil, triadimenol, flutriafol, guazatine as the active ingredient) became available, and the routine seed treatment of cereal seed continued without knowing whether treatment was necessary or not.

During the transition to mercury-free seed treatment fungicides, the question of whether seed treatment was necessary for all seed lots as a routine was asked. The new seed treatment fungicides were more expensive and had more specific effects, revealing a need for information about which pathogens to control in each seed lot. It was then decided in Norway that all seed lots of wheat, barley and oats should be treated only when seed health analyses showed that it was necessary (Brodal, 1993). This was part of the implementation of the first Norwegian action plan to reduce the use of pesticides (Anonymous, 1990), which included the policy of "*cereal seed treatment only according to need*". To avoid unnecessary fungicide seed

Table 4 In vitro and in vivo activities of BCAs to control seedborne pathogens

Biocontrol agent (BCAs)	Target pathogen	Crop	Inhibition of pathogen in vitro or in vivo on seeds/ seedlings (%)	Seed germination/ seedling emergence *vs*. control (%)	References
Bacillus thuringiensis	*Urocystis tritici*[a]	Wheat	54.8%-66.5[c]	-[d]	Tao et al. (2014)
Artemisia afra	*Fusarium graminearum*		95.0[c]	79.4–98.4[e]	Kena (2016)
	F. avenaceum[a]				
Leucosidia sericea	*Fusarium graminearum*[a]		91.0[c]	70.5–88.5[e]	
	F. avenaceum[a]				
Rhamnus prinoides	*Fusarium graminearum*[a]		77.0[c]	72.7–100[e]	
	F. avenaceum[a]				
Galla chinensis	*Microdochium majus*[a]		59.0[c]	72.0–77.0[e]	Vogelgsang et al. (2013)
Pseudomonas chloroaphis	*Bipolaris sorokiniana*		23.0–90.0	-	Liatukas et al. (2019)
Lactobacillus sakei, Pediococcus acidilactici, Pediococcus pentosaceus	*Fusarium* spp.[a]		73.5	83.0[f]	Suproniene et al. (2015)
	Bipolaris sorokiniana[a]		56.8		
	Alternaria spp.[a]		55.6		
Trichoderma viride	*Pyricularia oryzae*	Rice (*Oryza sativa*)	72.2	-	Arumugam et al. (2013)
	Bipolaris oryzae		74.4		
	Rhizoctonia solani		71.1		
	Sarocladium oryzae		66.7		
Pseudomonas fluorescens	*P. oryzae*		78.9		
	B. oryzae		75.6		
	R. solani		47.8		
	S. oryzae		68.9		
Stenotrophomonas maltophilia	*Pyricularia grisea*		66.7		Etesami & Alikhani, (2016)
Achromobacter xylosoxidans	*Pyricularia oryzae*[b]		11.0	-	Joe et al. (2012)
			32.0[c]		
Stenotrophomonas maltophilia	*P. oryzae*[b]		55.6		Fariman et al. (2022)
Trichoderma asperellum		Rice	78.1[c]	94.9[e]	Hashim et al. (2019)
Bacillus subtilis			79.6[c]	98.0[e]	
Trichoderma asperellum	*R. solani*[a]	Rice	100	-	Klaram et al. (2022)
			88.5[c]	92.0[g]	
Trichoderma harzianum			100	-	
			84.0[c]	92.0[g]	
Trichoderma hamatum			100	-	
			92.0[c]	90.5[g]	
Trichoderma viride			100	-	
			77.7[c]	90.5[g]	
Trichoderma longibrachiatum			100	-	
			78.1[c]	93.1[e]	

Table 4 (continued)

Biocontrol agent (BCAs)	Target pathogen	Crop	Inhibition of pathogen in vitro or in vivo on seeds/ seedlings (%)	Seed germination/ seedling emergence *vs*. control (%)	References
Pseudomonas brassicacearum	*Xanthomonas axonopodis* pv *phaseoli*[b]	Common bean (*Phaseolus vulgaris*)	38.4–65.3	-	Giorgio et al. (2016)
			28.5–55.3[c]	-	
P. putida			47.2–51.9	-	
			26.9–27.3[c]	-	
Bacillus megaterium			48.0	-	
			46.4[c]	-	
Pseudomonas fluorescens	*Colletotrichum lindemuthianum*[a]		17.7[c]	-	Amin et al. (2014)
Trichoderma viride			28.5[c]	-	
Trichoderma harzianum			25.0[c]	-	
Alcaligenes faecalis	*Plasmodiophora brassicae*[a]	Cabbage	51.4[c]	up to 90[g]	Jia et al. (2022)
Paenibacillus sp.	*Xanthomonas campestris* pv. *campestris*[b]	Rape (*Brassica napus*)	81.8[c]	76.0[e]	Mandiriza et al. (2018)

[a] natural contamination

[b] Artificially inoculated

[c] Inhibition of pathogen on seedling or plant

[d] Data not available

[e] Increased seed germination

[f] Reduce of seed germination

[g] Rate of seed germination equal to the control

treatment and be able to choose the appropriate chemical, every cereal seed lot in Norway intended for certification, and most farm-saved seeds, have since 1990 been analysed for infection by the most frequently occurring seedborne pathogens. Based on the results from seed health analyses, in addition to results from advisory germination analyses, including test treatment with a fungicide that is routine in Norway, the need for treatment was determined according to inoculum thresholds (Table 5).

In order to screen a large number of samples, simplified, low labour-intensive and low-cost methods were designed and established in the seed testing laboratory in Norway (an official laboratory at that time, now the semi-privatized, ISTA accredited, Kimen Seed Laboratory https://www.kimen.no/). The methods include a blotter method for detection of *P. graminea*/*P. teres* in barley, now an ISTA-method (ISTA, 2022a), a modified version of the same blotter method for *P. avenae* in oats (unpublished internal method at Kimen Seed Laboratory), a blotter method (ISTA, 1964) detecting symptoms of seedling blight (*Fusarium* spp., *Microdochium* spp.) in barley and oats, and an agar plate method for *P. nodorum*, *Fusarium* spp., and *Microdochium* spp. in wheat, modified after ISTA-methods (ISTA, 2022b, c).

Table 5 Inoculum thresholds for the recommendation of seed treatment of cereal seeds in Norway (Sources: Kimen Seed Laboratory https://www.kimen.no/analysetilbud/forklaring-til-analysebeviset-for-korn/ accessed 29 August 2022; Brodal et al., 1997)

Cereal species	Pathogen (disease)	Threshold levels (% seed infection)
Barley	*Pyrenophora graminea*/*P. teres* (leaf stripe, net/spot blotch)	≥10
	Bipolaris sorokiniana (leaf spot/blotch, foot/root rot)	≥10
	Fusarium spp./*Microdochium* spp. (seedling blight)	≥25
Oats	*Pyrenophora avenae* (leaf spot/blotch)	≥25
	Fusarium spp./*Microdochium* spp. (seedling blight)	≥15
Wheat	*Parastagonospora nodorum* (leaf/glume blotch)	≥5
	Bipolaris sorokiniana (leaf spot/blotch, foot/root rot)	≥10
	Fusarium spp./*Microdochium* spp. (seedling blight)	≥15

Table 6 Proportion of cereal seed lots recommended for treatment to control seedborne pathogens for seed harvested in the years 1990–1994, 2017–2021. Sources: Brodal (1995); pers. comm. Eivind Meen, Kimen Seed Laboratory

Year of harvest	Seed lots recommended for treatment (%)[b]			
	Barley	Oats	Spring wheat	Total
Prior to 1990[1]	90	50	100	80
1990	72	56	79	ND[c]
1991	71	58	90	ND
1992	67	31	77	ND
1993	65	25	87	ND
1994	25	10	35	20
Average 1990–1994	60	35	75	50
2017	56	71	61	ND
2018	20	14	5	ND
2019	56	54	44	ND
2020	61	71	89	ND
2021	46	65	71	ND

ND no data

[a] Estimated proportion of fungicide treated seed lots when seed health analyses were not routine (prior to 1990)

[b] Based on results from routine analyses of all cereal seed lots

Routine screening for seed health became part of the cereal seed quality assessment, as a voluntary scheme, not officially required in the certification regulation. Since the beginning of the 1990s, 3000–4500 samples have been tested every year, representing close to 100% of the cereal seed lots used for sowing in Norway. The proportion of seed lots recommended for treatment over the years is shown in Table 6. To enable treatments only if necessary, routine analyses also ensure that heavily infected seed lots are identified and discarded.

A calculation of the extent of fungicide seed treatments on average for 1990–1994 showed that about 50% of the cereal seeds lots in Norway were recommended for treatment compared to the estimated extent of 80% before 1990 (Table 6), representing a reduction of about 35% (Brodal, 1995). This represented a reduction in fungicide, labour costs, and in environmental impact. The extent of treatment varied between cereal crops and from year to year. Before 1990, 100% of spring wheat seed, 90% of barley seed and 50% of oat seed were normally treated vs 75%, 60% and 35%, respectively, on average for the years 1990 to 1994 (Table 6). The warm and dry summer 1994 resulted in exceptionally low infection frequencies in cereal seeds. Only 20% of the cereal seed lots produced that year showed a need for treatment. 2018 was also extremely dry, resulting in the lowest need for seed treatment recorded so far.

Another important contribution in the reduction of fungicide for seed treatment in cereals is the use of hot, humid air which also is applied after assessing the need for treatment (Forsberg et al., 2005). Since 2012, one of the seed companies in Norway has established two ThermoSeed® machines (https://www.lantmannen.com/contentassets/011c206e623c41c0af7a597fd1e4fc8d/thermoseed-12-pages_interaktiv.pdf, accessed August 18, 2022), which replaces a significant share of the seed treatment fungicides.

The routine seed health analyses and treatment according to need ensures a proper and targeted use of seed treatment fungicides and can be considered a major contribution to achieve IPM in disease management of cereals in Norway. The approach was well received by the seed companies as cost-saving and environmentally friendly. There have been no complaints regarding false negatives, i.e., the absence of treatment against seedborne diseases, since the system was introduced. The commercial use of moist heat treatment by a seed company further contributes to sustainability.

7 Conclusions

Seed treatment is still a critical disease management component for agriculture production today. Even a low level of seedborne inoculum can in certain cases develop into severe losses and damage, as well as enabling the introduction of a pathogen into a new environment, where it can affect the same and possibly also other crops. Seed contamination, even by weak pathogens, is grounds for several countries to establish a trade barrier to prevent importation and protect domestic production. Reducing the use of pesticides and increasing that of organic farming is currently a major challenge in several countries. Setting protocols for management of seedborne pathogens based on the use of natural compounds, including basic substances and potential basic substances, complemented by physical means and BCAs can meet the requirements of the new agricultural policies and of markets. However, considering all the benefits of seed treatment, we also have to take into proper consideration cases when a threshold of seed contamination can be considered acceptable and seed treatment can be avoided. Further investigations are required to better understand the mechanisms involved in each type of seed treatment and its eventual effect on the seed microbiome.

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Declarations

Conflict of interest The authors declared that they have no conflict of interest.

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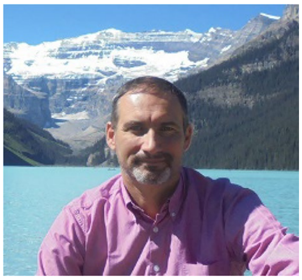

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