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***Review Article***

# Resistance inducers and their role in reinforcing wheat defense system against fungal pathogens

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## Abstract

**Plant resistance inducers (PRI) are considered as a novel and prospective option to manage fungal diseases. They offer an improved plant protection strategy in an environmentally safe and economically sound manner. A galaxy of resistance inducing compounds of different origins have been reported and tested successfully in different plant-pathogen systems. The published literature illustrates that the mechanism of action of PRI molecules differs from other agrochemicals as they protect plants from pathogen via stimulating plant defense machinery. Moreover, resistance inducers can be integrated with biological control agents and even fungicides, which could result in reduced use of agrochemicals in agriculture. A plenty of biological control agents are identified and validated for field usages, but further expansion in product development and their effective deployment in wheat and other disease management will inevitably require in depth knowledge and understanding of multifaceted interactions operating between plant and microbe. The current review offers an overview of PRI's that have been tested in wheat in order to activate its own defense system for attaining durable protection against fungal invasions. Additional attempts have been made to highlight the nature and applications of biological control based on different resistance inducers and their mechanism of action along with contemporary status and future developments with other measures of disease tactics in spatiotemporal manner.**

**Key words:** Defense, fungus, ISR, jasmonic acid, rust, SAR, salicylic acid, sustainability, wheat, yield

## 1. Introduction

Wheat (*Triticum aestivum* L.) is regarded as one of the most vital food crops which provide daily nourishment to a large section of global population. Several reports have indicated that global wheat production would need to be enhanced by 60% to match the food needs by 2050 (Kumar *et al.*, 2021). This target seems difficult to achieve in light of present scenario of diminishing arable land, scarcity of water resources and unpredictable climatic change (Jasrotia *et al.*, 2018). Moreover, regular invasion of fungal pathogens also causes drastic reduction in the wheat yield as well as on quality seed production (Goyal and Prasad, 2010). The major fungal diseases of wheat include rusts (yellow, brown and black), Karnal bunt, foliar blight, powdery mildew and loose smut (Kumaran *et al.*, 2021; Khan *et al.*, 2021; Bishnoi *et al.,* 2020; Kashyap *et al.*, 2020a; Gupta *et al.*, 2017; Al-Maaroof *et al.*, 2015; Jindal *et al.*, 2012; Park, 2007; Joshi *et al.,* 2004). Besides this, in literature several other region specific diseases of minor significance, for instance, head scab, wheat blast, flag smut, foot rot, hill bunt, viral and bacterial diseases have been documented throughout the globe (Singh *et al.*, 2020; Kashyap *et al.*, 2020b; Mehta *et al.*, 2014). The published reports indicate that diseases alone have the ability to cause 15-20% yield loss annually, but reports of more than 50% yield loss in wheat have also been documented (Figueroa *et al.*, 2018; Griffey *et al.*, 1993). To date, systemic and protectant fungicides are widely used for the management of fungal diseases in wheat for maximum harvest (Basandrai *et al.,* 2020; Kumar *et al.* 2018; Selvakumar *et al.*, 2015; Mahapatra and Das, 2013). Unfortunately, regular and injudicious usages of agrochemicals have resulted in numerous negative impacts including the upsurge in residue levels of agrochemicals, emergence of fungicide-resistant fungal strains and human health hazards (Sharma *et al.*, 2019; Kashyap *et al.* 2019; Kashyap *et al.*, 2018b; Bruce, 2010). Therefore, induced resistance (IR) could be an alternative approach for improving wheat productivity by avoiding losses caused by biotic stresses.

Advances in research efforts involving IR in plants have resulted in the discovery and identification of new class of chemical inducers with better efficacy, stability and environment benevolent nature in comparison to existing traditional agrochemicals (Yassin *et al.*, 2021; Sandroni *et al.* 2020). There are several reports that highlight the role of IR compounds in enhancing agricultural productivity by reducing the yield losses and by enhancing the stress tolerance levels (Sandroni *et al.*, 2020; Oliveira *et al.*, 2016). A large number of compounds derived from elicitor molecules (molecules released during the first stage interactions between the plant–pathogens) have been identified (Abdul Malik *et al.*, 2020; Jamiołkowska, 2020; Wiesel *et al.*, 2014; Angelova *et al.*, 2006). Biochemically, elicitors reported as RI compounds represent carbohydrate polymers, glycoproteins and lipids. They are reported to be either synthesized by microorganisms or can be extracted from the cell walls of plant, fungi and bacteria (Sandroni *et al.* 2020; Abdul Malik *et al.*, 2020, Thakur and Sohal, 2013). S-methylbenzo [1,2,3]thiadiazole-7-carbothiate (acibenzolar-S-methyl) (ASM) was the first molecule released as IR compound at commercial scale for agriculture use (Lyon and Newton, 2007). Later, compounds that resemble the action of salicylic acid (SA) include 2, 6-Dichloroisonicotinic acid (INA) and ASM have also become available in the market and are currently being used in agriculture (Dewen *et al.*, 2017). The major merit of these compounds is that by using these, the number of sprays of conventional fungicides may be reduced (Sandroni *et al.*, 2020). All the resistance inducers (RIs) have few characteristic features which include their preventive mode of action and augmentation of natural plant defense system. Additionally, they also help in reducing the number and frequency of preventive fungicide applications for the effective and precise management of biotic stresses (Llorens *et al.*, 2017). Usually, the phenomenon of induced resistance is operated throughout the plant cell and is strong enough to safe guard the plants from moderate level of stresses. However, it is important to mention here that, heavy inoculum pressure can breach the natural defenses of the plant (Pagán and García-Arenal, 2018), but under such situation, integrated application of plant resistance inducers (PRIs) with recommended fungicides offer complete protection (Llorens *et al.*, 2017). Further, it has been reported that, an accurate and synchronized schedule of resistance inducing compounds with traditional fungicides offers dual advantages in the form of disease severity and chemical residue reduction (Llorens *et al.*, 2017). Further, published literature also indicates that the integrated application of plant resistance PRI's with fertilizers or beneficial microbes could be a promising preventive and therapeutic option against harmful pathogens (Ons *et al.*, 2020). The amalgamation of PRIs in any disease management modules, either individually or in combination with other conventional disease management tools, could be a trust worthy way for reducing the yield losses as well as chemical residue problems in the environment. In summary, the present article provides an up to date knowledge of resistance inducing compounds that have been successfully tested for safeguarding wheat crop from fungal pathogens by activating the plant's own defense system.

## 2. Induced resistance (IR) and its types

In simple words, induced resistance (IR) can be defined as a physiological state of heightened plant defense where plant's basal defenses activates in robust and prompt manner to circumvent misuse of resources and to curtail tradeoffs between defenses against abiotic and biotic stresses. On the basis of elicitor nature and regulatory pathways engaged in the generation of molecules, IR can be divided into induced systemic resistance (ISR) and systemic acquired resistance (SAR) (Durrant and Dong, 2004; van Loon *et al.*, 1998). Several research evidences indicate that microbes of virulent, avirulent and nonpathogenic nature when come in contact with the plant have the ability to activate SAR (Pieterse *et al.,* 2014). Host plant and elicitors are two critical factors and act as determinant factor for deciding the specific time period required for the stimulation and establishment of SAR as a consequence of synthesis of pathogenesis-related (PR) proteins (chitinase and glucanase) and SA (Choudhary and Johri, 2009; Walters *et al.*, 2005). Principally, SAR indicates rise of salicylic acid (SA)-mediated basal resistance, while ISR represents augmentation of jasmonate/ethylene (JA/ET)-mediated basal resistance (Cortes-Barco *et al.*, 2010). Besides this, the mode of action of ISR also relies on the defense mechanisms triggered by inducing agents. Research evidences also revealed that multiple defense mechanisms expressed in response to ISR stimulation are tightly linked with the rapid production and accumulation of chitinases, peroxidases and β-1, 3-glucanases (Anand *et al.*, 2007; Maurhofer *et al.*, 1994). Another important trait of ISR includes wide number of pathogens that can be regulated by a single inducing agent (Hoffland *et al.*, 1996). Overall, it seems that ISR triggers as a consequence of multiple mechanisms which operate altogether to provide protection against spectrum of plant pathogens. Both 'induced responses' and 'induced resistance' have been extensively explored, well documented and are reported in wide range of plant species (Puyam *et al.*, 2019; Silva *et al.,* 2018; Alexandersson *et al.,* 2016; Srivastava *et al.*, 2012; Kashyap and Dhiman 2009; Heil and Bostock, 2002; Karban and Baldwin, 1997). The major advantage of PRIs in comparison to agrochemicals is the compatibility of PRIs with biocontrol agents (BCA). Another advantage offered by PRIs is the induced resistance (IR) via priming, which results in an augmentation of basal defense resistance regulated by a series of defense related plant genes (Bruce *et al.*, 2017; Ahmad *et al.*, 2010). Owing to these features, IR provides a durable form of protection, since the augmentation of multigenic resistance is difficult to breach by pathogens (Ahmad *et al.*, 2010; Gardner *et al.*, 1999). Thus, the potential of broad-spectrum disease management using the plant's self-resistance modules has led to amassed motivation in the identification, characterization and development of agents which can mimic and act as natural inducers of resistance.

## 3. Resistance inducing compounds and their applications

The resistance potential of wheat crop against fungal pathogen, infection can be augmented by exogenous treatment of a series of biotic and abiotic inducers (Table 1). Biotic inducers include infection by hemibiotropic pathogens, plant-growth-promoting microbes and treatment with non-pathogens or cell wall fragments (Walters *et al.*, 2013; Kashyap *et al.*, 2017). Another category of abiotic inducers encompasses the chemical compounds that act at innumerable points in the signaling pathways associated with disease resistance as well as other forms of abiotic stresses such as drought, heat shock and pH stress etc. (Walters *et al.*, 2005). Most importantly, resistance triggered by resistance inducer (RI) compounds is broad-spectrum, durable and long lasting (Yassin *et al.*, 2021; Věchet and Šerá *et al.*, 2015).

### *3.1 Chemicals and non-biological inducers*

### *3.1.1 Chitosan*

Chitosan is discovered by Rouget (1859) and structurally composed of β-(1-4)-linked d-glucosamine and N-acetyl-d-glucosamine and randomly present within the polymer. In fungi, chitosan is present in the cell walls of Zygomycetes fungi (Batista *et al.*, 2018; Raafat and Sahl, 2009). The characteristics properties of chitosan include biocompatibility, non-toxicity, low allergenicity and biodegradability. In addition, it is cationic in nature. Several published articles comprehensively portrayed the practical applications of chitosan in plant growth promotion and protection (Maluin and Hussein, 2020; Kashyap *et al.*, 2015). It has been documented that chitosan chelates the essential elements required for the optimal growth of plant pathogens and also deposits on plant and pathogen surface and forms biofilms that results in the deprivation of the nutrient availability for microorganisms and thereby restricting the normal growth of the pathogens (Xing *et al.*, 2015). More interestingly, the characteristics feature of chitosan to induce resistance in plants is tightly associated with its elicitor-like properties, which trigger the early activation of pathogenesis-related proteins and augment the plant resistance. For instance, in case of wheat, application of chitosan provides protection

**Table 1:** Principle studies illustrating potential of resistance inducing (RI) compounds in stimulating wheat defense system against fungal pathogens

| Resistance Inducer | Disease | Pathogen | Effective concentration | Phenotypic effect | Reference |
|---|---|---|---|---|---|
| Acibenzolar-S-methyl | Wheat blast | *Pyricularia oryzae* | 0.5 mM | Positive regulation of the resistance of wheat to blast; reduction of lesions per $cm^2$ of leaf area; and area under blast progress curve | Rios *et al.* (2014) |
|  | Wheat blast | *P. oryzae* | 300 mg $L^{-1}$ | Positive regulation of the resistance of wheat to blast; reduction of lesions per $cm^2$ of leaf area; and area under blast progress curve | Rios *et al.* (2014) |
| Ascorbic acid | Leaf blotch | *M. graminicola* | 50 mg $L^{-1}$ | Inhibition of *in planta* spore germination, hyphal growth, leaf penetration, substomatal colonization and infection level reduction by more than 75% | Somai-Jemmali *et al.* (2015) |
| Benzo(1,2,3)thiadiazole-7-carbothioic acid S-methyl ester | Powdery mildew | *B. graminis* f. sp. *tritici* | 30 g $ha^{-1}$ | 35% reduction in disease symptom expression | Gorlach *et al.* (1996) |
|  | Karnal bunt | *T. indica* | 1 mM | Augmentation of wheat protection from *Tilletia indica* infection | Kashyap *et al.* (2018a) |
|  | Leaf blight | *Zymoseptoria tritici* | 2 mM | Delayed *Z. tritici* growth during the early seed germination stage | Bellameche *et al.* (2020) |
| Benzothiadiazole | Powdery mildew | *Blumeria graminis* f. sp. *tritici* | 1.2 mM | 65 % reduction in powdery mildew infection | V chet and Šerá (2015) |
| Calcium phosphate | Spot blotch | *B. sorokiniana* | 1.63 g of per kg soil | Inhibition of fungal growth and limited number of epidermal cells showing browning | Domiciano *et al.* (2013) |
| Calcium silicate | Wheat blast | *M. oryzae* pathotype *Triticum* | 300 kg $ha^{-1}$ (pre-plant furrow application) and 1 ton $ha^{-1}$ as top soil application | Reduction in incidence and severity of blast diseases in the spike | Pagani *et al.* (2014) |
|  | Spot blotch | *B. sorokiniana* | 0.30 g / Kg of soil | 58.5% reduction in the AUDPC of spot blotch, rise in the incubation period and decline in the number of lesions per $cm^2$ of leaf area and disease severity | Domiciano *et al.* (2010) |
|  | Wheat blast | *P. oryzae* | 1.25 g $Kg^{-1}$ of soil | 31 % reduction in the area under blast progress curve and 45% reduction in the number of disease lesions per $cm^2$of leaf area | Filha *et al.* (2011) |

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| | Powdery mildew | *B. graminis* f. sp. *tritici* | 3 tonnes ha$^{-1.}$ | Disease severity reduction along with restricted fungal colonization on leaf tissue | Bélanger *et al.* (2003) |
| | Powdery mildew | *B. graminis* f. sp. *tritici* | 4480 kg ha$^{-1}$ | Suppression of powdery mildew infection with yield increase | Provance-Bowley *et al.* (2010) |
| Chitosan | *Fusarium* head blight | *F. graminearum* | 1000 ppm | Reduction in disease severity with dehydration and deformation of mycelium | Kheiri *et al.* (2016) |
| Chitosan + liquid seaweed extract (LSE) from brown macroalga | *Fusarium* head blight | *F. graminearum* | 0.001% | Reduction in disease severity | Gunupuru *et al.* (2019) |
| Chitosan + *P. fluorescens* MKB 158 | *Fusarium* head blight | *F. graminearum* | chitosan (1000 µ g l$^{-1}$) and *P. fluorescens* MKB 158 (log CFU ml$^{-1}$= 7.0) | 74% reduction in the severity of FHB symptom development | Khan and Doohan (2009) |
| Chitosan Hydrochloride | *Fusarium* head blight | *F. graminearum* | 0.5% | Suppression of *Fusarium graminearum* growth and virulence; enhanced wheat growth, development and SAR activation | Francesconi *et al.* (2020) |
| Glycerol | Powdery mildew | *B. graminis* f. sp. *tritici* | 3% | Induced powdery mildew resistance in wheat by regulating fatty acid metabolism, plant hormones cross-talk, and expression of pathogenesis related genes | Li *et al.* (2020) |
| Glycine betaine | Powdery mildew | *B. graminis* f. sp. *tritici* | 0.3 M | 30 % reduction in powdery mildew infection in wheat | V chet and Šerá (2015) |
| Heptanoyl salicylic acid | Powdery mildew | *B. graminis* f. sp. *tritici* | 1 gl$^{-1}$ | 70% protection against powdery mildew infection in wheat | Muchembled *et al.* (2006) |
| Iturin A | Head blight | *F. graminearum* | 50 µg ml$^{-1}$ | Phenotypic alterations in conidia and hyphal distortion of *F. graminearum* | Gong *et al.* (2015) |
| Jasmonic acid | Leaf blotch | *Stagonospora nodorum* | 100 µM | Reduction in leaf blotch disease; induction of accumulation of β-1,3-glucanase and thaumatin-like proteins in wheat | Jayaraj *et al.* (2004) |
| | Wheat blast | *P. oryzae* | 0.1 mM | Reduction in the lesions per cm$^2$ of leaf area and area under blast progress curve | Rios *et al.* (2014) |
| | Karnal bunt | *T. indica* | 40 µl | Reduction in the Karnal bunt symptom development | Mandal *et al.* (2006) |

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| | Karnal bunt | *T. indica* | 1 µg µl$^{-1}$ | Stimulation of cystatin gene expression to restrict *T. indica* invasion | Dutt and colleagues (2011) |
| | *Fusarium* head blight | *F. graminearum* | 1 mM | Suppression of growth and head blight symptom expression by stimulating cross talk between defense related genes | Qi *et al.* (2016) |
| | Common bunt | *T. caries* | $10^{-7}$ M | Improving wheat resistance by stimulating $H_2O_2$ accumulation and defense related proteins (oxalate oxidase, peroxidase and proteinase inhibitor) in wheat seedlings | Yarullina *et al.* (2018). |
| Magnesium silicate | Wheat blast | *M. oryzae* pathotype *Triticum* | 300 kg ha$^{-1}$(pre-plant furrow application) and 1 ton ha$^{-1}$ as top soil application | Reduction in incidence and severity of blast disease in the spike | Pagani *et al.* (2014) |
| Methyl jasmonate | Leaf rust | *Puccinia recondita* f.sp. *tritici* | | Reduction in disease severity due to rapid and enhanced activities of POX, CHI and phenolic compounds | Haggag and Abd-El-Kareem (2009) |
| | Powdery mildew | *B. graminis* f. sp. *tritici* | 1 mM l$^{-1}$ | Reduction of infection of *Blumeria gramimis* f.sp. *tritici* in wheat | Duan *et al.* (2014) |
| | Crown and root rot disease. | *F. culmorum* | 1 mM | Augmentation in the activities of pathogen responsive defense-related enzymes, total phenols and callose contents in wheat host | Motallebi *et al.* (2015) |
| | Dwarf bunt | *Tilletia controversa* | 20 mM | Activation of defense genes to eliminate the fungal pathogen movement to upper parts of the plants | Muhae-Ud-Din *et al.* (2020) |
| Milsana® (plant extract of giant knotweed) | Powdery mildew | *B. graminis* f. sp. *tritici* | 0.3% | 85 % reduction in powdery mildew infection | Randoux *et al.* (2006) |
| | Powdery mildew | *B.* graminis f. sp. *tritici* | 100g L$^{-1}$ | 72 % reduction in powdery mildew infection | Věchet and Šerá (2015) |
| Mycosubtilin + surfactin + fengycin | Septoria leaf spot | *Zymoseptoria tritici* | 4.5 mg L$^{-1}$ | Significant inhibition of fungal growth | Mejri *et al.* (2017) |
| NaSA and INA | *Fusarium* head blight | *F. graminearum* | 10 mM | Reduction in FHB severity | Zhang *et al.* (2007) |

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| Oligogalacturonides | Powdery mildew | *B. graminis* f. sp. *tritici* | 5 g L$^{-1}$ | 57-58% reduction in the infection level | Randoux *et al.* (2010) |
| Plipastatin A | Head blight | *F. graminearum* | 100 µg ml$^{-1}$ | Phenotypic alterations in conidia and hyphal distortion of *F. graminearum* | Gong *et al.* (2015) |
| Potassium silicate | Wheat blast | *M. oryzae* pathotype *Triticum* | 20 g l$^{-1}$ | Reduction in the leaf blast severity | Cruz *et al.* (2011) |
| | Wheat blast | *M. oryzae* pathotype *Triticum* | 1ml l$^{-1}$ | Reduction in the incidence and severity of blast disease in the spike | Pagani *et al.* (2014) |
| Saccharin | Powdery mildew | *B. graminis* f. sp. *tritici* | 3–5 mM | Significant reduction of powdery mildew infection in wheat | Phuong *et al.* (2020) |
| | Dwarf bunt | *T. controversa* | 100 µM | Activation of wheat defense genes to eliminate the fungal pathogen movement to upper parts of the plants | Muhae-Ud-Din *et al.* (2020) |
| | Leaf blotch | *Stagonospora nodorum* | 1 mM | 56 % reduction in the incidence of leaf blotch disease; Rapid accumulation of β-1,3-glucanase and thaumatin-like proteins in wheat | Jayaraj *et al.* (2004) |
| | *Fusarium* head blight | *F. graminearum* | 100-400 mM | Reduction in efficiency of fungus germination, growth and symptom development | Qi *et al.* (2012) |
| | Powdery mildew | *B. graminis* f. sp. *tritici* | 1 mM | 25 % reduction in the powdery mildew infection | Věchet and Šerá (2015) |
| | Karnal bunt | *T. indica* | 1 mM | Augmented wheat protection from *T. indica* infection | Kashyap *et al.* (2018a) |
| | Common bunt | *T. caries* | 0.05 mM | Imparting resistance in wheat against fungus by stimulating the transcriptional activity of the genes encoding peroxidase, oxalate oxidase, and proteinase inhibitors | Yarullina *et al.* (2018) |
| | Spot Botch | *B. sorokiniana* | 10-5 M | Impart resistance against fungus in wheat and reduce the need of one or more foliar spray at boot leaf stage of the crop | Devi *et al.* (2018) |
| Silicon | Powdery mildew | *B. graminis* f. sp. *tritici* | 1.7 mM | 80% reduction in *B. graminis* f. sp. *tritici* infection in wheat seedlings | Guével *et al.* (2007) |
| Silicon | Wheat blast | *M. oryzae* pathotype *Triticum* | 2 mM | 70% reduction in the leaf blast severity and 78% reduction in the area under diseases progress curve | Aucique Perez *et al.* (2014) |

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| Sodium diethyldithiocarbamate | Powdery mildew | *B. graminis* f. sp. *tritici* | 10 mM | Enhancement in wheat immunity and reduction the severity of disease | Li *et al.* (2020) |
| Tramesan (α-heteropolysaccharide) | Leaf blotch | *Stagonospora nodorum* | 3.3 μM | Protects wheat by eliciting plant defenses and reduce infection by 99 and 25 % under glass house and field conditions | Scala *et al.* (2020) |
| | Leaf blotch | *Septoria tritici* | 3.3 μM | Protects wheat by eliciting plant defenses and reduce infection by 75 and 30 % under glass house and field conditions | Scala *et al.* (2020) |
| Trehalose | Powdery mildew | *B. graminis* f. sp. *tritici* | 15 g L$^{-1}$ | 50- 95% protection from fungal infection depending on the number and frequency of spray | Reignault *et al.* (2001) |
| Z-3-hexenyl acetate | *Fusarium* head blight | *F. graminearum* | 70 μL | Reduced fungal growth *in planta,* however, produced more deoxynivalenol | Ameye *et al.* (2015) |
| β-aminobutyric acid | Karnal bunt | *T. indica* | 1 mM | Enhanced level of wheat protection from *T. indica* infection | Kashyap *et al.* (2018a) |
| | Septoria leaf spot | *Zymoseptoria tritici* | 15 mM | Delayed *Z. tritici* growth during the early seed germination stage | Bellameche *et al.* (2020) |

from *F. graminearum* infection (Reddy *et al.*, 1999). It has been observed that chitosan can also stimulate induced resistance in winter wheat in response to the challenge inoculation of snow mould pathogen *Microdochium nivale* (Hofgaard *et al.*, 2005). The similar group of researchers also documented that exogenous application of chitosan on wheat increased chitinase gene expression, but chitosan molecule also showed growth inhibition of *M. nivale* under *in vitro* experimentation (Hofgaard *et al.*, 2005). Therefore, these research evidences clearly indicate the possibility of dual action of chitosan (i.e. induced resistance and direct antifungal action) in restricting the growth of *M. nivale* on wheat. Additionally, Hofgaard *et al.* (2005) also pointed out that these disease protection levels vary with disease pressure. Khan and Doohan (2009) evaluated the efficacy of chitosan for the management of *F. graminearum* and its associated mycotoxin contamination in wheat grains. They demonstrated that foliar spray of chitosan (1 mg ml$^{-1}$) provided 81% and 76% reduction in expression of head scab disease symptoms in greenhouse and field experiments, respectively. Further, they also observed ≥74% reduction in the concentration of deoxynivalenol (DON) toxin under both glasshouse and field conditions in response to foliar spray of chitosan. Later, research evidences regarding the efficacy of chitosan as a seed treatment to elicit resistance against *F. graminearum* in durum wheat has been published by Orzali *et al.* (2014). The results of both field and greenhouse trials revealed that seed treatment with chitosan (0.5%) provided effective protection against the root and foot rot disease caused by *F. graminearum.* Kheiri *et al.* (2016) also provided supporting evidences regarding the inhibitory effect of chitosan against *F. graminearum* infection in wheat. They reported that foliar spray of both chitosan (0.1%) and chitosan based nanoparticles (0.5%) can be applied as antimicrobial agents owing to their biocompatibility, antimicrobial potential and a lower toxicity towards mammalian cells. Recently, Francesconi *et al.* (2020) tested the effect of foliar application of chitosan (0.5%) at the flag leaf stage of wheat that resulted in the significant rise in plant growth and nitrogen balance index. However, it suppressed head scab disease caused by *F. graminearum* by down regulating the transcript of key genes associated with the cell growth, respiration, virulence, and trichothecene biosynthesis of the fungus. On parallel lines, Buzón-Durán *et al.* (2020) also demonstrated antifungal activity of chitosan oligomers

(COS)–amino acid conjugate complexes (1500 µg ml$^{-1}$) against *F. culmorum.* They noticed that COS–amino acid conjugate complexes reduced the head blight symptom development by 50-83.5% in *Triticum spelta.* These aforementioned research evidences clearly signify that the prior induction of resistance by non-toxic chitosan in plants has not only opened new frontiers for an eco-friendly disease management but also reduced the use of conventional health hazardous chemicals for plant disease.

### *3.1.2 Salicylic acid (SA) and its derivatives*

Salicylic acid (SA) plays an essential role in regulating plant defense system and assisting plants to build resistance against biotrophic and hemibiotrophic pathogens (Grant and Lamb, 2006). SA and its functional analogs [e.g. β-amino-n-butyric acid (BABA), 2, 6-dichloroisonicotinic acid (INA), and benzothidiazoles (BTH)] are the most commonly investigated chemical group of molecules for inducing disease resistance in plants (Kashyap *et al*., 2018b; Kim *et al*., 2013; Conrath, 2006). Historically, the role of SA and its analogues (BTH) in augmentation of defense gene expression has been established by Görlach *et al.* (1996), while studying the effect of BTH (0.3 mM) on wheat seedlings between 4-7 days prior to challenged inoculation with powdery mildew fungus, *B. graminis* f. sp. *tritici* (Görlach *et al*., 1996). In this study, they also noticed that BTH is beneficial in inducing resistance in wheat against multiple pathogens such as *Septoria* spp. and *Puccinia recondita* causing leaf blight and brown rust disease, respectively. More interestingly, they observed that a single application of BTH (30g ha$^{-1}$) is adequate to provide complete protection against powdery mildew fungus (*B. graminis* f. sp. *tritici*) in wheat throughout the season. Since then, this molecule has been tested and evaluated against a series of pathogens and host systems. As a consequence of encouraging results of resistance induction against a wide range of pathogens, this molecule has been released commercially in Europe and USA under the trade name Bion® and Actigard®, respectively (Eyles *et al*., 2010). It is important to mention here that the under field conditions, the performance of chemical elicitors varied in spatio-temporal manner and clearly evident in case of benzothiadiazoles (BTH), where plant host respond differently at different time points in response to chemical elicitor application (Bektas and Eulgem, 2015). On parallel lines, Heier *et al.* (2005) studied the effect of nitrogen fertilization, fungicides and resistance induction on *Fusarium* head blight (FHB) and related mycotoxin accumulation in wheat in response to BTH and *Spirulina platensis* application and reported equivalent effectiveness of PRI compounds and traditional fungicides. Further, they also noticed that excessive N-fertilization has the ability to influence the efficacy of BTH and *Spirulina platensis* as mycotoxin levels rise in wheat grains, even under hostile conditions for *Fusarium* spp. The observations of environment influence on resistance induction in plants were supported by the study of Pasquer *et al.* (2005), where they reported a general high level expression of defense genes in plants grown under normal field conditions than glasshouse grown plants. Zhang *et al.* (2007) evaluated SA, 2, 6-dichloroisonicotinic acid (INA), β-aminobutyric acid (BABA) and sodium salt of salicylic acid (NaSA) for the management of FHB disease in wheat. The results revealed that foliar spray of NaSA and INA at 10 mM on wheat heads at three days prior to pathogen challenge with *Gibberella zeae* significantly decline the severity level of disease. Further, they also noticed that 1 mM concentration of NaSA, INA, and BABA is also equally effective in achieving same level of reduction in FHB disease severity, when applied on wheat head initiation stage at ten days prior to challenge inoculation with *G. zeae.* Interestingly, induction of FHB resistance in wheat is also possible with similar results, even at much lower concentration (0.1 mM) of INA. Thabet (2008) experimentally showed that BTH and SA inhibit the leaf rust infection in wheat by stimulating the synthesis of pathogenesis related (PR) protein and other peroxidase and phenolic compounds. Later, the effect of BTH (1 mM) and SA (1000 µg ml$^{-1}$) on ISR was investigated by Al-Maaroof *et al.* (2014) in wheat against yellow rust disease incited by *Puccinia striiformis* f. sp. *tritici.* They reported that BTH (1 mM) and SA (1000 µg ml$^{-1}$) are effective in reducing the infection level of *P. striiformis* f. sp. *tritici.* Further, they also demonstrated that the resistance to *P. striiformis* f. sp. *tritici* has been induced by these chemical inductors in wheat genotypes due to the rapid synthesis of peroxidase, phenylalanine ammonia-lyase (PAL) and total phenolic compound in both moderately susceptible (cv. Tamuz-2) and susceptible (cv. AL-8/70) wheat genotypes. BTH, BABA and SA at 1 mM concentration were also tested to manage Karnal bunt (*T. indica*) under glass house conditions by Kashyap *et al.* (2018b). Results indicated that 1 mM concentration of these compounds is adequate to suppress *T. indica* infection in wheat grown under greenhouse conditions. Moreover, elevated accumulation of *PDF1.2, PR1* and *PR5* with all tested compounds at three days post-inoculation was also noticed. Results suggest that these compounds primed wheat seedlings to show prompt, rapid and strong response to *T. indica* infection by triggering SA and JA/ ET mediated defense pathway. Yarullina *et al.* (2018) also observed stimulatory effect of SA (0.05 mM) in imparting resistance against *T. caries* by stimulating the accumulation of $H_2O_2$ and transcriptional activity of the genes encoding peroxidase, oxalate oxidase and proteinase inhibitors. Devi *et al.* (2019) reported that seed soaking with SA ($10^{-5}$ M) induced resistance against *B. sorokiniana* fungus in wheat. Further, they also mentioned that for prolonged effect of tested inducers on disease resistance requires one or more foliar sprays at boot leaf stage of the crop. Muhae-Ud-Din *et al.* (2020) showed that exogenous application of SA (20mM) was able to reduce the infection of *T. controversa* in wheat roots, coleoptiles and anther tissues of a highly susceptible wheat cultivar (cv. Dongxuan 3). Bellameche *et al.* (2020) explored the prospect of chemical inducer application in the management of *Zymoseptoria tritici* infection on wheat. Their study concluded that BABA (15 mM) applied as a soil-drench effectively safeguards the wheat seedlings from *Z. tritici* infection. However, soil-drenching of wheat seedlings with BTH (2 mM) results in delayed *Z. tritici* growth during the early seed germination stage.

Heptanoyl salicylic acid (HSA) obtained by esterification of 2-OH benzoic acid with heptanoic acid have been reported to provide protection in wheat against powdery mildew fungus. Muchembled and colleagues (2006) demonstrated that single foliar spray of 1 $gl^{-1}$ solution of HSA is able to provide 70% protection against *B. graminis* f. sp. *tritici* infection in wheat plants.

### 3.1.3 Jasmonic acid

Jasmonic acid (JA) plays an imperative part in enhancing plant resistance to diverse types of plant pathogens. The efficacy of JA in stimulating defense resistance against *Stagonospora nodorum* fungus in wheat has been studied by Jayaraj *et al.* (2004). The results of the study indicated that one day prior to challenge inoculation of *Stagonospora nodorum*, JA (100 µM) provided 56% reduction in the incidence of leaf blotch disease in wheat seedlings under greenhouse conditions. Similarly, Dutt and colleagues (2011) treated resistant (HD-29) and susceptible (WH-542) wheat varieties with JA (1 µg $\mu l^{-1}$) followed by artificially challenged inoculation of *T. indica* sporidial suspension to study its influence on Karnal bunt disease development. They observed that exogenous application of JA helps in improving wheat defense system against KB by stimulating cystatin gene expression. Similar report of defense activation in susceptible wheat varieties (cv. Chinese Spring and Pumai 9) by exogenous application of methyl jasmonate (MeJA; 1 mM $l^{-1}$) against powdery mildew exposure has been published (Duan *et al.*, 2014). Further, it has been noticed that after exogenous application of MeJA, it passes into plant tissue via stoma and trigger esterase driven hydrolysis in the cytoplasm to produce endogenous JA, which is responsible for long-distance signal communication between plants to activate defense system against *B. gramimis* f.sp. *tritici* and reached maximum within 2- 5 h post-inoculation. Besides this, it has been observed that JA also induce elevated expression level of *PR1*, *PR2*, *PR3*, *PR4*, *PR5*, *PR9*, *PR10* and *Ta-JA2* genes in wheat plants. Motallebi and team (2015) also explored the effect of MeJA (1 mM) in wheat genotypes after artificial exposure of *F. culmorum* fungus responsible for crown and root rot disease. They observed augmented activities of pathogen responsive defense-related enzymes (PAL, SOD, POX, CAT, LOX and PPO), total phenols and callose (glucose residues linked together through β-1,3-linkages) contents in wheat host. Exogenous application of JA (1 mM) is also reported to suppress *F. graminearum* growth and head blight symptom expression in wheat by triggering cross talk between a series of defense related genes (*ATB2*, *ExpB6*, *LEA Td16*, *PR1*, *Pdf*1.2 and *PR4*) (Qi *et al.,* 2016). Protection potential of JA in wheat plants infected with *T. caries* has been demonstrated by Yarullina *et al.* (2018). Further, they highlighted that soaking of wheat seeds for three hours in JA ($10^{-7}$ M) helps in improving resistance against pathogen by stimulating accumulation of defense related proteins (oxalate oxidase, peroxidase and proteinase inhibitor) in plant tissues. Recently, Muhae-Ud-Din *et al.* (2020) revealed that the invasion capability of *T. controversa* decreased in temporal manner after root and seedling treatment with MeJA (100 µM) by activating *COI1-1* and *COI1-2* genes mediated defense signaling system. The above mentioned research evidences clearly supported the hypothesis that JA and its analogues protect wheat seedlings by activating defense signaling systems in spatio-temporal manner.

### *3.1.4 Lipopolysaccharides*

Lipopolysaccharides (LPS) and lipooligosaccharides are generally found in the exterior surface of Gram negative bacteria and are reported to impart disease resistance against diverse types of plant pathogens (Ranf, 2016; Erbs and Newman, 2003). For instance, Ortmann and Moerschbacher (2006) reported the spent growth medium and *Pantoea agglomerans* derived exopolysaccharides (EPS) served as important priming molecules to impart stress resistance in suspension-cultured wheat cells. Similar protection evidences in wheat against *P. recondita* f. sp. *tritici* has been achieved, when culture filtrate of *P. agglomerans* were sprayed on wheat leaves (Kempf and Wolf 1989). Similarly, lipopeptides (surfactin, mycosutilin and fengycin) produced by *Bacillus subtilis* have been reported to induce resistance and protect wheat from *B. graminis* f.sp. *tritici* infection (Khong *et al*., 2012). Under field conditions, surfactin and mycosubtilin provided 41% and 44% protection, respectively, when sprayed on wheat leaves at rate of 4g ha$^{-1}$. Here, it is important to mention that no direct antifungal effect of LPS was recorded against conidial germination of *B. graminis* f. sp. *tritici*, irrespective of the tested concentrations (Khong *et al*., 2013). Further, they also performed gene expression analysis to investigate elicitor and priming effects of surfactin and mycosubtilin on the activation of defense-related genes (*POX2, POX381, LOX*, AOS and *PR1*) in response to pathogen inoculation. Interestingly, only surfactin displayed stimulation in the expression of defense-related genes in response to *B. graminis* f.sp. *tritici* exposure, while mycosubtilin did not exhibit any priming effect (Khong *et al*., 2013). These research evidences clearly illustrate that the role of LPS in disease resistance induction through elicitation or augmentation depends on the targeted pathogen and LPS type. In addition to rhizospheric plant growth promoting rhizobacteria (PGPRs), cyclic lipo-polysacharides (CLP) production from phyllospheric microbes have also been reported for resistance induction. For instance, *Bacillus liquefaciens* isolated from wheat spikes infected with *Fusarium graminearum* has been reported to synthesize CLPs (iturin, plipastatin and surfactin) with strong inhibitory activities against *F. graminearum* (Gong *et al*., 2015). The optical and fluorescence microscopy analysis clearly showed the significant phenotypic alterations in conidia and hyphal distortion of *F. graminearum*in response to iturin A (50 µg/ml) or plipastatin A (100 µg/ml) treatment. Mejri *et al.* (2017) also explored the antagonistic nature of CLPs (mycosubtilin, surfactin and fengycin) derived from *Bacillus subtilis* at a concentration of 100 mg L$^{-1}$ on wheat (cv. Dinosor and Alixan) against *Zymoseptoria tritici* and recorded significant reduction of disease severity, when applied two days prior to fungal inoculation. Further, they also got success in achieving 82% disease reduction by applying mycosubtilin+surfactin containing formulations on Dinosor genotype. Further, *in vitro* and *in planta* research evidences also support the conclusion of significant inhibition of fungal growth by mycosubtilin based formulations. However, it is worth to mention here that 1.4 mg L$^{-1}$concentration of both mycosubtilin and mycosubtilin + surfactin and 4.5 mg L$^{-1}$ of mycosubtilin + surfactin + fengycin showed maximal inhibitory activity and thus indicating that efficacy of these products depends largely on antagonistic activity. In contrast, surfactin and fengycin did not show any direct antifungal action against the fungus and therefore signifying their role as resistance inducers rather than biofungicides against *Z. tritici* in wheat. On parallel lines, Mire and colleagues (2018) also demonstrated that surfactin extract of *B. amyloliquefaciens* S499 impart protection against *Z. tritici* in wheat by triggering both SA- and JA mediated defense system. It has been observed that surfactin is able to provide 70% protection in wheat against *Z. tritici* and equivalent in antagonistic nature of commercialized elicitor product, Bion®50WG (Mire *et al*., 2018). In summary, the aforementioned studies clearly indicate the potential of LPS to protect wheat seedlings against fungal infection and their involvement in the activation of defense signaling pathway.

### *3.1.5 Proteins and peptides*

A plenty of studies have revealed that proteins and peptides play an important role in disease-resistance against fungal pathogens in plants. For instance, cell wall proteins derived from *Pythium oligandrum* is reported to decline the infection and symptoms caused by *F. graminearum* on wheat spikelets (Takenaka *et al*., 2003). This concept has been developed and commercialized by Novartis (now Syngenta) as Bion® (Kessmann *et al*., 1996). Research evidences highlighted that this compound is highly effective and provides protection up to 10 weeks against powdery mildew infection in wheat (Görlach *et al.*, 1996). Besides this, Reignault and team (2004) also evaluated the efficacy of other proteins and peptides compound such as Iodus 40®, Milsana®, salicylyl heptanoate, trehalose, and pectic oligosaccharides against powdery mildew disease of wheat and attained significant reduction in the level of infection after application of these compounds. Another peptide 'syringolin' isolated from *P. syringae* pv. *syringae* bacterium (Wäspi *et al.*, 1998) was also studied for inducing resistance in wheat against fungal infection. It has been observed that Syringolin A induces resistance in wheat towards powdery mildew fungus by accumulating defense gene transcripts when applied before inoculation (Wäspi *et al.*, 2001). Naguib *et al.* (2018) investigated the efficacy of wheat seed priming with defensin-like protein to protect wheat against *F. oxysporum* infection. They observed that priming with defensin protein helps the wheat seedlings to overcome the *Fusarium* infection by improving the antioxidant system as well as hydrolysis processes. Further, they also confirmed that defensin priming enhanced the phosphatase and amylase activities and helped in the solubilization of phosphate and sugar, which in turn served in the augmentation of the metabolic activity of the defensin-primed plants.

### *3.1.6 Trehalose*

Trehalose (TH; α-D-glucopyranosyl-[1–1]-α-D-glucopyranoside) is a natural non-reducing disaccharide. It has been reported to present in diverse types of living organisms including fungi. Several researches revealed that trehalose is able to impart resistance against biotic and abiotic stresses in plants (Yogita *et al.* 2015; Luo *et al.*, 2021; Sadak *et al.*, 2019; Drennan *et al.*, 1993). For instance, significant decline in infection intensity of *B. graminis* f. sp. *tritici* fungus have been observed in response of exogenous application of trehalose (Reignault *et al.*, 2001). It has been reported that wheat plants sprayed with a trehalose solution (15 g L$^{-1}$), 48 hours prior to inoculation with *B. graminis* f. sp. *tritici* provided 50-95% protection from fungal infection. However, the level of protection depends on the number and frequency of trehalose solution spray (Reignault *et al.*, 2001). Later, Tayeh *et al.* (2014) also explored the priming effect of trehalose in wheat against powdery mildew infection and noticed that exogenous application of trehalose enhanced the expression level of multiple types of defense related genes (e.g. *chi*, *chi1*, *chi4* precursor, *PR1* and oxalate oxidase). Further, they also noticed that trehalose spraying may alter the lipid metabolism and boost wheat defense system by enhancing lipoxygenase and lipid-transfer protein (LTP) gene expression in wheat (Tayeh *et al.*, 2014). These limited and preliminary investigations clearly indicate the potential of exogenous application of trehalose to protect wheat plants from fungal infection.

### *3.1.7 Silicon*

There are many recent reports which highlighted the role of silicon (Si) in reducing disease severity levels in plants by different means which includes: i) averting pathogen ingression via structural reinforcement; ii) hampering pathogen colonization through activation of SAR; iii) inhibiting pathogen by triggering production of antimicrobial compounds; and iv) activation of multiple signaling cascades associated with the augmentation of defense-related gene expression (Islam *et al.,* 2020; Wang *et al.*, 2017; Remus-Borel *et al.*, 2005). The prime advantage provided by Si in reference to plant resistance against fungal infections is the accumulation of Si in epidermal tissue followed by activation of a series of processes such as formation of complexes with organic compounds in cell walls, generation of phenolic compounds and other compounds such as phytolexin, glucanase and peroxidase for regulating pathogenicity as well as other stress-related gene expression, which ultimately lead to prevent pathogen invasion and colonization in plant cell (Sakr, 2016; Belanger *et al.*, 2003). Bélanger and associates (2003) noticed that that exogenous application of Si amendments in the form of nutrient solution or calcium silicate slag provided protection against *B. graminis* f.sp. *tritici* infection in wheat. Further, it has been demonstrated that epidermal cells of plants supplied with Si helps to restrict the fungus growth by arresting papilla formations. Moreover, it has been observed that phenolic material not only stacked along the cell wall, but also associated with altered integrity of haustorian and collapsing of conidial chains of *B. graminis* f.sp. *tritici* in Si primed plants. Si (100 mg L$^{-1}$) amendment in soil reported to enhance wheat tolerance against diseases incited by *B. graminis* f.sp. *tritici*, *Phaeosphaerian odorum* and *P. recondita* (Rodgers-Gray and Shaw, 2004). Rémus-Borel and colleagues (2005) highlighted that wheat plants treated with Si produce antifungal aglycones metabolites in response to *B. graminis* f.sp. *tritici* infection than plants deprived of Si treatment. Later, Guével *et al.* (2007) documented that wheat roots treated with Si (1.7 mM) resulted in the reduction of *B. graminis* f.sp. *tritici* infection by 80%. Chain *et al.* (2009) revealed that *B. graminis* f. sp. *tritici* infection can alter about 900 genes in wheat seedlings. However, in case of Si-primed wheat seedling, they noticed very minor alterations in gene expression when exposed to fungal infection, concluding that Si is helpful in preventing the stress triggered by *B. graminis* f. sp. *tritici* infection in plant (Chain *et al.*, 2009). Further, disease protection evidences of Si-amendments in soil against wheat blast disease have been provided by Filha *et al.* (2011). They demonstrated that the area under blast progress curve and the number of lesions significantly reduced in response to Si treatment in wheat, however, incubation period of *Pyricularia grisea* was significantly enhanced by 28.2% in case of Si-treatment. They also confirmed that augmentation of chitinase and peroxidase activity defined the potential of Si to reduce wheat susceptibility to blast disease. Sousa *et al.* (2013) revealed that exogenous application of Si restricts the hyphal penetration of *P. oryzae* upto the first-invaded epidermal cell of infected wheat leaves. On parallel lines, Domiciano *et al.* (2013) also reported that exogenous application of Si delays the penetration of *B. sorokiniana* infection in the epidermal cells and thereby reduces fungal colonization in foliar tissue of wheat. Pagani and team (2014) also studied the efficacy of foliar application of $SiO_2$ (30 g $l^{-1}$) along with furrow application of calcium and magnesium silicate (300 kg $ha^{-1}$) for wheat blast disease management under field conditions. They observed that wheat plants treated as foliar or furrow application of silicate showed significantly low disease incidence, although effect was genotype dependent as BRS-264 genotype is more responsive to Si applications compared to BR-18 genotype. Later, Silva *et al.* (2015) conducted histochemical study and confirmed the involvement of Si in the potentiation of flavonoids biosynthetic pathway in wheat leaves suffered from *P. oryzae* infection. Overall, it seems that Si is involved in imparting resistance against wheat diseases by modulating interactive defense gene based signaling and enzymatic production.

### *3.1.8 Phosphites*

A plenty of published literature described phosphites as a metal salts of phosphorous acid and possess unique characters of low toxicity, high solubility, systemic (both upward and downward) translocation (Carmona *et al.* 2018; Deliopoulos *et al.*, 2010; Reuveni, 1997). Besides this, they have been reported to elicit systemic acquired resistance. For instance, potassium phosphite ($K_2HPO_3$) has been reported to control numerous plant pathogens (Kashyap and Dhiman, 2009; Lovatt and Mikkelsen, 2006; Forster *et al.*, 1998). In wheat, Cruz and team (2011) reported the role of phosphite (1500 ml $ha^{-1}$) in reducing the severity of wheat blast disease under controlled conditions. Similar positive effect of phosphite (1 ml $l^{-1}$) in protecting wheat from *Magnaporthe grisea* infection under two years' field experimentation has been reported by Pagani *et al.* (2014). Besides this, Santos *et al.* (2011) has also obtained positive effects of phosphite treatment in reducing the infection of *Drechslera tritici-repentis* and *B. sorokiniana* in wheat plants, although, the effect varied with the type of wheat species and pathosystem.

### *3.1.9 Glycerol*

Several studies recognized glycerol as an on-toxic, environmental friendly, edible and biodegradable sugar alcohol. Li *et al.* (2016) provided evidences that foliar spray application of glycerol (3%) stimulates wheat defense without showing any significant injury to wheat leaves when challenged inoculations were made with *B. graminis* f. sp. *tritici* at least 1–2 days' post glycerol treatment. Further, they also observed that exogenous treatment of glycerol stimulates the expression level of glycerol-3-phosphate (G3P), pathogenesis-related genes (*TaPR-1, TaPR-2, TaPR-3, TaPR-4*, and *TaPR-5*) and produces reactive oxygen species before fungal infection along with SA accumulation in the wheat leaves. Under field conditions, it was noticed that glycerol sprays significantly lessen powdery mildew disease severity without hampering wheat seed quality. Recent whole transcriptome analysis of wheat plants infected by *B. graminis* f. sp. *tritici* after glycerol exposure highlighted that glycerol (3%) treatment regulates fatty acid metabolism (e.g. *TaGLI1*, *TaACT1*, and *TaSSI2)* and hormones cross-talk and also supports the earlier reports of enhanced expression of *PR* genes (*PR-1*, *PR-3*, *PR-10*, *callose synthase*, *PRMS*, *RPM1*, peroxidase, *HSP70* and *HSP90)* which together can strengthen wheat resistance potentialities against *B. graminis* f. sp. *tritici* (Li *et al.,* 2020). Further, it has been noticed that glycerol induced JA and SA levels, while reduced the auxin (IAA) levels in wheat in response to fungal infection lead to the accumulation of glycerol-3-phosphate (G3P) and oleic acid (OA18:1) metabolites at the zone of infection. More importantly, it is worth mentioning here that glycerol used as a cosolvent medium for agrochemicals and therefore seems to have potent application in wheat field as an eco-compatible agrochemical to protect crop from pathogens of different nature.

### *3.2 Biological inducers*

There are lot of published documents that highlight the positive effects of microbes on disease supersession by eliciting ISR (Kashyap *et al.*, 2018b; Srivastava *et al.*, 2012). The first evidence in context to the microbe mediated induction of induced resistance (IR) to protect wheat from diseases came from pioneering research of Kilic-Ekici and Yuen (2003). These researchers experimentally illustrated that both live and heat killed cells of *Lysobacter enzymogenes* strain C3 have the ability to induce resistance against *B. sorokiniana* and reduced *Bipolaris* leaf spot development on tall fescue and wheat. Additionally, they also reported that the *L. enzymogenes* application induces non-specific and durable resistance with elevated activities of peroxidase enzymes in response to the challenged inoculation of *B. sorokiniana* inoculation on wheat (Kilic-Ekici and Yuen, 2003). Al-Ani and colleagues (2011) reported that *Pseudomonas fluorescence*, *Azospirillum irakense*, sea force extract and elsa fungicide (1 ml $l^{-1}$) have the potential to stimulate ISR and enhance wheat and barley growth when exposed to barley yellow dwarf virus infection. Further, they also observed that *P. fluorescence* is more efficient in controlling barley yellow dwarf virus in comparison to *A. irakense*, Sea force extract and Elsa. They also noticed that the effect of treatment is more pronounced in partially resistant genotypes (cv. IBA 99, Arivate and Karonea) than the susceptible ones (Hashmia and Kara).

The research evidences on the involvement of rhizosphere microbe in the induction of phenylpropanoid cascade and subsequent stimulations of ISR against *B. sorokiniana* in wheat has been provided by Singh *et al.* (2016). They revealed the up-regulation of phenylpropanoid cascade and manifold rise in the activities of PAL, peroxidase and chitinase are responsible for the induction of ISR in plants co-inoculated with *B. amyloliquefaciens* B-16 and *T. harzianum* UBSTH-501 strains. Similar observations were also noticed by Singh and Jha (2017), where plant growth promoting bacterium, *Stenotrophomonas maltophilia* SBP-9 was reported to induce ISR to protect wheat plants against *F. graminearum* by rising the activities of defense enzymes (e.g. PAL, β-1, 3 glucanase, PO and PPO). Samain *et al.* (2017) identified the potential of paenimyxin lipo-polypeptide elicitor of *Paenibacillus* sp. strain B2 in stimulating ISR against *Septoria tritici.* Further, they also mentioned that *Paenibacillus* strain B2 is able to provide more than 59% protection against *Septoria tritici* blotch by ISR triggered as a consequence of rise in expression level of *pr1*, *lox*, *Aos*, peroxidase, *oxo* and *gst* genes. Moreover, they also highlighted role of paenimyxin elicitor in providing 76% local protection against *Septoria tritici* with strong activation of defense related genes (e.g.*glu*, *lox*, *aos*, *pal*, chs, oxo, and *gst*). Here it is important to mention that *Paenibacillus* sp. PB2 strain is also reported to stimulate wheat root colonization by *Curtobacterium plantarum* strain EDS (Samain *et al.*, 2017) and therefore results in wheat growth promotion.

A large body of published literature outlines the biocontrol potentialities of *Bacillus* species, owing to their inherent abilities to be heat tolerant, produce desiccation-resistant endospores and survive under high temperature, nutrient deprived niches and unfavorable pH with better fitness and stability (Kushwaha *et al.* 2020; Solanki *et al.*, 2015; Singh *et al.* 2014; Solanki *et al.* 2012). Burkhanova *et al.* (2017) documented that *B. subtilis* and *Bacillus thuringiensis* also have the ability to stimulate ISR in wheat plants against *Septoria nodorum* infection. They observed that *Bacillus* strains have the capacity to survival endophytically with strong antagonistic interaction towards *S. nodorum* infection. Interestingly, they also reported that *B. subtilis* 26D reduce leaf blotch symptom by suppressing the catalase activity and augmenting the enzymatic activities of peroxidase and $H_2O_2$ content along with strong expression of pathogenesis related defense genes (e.g. *PR-1*, *PR-6*, and *PR-9*), which signifies the involvement of SA-dependent pathway, however, *B. thuringiensis* V-5689 and V-6066 are also observed to stimulate JA/ET-dependent pathway (Burkhanova *et al.*, 2017).

The genus *Trichoderma* has received significant prominence in past several decades because of their strong antagonistic abilities against a wide spectrum of fungal pathogens and plant growth promotion triggered by ISR (Kashyap *et al.* 2020c; Kashyap *et al.*, 2017; Rai *et al.*, 2016a; Rai *et al.*, 2016b; Srivastava *et al.*, 2012; Solanki *et al.*, 2011). Cordo *et al.* (2007) reported that *Trichoderma* spp. can protect wheat plants from *S. tritici* infection by triggering host defense. Seed coating with *T. harzianum* Th5 is reported to be the most efficacious application technique for restricting the spread of leaf blotch disease in wheat. It has been observed that seed coating of *T. harzianum* has the ability to reduce the antifungal proteolytic activity in wheat apoplast when exposed to *S. tritici* infection. Moreover, it has been noticed that endogenous germin-like protease inhibitor coordinated the proteolytic action and stimulated ISR against *S. tritici.* On parallel lines, Stocco *et al.* (2015) also reported the induction of ISR by *T. harzianum*in wheat when exposed to *Z. tritici.* The reduction of the *Septoria* leaf blotch severity due to ISR activation has been strongly supported by the fact of strong expression of defense-related proteins at sites distant from the location of the *Trichoderma* strain when challenged inoculated with fungal pathogens. Biological control of *P. graminis* f. sp. *tritici* causing stem rust in wheat has been reported by the exogenous application of *Trichoderma* spp. and arbuscular mycorrhizal (AM) fungi based formulations (El-Sharkawy *et al.*, 2018). Under natural field conditions, it has been observed that AM fungi and *Trichoderma* spp. can improve the wheat growth and yield parameters and reduce disease pressure by rapid synthesis of peroxidase, polyphenol oxidase and total phenol content (El-Sharkawy *et al.*, 2018). It is worth to indicate here that the synergistic action of *Trichoderma* spp. and AM fungi helps in inducing the SA, JA and ET regulated defense mechanisms and thus clearly explains the superiority of the combined treatment (arbuscular mycorrhizal + *T. harzianum* HL1 + *T. viride* HL5) over individual (El-Sharkawy *et al.*, 2018). Draz *et al.* (2019) mentioned that prior applications of 10,000 mg L$^{-1}$ of plant extracts (e.g. *Acalypha wilkesiana, Lantana camara, Lawsonia inermis, Melia azedarach* and *Punica granatum*) under field conditions can induce resistance in wheat against *P. triticina* by triggering the synthesis of defense-related enzymes. In nut shell, it seems that biological inducers are one of best option and moreover they are thought to open the way towards the development of bio-control tools against wheat diseases and sustainable cultivation of wheat.

## 4. Induced resistance as a component of integrated disease management (IDM)

Biological control and resistance augmentation by microbes and chemicals have a prospective future to serve as an essential element in any integrated disease management module. Research evidences indicate that ASM has been explored extensively in combination with myriad of fungicides for the management of plant diseases. More specific evidence has come from the experimentation, where a tank mixture of ASM and Azoxystrobin has been reported to provide excellent control of powdery mildew and leaf blotch (*Septoria tritici*) disease in wheat (Stadnik and Buchenauer, 1999). Further, it has been observed that foliar applications of urea with BTH not only enhance wheat yields but also provides effective control of powdery mildew disease in wheat, regardless of the observation of increase in powdery mildew symptoms when urea (as a nitrogen source) applied alone (Stadnik and Buchenauer, 1999). Similarly, ASM has been reported to enhance the efficacy of Cypronidil against powdery mildew. In Denmark, Jorgensen *et al.* (1997) conducted several field trials of ASM efficacy as an integrated control strategy for cereal disease management and got excellent results against fungal infection in wheat (Jorgensen *et al.*, 1997). In Brazil, Santos and team (2011) demonstrated that combined application of phosphite with pyraclostrobin + epoxiconazole (400 ml ha$^{-1}$), pyraclostrobin + epoxiconazole (300 ml ha$^{-1}$) and pyraclostrobin + epoxiconazole (400 ml ha$^{-1}$) is effective in the management of leaf rust, powdery mildew and brown spot diseases of wheat.

## 5. Factors affecting induced resistance

A large body of evidences indicated that the expression of IR in wheat is greatly influence by the type of wheat genotype. For instance, Pagani *et al.* (2014) documented the influence of wheat genotypes on the expression of IR in wheat against wheat blast fungus, *M. oryzae* pathotype *Triticum.* They described that BRS 264 genotype is more predisposed to stimulate beneficial effect in response to Si treatment than BR 18 genotype. Similarly, Santos *et al.* (2011) also noticed positive response of phosphite treatment to manage *Drechslera tritici-repentis* and *B. sorokiniana* infection in wheat depending on the crop species and on the pathosystem. It is worth to mention here that the findings of both the studies came from the experiments employing single pathogen isolate or single host genotype which might lead to the wrong conclusions that may alter the efficacy of elicitors in practice. Newton *et al.* (2004) revealed that bacterial inocula applied in previous crop has the ability to influence fungal disease development in succeeding non-host crops and therefore indicates penalties for commonly practiced agronomic interventions including rotations. They also explained these results by corroborating the results with synergistic enzyme theory and explained the severe effects on hemi-biotrophic pathogens and powdery mildew disease in wheat is due to heavy load of bacterial inoculum. Further, they also explained that the disease outcome may not be directly attributed to the interaction between the bacteria and *B. graminis* inoculum, but there is also a possibility of induced susceptibility or even nutritional effect as heavy dosages of nitrogen is responsible for enhancing susceptibility of cereals towards mildew infection. Statistically, Newton *et al.* (2000) also determined that high nitrogen level enhance powdery mildew severity by 4.58 times in comparison to low level of nitrogen under high inoculum load. Besides this, expression of resistance is also reported to be influenced by various other organisms dwelling in the environment in direct or indirect fashion. Several workers explained that both humidity and light have strong effect on the expression of defense-related genes, including ROS production (Mateo *et al*., 2004; Zhou *et al*., 2004). Fobert and Després (2005) clearly mentioned that amount and duration of light directly affects the chloroplast and redox status of cells and thereby is directly involved in the alteration of SAR stimulation (Fobert and Després, 2005). This is true in case of wheat, where expression of yellow rust resistance gene is dependent on light intensity (Ash and Rees, 1994). All above mentioned studies highlighted that the expression of IR is not stable and is greatly influenced by host, plant age, tissue maturity and edaphic factors etc. Therefore, it is essential to take these factors into account when induced resistance is practiced under field conditions for the management of wheat diseases.

## 6. Consequences of resistance induction

Induction of resistance is reported as a costly relationship in terms of yield forfeit and more over it triggers under optimal conditions only after the pathogen recognition (Walters *et al*., 2013). It has been well documented that resistance (R) genes and matching virulence have been taking the energy from host in terms of fitness to the pathogen and its selection stabilization (Vanderplank, 1968). This has been experimentally confirmed by Tian *et al.* (2003) in *A. thaliana.* Heil *et al.* (2000) investigated the effects of ASM triggered IR on yield penalties in absence of pathogen pressure. They described that ASM treatment in wheat reduced biomass, ear and grain numbers and moreover got noticeable effects under nitrogen limited conditions. These results clearly reveal the allocation cost effect of ASM and supports the 'growth-differentiation balance' hypothesis of Herms and Mattson (1992), which indicates that a metabolic competition between processes engaged in the plant growth are obligatory for plant differentiation, such as synthesis of chemical and metabolites for plant defense. These findings clearly encourage the need of research on ecologically realistic manner in the agricultural systems to attain a reliable risk assessment of ISR in wheat protection for its successful application in agriculture.

## 7. Future challenges and directions

Recent research progress in the dissection of molecular basis for priming, plant immunity, SAR and ISR indicate a wider role for plant defense activating compounds. Several compounds of biological and non-biological origin are gaining significant momentum in curtailing the use of health hazardous chemicals for wheat disease management. Still, there are several researchable issues that need attention for effective amalgamation of resistance inducers into wheat protection package and for their wider use in farmer's fields, which are enlisted as follows:

- Compounds inducing resistance have played important functions in wheat–pathogen interactions. Therefore, research investigation on the structure and function of these compounds in plants, as well as the underlying genetic cascade of wheat-associated pathogens will be advantageous to develop effective disease management tools and to upsurge disease resistance in wheat plants.
- There is a need to discover more effective resistance inducers against wheat disease and the information attained in the last few years on SAR, ISR and RNA silencing mechanisms and the interactions between them, may guide researchers to develop new molecules effective against wheat pathogens.

Additionally, deep research efforts are sought to comprehend the effects of nutrition, timing and dosages of application and genotypic effects after application of resistance inducers.

- A deep insight into the genetic alterations as a consequence of defense priming and pathogen resistance will offer valuable information for developing disease-resistant varieties by exposing parental plants to resistance inducers, as well as for the synthesis of novel plant protection chemicals that can trigger plant's intrinsic disease resistance machinery.
- A number of reports have emphasized that ISR stimulating plant growth promoting microbes (PGPM) as beneficial tool to control wheat diseases that are sensitive to JA- and ET-dependent defenses. Thus, incorporating ISR stimulating PGPM into disease management framework in juxtaposition with other stratagems will be worth to explore in the present arena of climate change.

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No commercial or financial relationships that could be construed as a potential conflict of interest.

## Compliance with ethical standards

Yes

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