



SEED GERMINATION PROMOTING CHEMICAL COMPOUNDS AND THEIR POTENTIAL USE IN THE MALTING INDUSTRY

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Abstract

Malting of barley grains is a procedure known for centuries, however, the technology of malt production is constantly being studied and optimized. The optimizations comprise different conditions of barley steeping, as well as using different additives to improve seed germination. Among the most famous group of seed germination regulators, gibberellins, a broad spectrum of diverse chemical substances also have stimulatory effects on seed germination. This review summarizes what is known about multiple barley seed germination promoting compounds, as well as other chemical/hormonal seed germination regulators described in other plant species. The goal is to provide an impulse for testing new stimulatory substances with potential applications in malting process optimization.

Keywords: seed germination stimulation, barley, gibberellins, hydrogen peroxide

1 Introduction

The brewing industry in the Czech Republic has a long tradition, and its products are one of our most renowned market commodities. The taste and quality of beer highly correlates with the quality of its three basic components: water, hops and malt. The principle of malt production exploits the natural processes of seed germination. During this process, raw grains are imbibed in water, partly germinated, and then the germination is halted by drying with hot air. As a result, seed storage biopolymers are enzymatically converted into less complex compounds. Most importantly, starch is partially converted into monosaccharides and higher sugars, which are accessible for yeast fermentation (alcohol production). To produce high-quality malt, fast and uniform seed germination has to be maintained to provide an optimal level of catabolic processes in grains. For this purpose, multiple approaches to seed germination regulation can be employed, including the use of various plant growth regulators. However, the use of such regulators requires a deep

knowledge about the complexity of the germination regulatory machinery.

In the temperate climate zone, mature seeds undergo a period of intensive desiccation and become dormant (a period when the seeds are not able to germinate even though the environmental conditions are optimal). In this state, all metabolic processes are minimized and when stored properly, seeds can retain their viability for tens or hundreds of years. Control of the length of seed dormancy has been shown in a generally known model to be mostly driven by the ratio of two opposing phytohormones: abscisic acid (ABA) and gibberellins (GAs). ABA deepens the seed dormancy and thus inhibits premature seed germination (vivipary). ABA also ensures the accumulation of storage and protective compounds during the seed maturation (Bewley et al., 2012). In contrast, GAs are involved in overcoming dormancy, embryo growth activation, endosperm and seed coat weakening, and mobilization of storage compounds.

Seed germination is a highly complex process, controlled by multiple regulatory pathways. As such, seed germination can be affected by a broad spectrum of chemical substances. This review summarizes the most important classes of seed germination regulators, as well as less-known chemicals that have been proposed to improve seed germination (Table 1). The testing of new seed germination regulating substances may open the possibility to optimize the malting process. Even though malt can be made from different cereals, such as wheat or sorghum, barley is considered to be the most suitable for malt and beer production and this review is therefore preferably focused on barley grains. Finally, despite the huge importance of the chemical harmlessness in food/beverage industry, the potential health impact of these substances is not discussed here.

2 Hormonal treatments

Being the key natural regulators of plant developmental processes, phytohormones are widely employed for plant growth modulation to produce economic benefits. The highest commercial importance is attributed to GAs which, among others, are commonly used during malt production. While the involvement of phytohormones in the regulation of seed germination is not fully understood, multiple studies suggest a range of different roles for these various compounds (Miransari and Smith, 2014).

2.1 Gibberellins

GAs are an important class of plant hormones with a tetracyclic diterpene acid structure. GAs are well known to facilitate the regulation of multiple developmental processes, such as plant height, floral initiation, fruit set, and seed germination. Although more than 130 different gibberellin forms have been isolated from plants, fungi and bacteria, only a few are biologically active, namely GA1, GA3, GA4 and GA7 (Daviere and Achard, 2013).

The history of GA research dates back to the late 19th century. In Japan, so-called bakanae disease caused significant losses in rice crops. In 1926, it was found that the disease is caused by *Fusarium* fungus (*Gibberella fujikuroi*) which produces active compounds, gibberellins, with hormone-like effects. These were first isolated from the fungus in 1935 and, 23 years later, GAs were isolated from immature runner bean seeds, which was the first evidence of GAs biosynthesis in plants (Hedden and Sponsel, 2015). The signaling of bioactive GAs was originally studied using a model of barley caryopses, based on the observation of T. Hayashi (1940) who showed an increased α -amylase activity after GA treatment. The first

malting studies using GAs were done by Sandegren and Beling (1958). Since that time, the great potential of GAs as plant growth regulators has been investigated in detail (e.g. Bawden et al., 1959; Briggs, 2002). Gibberellic acid (GA3) was shown to be highly effective in breaking seed dormancy (Pollock, 1959). In former Czechoslovakia, Maštovský et al. (1959) developed a methodology for time reduction of the malting process using GA3, which was subsequently optimized by Sekrt et al. (1961). Further research showed that GAs stimulate multiple hydrolytic enzymes, leading to the increased levels of simple substances, such as sugars, amino acids, nucleotides and inorganic phosphate. For example, GAs enhanced the activity of β -glucosidases and β -glucanases, resulting in more intensive breakdown of β -glucans and improved beer filtering step (Guido and Moreira, 2014; Shahpiri et al., 2015). GAs were also shown to stimulate limit dextrinase activity (as well as α -amylase activity), whereas β -amylase was unchanged (Evans et al., 2009). Thanks to the current large-scale omic technologies, the effects of GA treatment on germinating barley grains were described at the level of transcriptome (Chen and An, 2006), metabolome (Huang et al., 2016) and proteome (Huang et al., 2017). However, even though the benefits of GAs were evident, their use is connected with a few negative effects on malt quality (e.g. high proteolytic activity) and economical effectivity (Kosař et al., 1989).

2.2 Abscisic acid

Even though ABA is crucial for seed formation, content of storage compounds, and seed survival under unfavorable environmental conditions, the seed germination process itself requires a low ABA level. Thus, the inhibitors and antagonists of ABA represent a group of potential seed germination promoters. For example, the well-known herbicides fluridone and norflurazon target phytoene desaturase, a key enzyme of carotene biosynthesis and ABA precursor (e.g. Kusumoto et al., 2006). However, no effects on malting have as yet been reported.

2.3 Karrikins

Karrikins are butenolide-like compounds discovered in the smoke from burning plant material (Flematti et al., 2004; Van Staden et al., 2004). So far, the karrikin compound family is composed of six members (e.g. KAR1, 3-Methyl-2h-Furo[2,3-C]pyran-2-One) with strigolactone-related structures and phytohormone-like properties. These heterocyclic molecules were shown to promote seed germination of fire-following plant species. However, the stimulatory effect, comparable to that of GAs, was observed also in other plant species, including a model plant *Arabidopsis thaliana* (Nelson et al., 2010;

Nelson et al., 2012), *Lactuca sativa* (Flematti et al., 2004), *Brassica tournefortii* (Stevens et al., 2007) and others (Van Staden et al., 2006). Interestingly, the karrikinresponse was found also in *Poaceae* (a family which includes important cereals), such as rice (Kulkarni et al., 2006), *Avena fatua* (Long et al., 2011) and *Hordeum leporinum* (Stevens et al., 2007). The vast majority of tested plant species showed the highest sensitivity to KAR1 (Waters, 2017), however, *A. thaliana* showed KAR2 preference (Nelson et al., 2010).

2.4 Ethylene

Ethylene is a gaseous plant hormone involved in multiple developmental processes including senescence and fruit ripening. In seeds, the effect of ethylene is species-specific. For instance, a massive increase in ethylene biosynthesis takes place during seed germination of multiple plant species, such as *Arabidopsis*, pea and tobacco (Linkies and Leubner-Metzger, 2012). Further, exogenously applied ethylene or its precursors (1-aminocyclopropane-1-carboxylic acid - ACC; ethephon - ETP) showed a stimulatory effect on seed germination of multiple plant species, such as beech (*Fagus sylvatica*), sunflower (*Helianthus annuus*), sugar beet (*Beta vulgaris*) and apple (*Malus domestica*) (Esashi, 2018). Ethylene is involved in barley seed germination which was shown by a decreased rate of seed germination in the presence of ethylene perception antagonists (Locke et al., 2000). The stimulatory effect of ethylene is carried out at different levels. Multiple studies showed the ethylene counteracting the inhibitory effect of ABA, while others proposed the role of ethylene in endosperm weakening (Corbineau et al., 2014; Bogatek and Gniazdowska, 2012).

2.5 Cytokinins

Cytokinins are highly important phytohormones orchestrating diverse developmental processes including cell growth and division. Cytokinins are usually considered to be seed germination promoters in stress conditions (Nikolić et al., 2006). The seed size can be also determined by cytokinins (Jameson and Song, 2015), as well as the level of seed dormancy (Nambara et al., 2010). Kinetin (a cytokinin-like compound) was found to promote barley seed germination (Pollock, 1959). Moreover, Khan (1969) suggested cytokinins (kinetin and benzyladenine) to be antagonists of seed germination inhibitors (ABA and coumarin). The stimulatory effect of cytokinins was also observed in light-requiring species (e.g. Biddington and Thomas, 1976). On the other hand, *Arabidopsis* cytokinin receptor loss-of-function mutants showed rapid seed germination (Riefler et al., 2006). The same results were obtained by using cytokinin antagonists PI-55 and LGR-991 (Nisler et al., 2010).

2.6 Other phytohormones

Strigolactones were first shown to induce seed germination of parasitic plants *Striga*. More recently, the stimulatory effect was observed also in some non-parasitic plants. It was also proposed that strigolactones allow thermo-inhibited seeds to germinate by interacting with GAs, ABA and ethylene (Toh et al., 2011). Finally, brassinosteroids participate in promotion of endosperm rupture by counteracting the inhibitory effects of ABA (Leubner-Metzger, 2001; Hu and Yu, 2014).

3 Chemical treatments

The potential effects of different chemical substances (non-phytohormone) in relation to stimulation of seed germination have also been studied for many years. A review of chemicals with seed germination promoting effects is briefly described in the following sections.

3.1 Hydrogen peroxide

Significant seed stimulatory effects can be seen with the well-known chemical hydrogen peroxide (H_2O_2). H_2O_2 is a unique member of reactive oxygen species (ROS) and was originally thought only to be a toxic molecule causing significant oxidative damage in living cells. Nowadays, H_2O_2 is also considered to be an important signaling molecule, with phytohormone-like properties (Habánová and Berka, 2018). The switch between toxic and signaling behavior is dose-dependent and tissue-specific. In improperly stored dry seeds, increased H_2O_2 production combined with minimal metabolism activity may induce significant defects leading to the reduction of seed viability. On the other hand, the presence of H_2O_2 (both internal and externally supplied) could significantly improve seed germination due to its positive role in the removal of phytohormonal and mechanical barriers that inhibit seed germination. Briefly, H_2O_2 participates in weakening of endosperm and seed coats, mediating selective oxidation of mRNA and proteins and modulating metabolism of ABA and GAs (Černý et al., 2018). The stimulatory effect of H_2O_2 was described in multiple plant species, including barley (e.g. Kilic and Kahraman, 2016; Ishibashi et al., 2017). Moreover, H_2O_2 was shown to be involved in co-regulation of α -amylase activation and the programmed cell death in the aleurone cells.

3.2 Nitric oxide and cyanides

Nitric oxide (NO), as well as some NO precursors was proposed to break seed dormancy in different plant species. A promising promoter of *Arabidopsis* seed germination is sodium nitroprusside (SNP) which releases NO and cyanide (Bethke et al., 2006). Interestingly, Esashi et

Table 1 The list of compounds promoting seed germination of barley and other plant species.

Stimulatory compounds	Water solubility	Examples of published effects on seed germination	
Gibberellins (GA1, GA3, GA4, GA7)	very low	Endogenous seed germination stimulator of most plant species (nM– μ M range)	Hedden and Sponsel, 2015 (review)
Cytokinins (e.g.: tZ, K, BA)	very low	<i>A. graveolens</i> (10 μ M BA) <i>L. corniculatus</i> (0.08–3.5 μ M) <i>H. vulgare</i> (25 ppm K)	Biddington and Thomas, 1976 Nikolić et al., 2006 Pollock, 1959; Khan, 1969
Ethylene (precursors: ACC, ETP)	good*	<i>M. domestica</i> (10 mg/l ETP) <i>F. sylvatica</i> (700 μ M ETP), <i>B. vulgaris</i> (1 mM ACC) <i>H. vulgare</i>	Sińska, 1989 Calvo et al., 2004 Hermann et al., 2007 Locke et al., 2000
Karrikins (KAR1–KAR6)	very low	<i>L. sativa</i> (from 1 ppt KAR1) <i>A. fatua</i> , <i>H. leporinum</i> (0.67–6.7 μ M KAR1)	Flematti et al., 2004 Stevens et al., 2007
Strigolactones (e.g. GR24, 3RAS)	very low	<i>A. thaliana</i> (20 μ M GR24) <i>A. fatua</i> (100 μ M 2RAS, 3RAS)	Toh et al., 2011 Bradov et al., 1990
Brassinosteroids (e.g. BL)	very low	<i>N. tabacum</i> (10 nM BL)	Leubner-Metzger, 2001
ABA inhibitors (Fluridone, Norflurazon)	very low	<i>L. sativa</i> (50 μ M F) <i>C. arabica</i> (50 μ M F) <i>S. asiatica</i> (100 μ M N)	Yoshioka et al., 1998 Silva et al., 2004 Kusumoto et al., 2006
Phthalimides (e.g. AC-94377)	very low	<i>A. fatua</i> (100 μ M) <i>A. graveolens</i> (500 mg/l)	Upadhyaya et al., 1986 Gott and Thomas, 1986
Hydrogen peroxide	good	<i>P. sativum</i> (20–80 mM) <i>A. thaliana</i> (5–10 mM) <i>S. oleracea</i> (0.3%) <i>H. vulgare</i> (10–100 mM)	Barba-Espin et al., 2012 Liu et al., 2010 Katzman et al., 2001 Ishibashi et al., 2017
Sodium nitrate, sodium nitrite	good	<i>O. sativa</i> (10 mM NaNO ₃ , NaNO ₂) <i>H. vulgare</i> (0.5% NaNO ₃ , NaNO ₂)	Cohn et al., 1983 Pollock, 1959
Nitric oxide (precursor: SNP) and cyanides	good*	<i>A. thaliana</i> (50 ppm NO) <i>H. annuus</i> (1 mM HCN) <i>H. vulgare</i> (100 μ M SNP)	Libourel et al., 2006 Oracz et al., 2008 Bethke et al., 2004
Hydrogen sulfide (precursor: Na ₂ S)	good*	<i>Z. mays</i> , <i>P. vulgaris</i> (10 μ M–1 mM H ₂ S) <i>H. vulgare</i> (250–1,000 ppm H ₂ S)	Dooley et al., 2013 Pollock, 1959
Formic acid esters	good	<i>O. sativa</i> (30–130 mM) <i>H. vulgare</i>	Cohn et al., 1989 Reuss et al., 2003
Potassium bromate	good	<i>H. vulgare</i> (0.5%)	Pollock, 1959 Briggs, 1998

Legend: ACC – 1-aminocyclopropane-1-carboxylic acid; ETP – ethephon; tZ – trans-zeatin; K – kinetin; BA – benzyladenin; SNP – sodium nitroprusside, GR24 and 3RAS – synthetic analogs of strigolactones, BL – brassinolide, AC-94377 – 1-(3-chlorophthalimido)cyclohexanecarboximide

* gaseous substances could be supplied either directly in gas phase, or they could be generated from precursors (Na₂S → H₂S; SNP → NO; ACC or ETP → ethylene). In such cases, water solubility information is related to the precursor.

al. (1991) showed that cyanides are produced by seeds and exogenously applied cyanides stimulate dormancy release (Oracz et al., 2008; Bethke et al., 2006). Such substances, as well as karrikins, were also shown to be present in the smoke from burning vegetation (Flematti et al., 2011). It is worth to say that cyanide salts are highly toxic which would be incompatible with their use as malt additives. However, other cyanide-based substances, such as potassium ferrocyanide, are nontoxic.

3.3 Phthalimides

Phthalimides are imide derivatives of phthalic anhydride, which were shown to have GA-like activity (Metzger, 1983). The most active phthalimide compounds were

described as AC-94377 [1-(3-chlorophthalimido)cyclohexanecarboximide], AC-92803 [2-(3-chlorophthalimido)-2-methyl-2-isobutyl - acetamide] and AC-99524 [1-tetrahydrophthalimido-cyclohexane-carboximide].

The highest effectivity, which was even slightly higher than in case of GA3, was attributed to AC-94377. The seed stimulatory effect was observed in several plant species, including wild oat (*Avena fatua*), a member of Poaceae family (Metzger, 1983; Upadhyaya et al., 1986). Being a highly promising seed germination regulator, the mode of AC-94377 functioning was deeply analyzed. Despite the structural differences between GA3 and AC-94377, Jiang et al. (2017) demonstrated that AC-94377 binds to the At-GID 1, an *Arabidopsis* GA receptor.

3.4 Other chemicals

This last section is dedicated to less-known potential seed germination promoters. As an early example, we can use a previously mentioned pioneer work of Pollock (1959) who tested a wide spectrum of chemical substances and their effects on barley seed germination. Among others, hydrogen sulfide was found to be highly effective in breaking seed dormancy. Recently, hydrogen sulfide, as well as nitric oxide, are considered to be important gas-transmitters with important physiological functions. The potential of hydrogen sulfide increases thanks to the evidence that this substance promotes seed germination of multiple plant species (Dooley et al., 2013). Next, Pollock (1959) suggested sodium nitrate and sodium nitrite to enhance barley seed germination. Similar results were found for example in red rice seeds (Cohn et al., 1983). More recently, Reuss et al. (2003) found ethyl and methyl formate to be promising stimulators of seed germination. Finally, it is worth mentioning potassium bromate. Bromate ions were shown to inhibit some proteolytic enzymes. Since the proteolytic activity is too high in the presence of GAs, potassium bromate treatment during malting process was shown to be beneficial (Briggs, 1998). However, the use of potassium bromate is connected with health-related controversies (Kurokawa et al., 1990). Even though Food and Drug Administration prescribed safety conditions of potassium bromate use as an additive during malt production, this chemical is classified as a possible carcinogen.

4 Conclusion

Diverse classes of chemicals displaying stimulation of seed germination have been discussed here. Such chemicals included the most famous group of phytohormonal stimulators (gibberellins), other phytohormones, and chemical substances with described seed germination promoting effects. The resulting benefits of such additives are for example triggering of higher hydrolytic enzyme activity and reduction of malting-time. Recently, the climate change and extreme weather fluctuations cause serious yield losses as well as reduced seed quality, which may be negatively reflected in the process of seed germination. Thus, the proper use of seed germination stimulators may compensate the negative effects of abiotic stress on barley seed quality. Despite the fact that phytohormonal treatments are associated with higher financial costs, there are undisputed benefits due to their very low active concentrations (nM) and natural occurrence and signaling in plants. Impressive results were also reached with an inorganic compound, hydro-

gen peroxide, which was found to improve seed germination of multiple plant species including barley. Moreover, hydrogen peroxide is a highly reactive molecule with short life-span, being decomposed into simple nontoxic substances via enzymatic and non-enzymatic processes. Here, hydrogen peroxide surpasses other more complex seed germination stimulators, whose health effects may be at least questionable.

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