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SILICON APPLICATION UNVEILED: A REVIEW OF INSIGHTS INTO PLANT DEFENSE MECHANISMS UNDER BIOTIC CHALLENGES

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Abstract

Silicon (Si) is the second most abundant element after oxygen in soil. Nevertheless, it was not considered essential for plant growth and development. In the last decades, many researchers have reported that silicon can mitigate to some extent the adverse effects of variable biotic and abiotic stresses caused by salinity, chilling, heating, nutritional imbalance, heavy metals, diseases, herbivores, and many others. There are different hypotheses regarding the mechanisms of the silicon mode of action. Some of them propose that the silicon treatment is probably related to the structural modification of the plant cells and tissues. Others speculate that silicon could be involved in plant metabolism. The interaction between the two mechanisms is also a very reliable hypothesis. Most of the studies focused on the influence of silicon on alleviating the negative effects of abiotic stress factors. The reports about the effect of silicon under biotic stress are not so abundant. Today, there is no doubt about the positive effect of silicon application in alleviating stress and reducing the pest and disease incidence and severity. However, the mechanisms of the silicon-induced plant responses are not yet completely clear. This motivated the current study to analyze the data presented about the silicon-induced alleviation of biotic stress.

Keywords: silicon, stress, disease, pest, physical barrier, plant metabolism

INTRODUCTION

Silicon (Si) is the second most abundant element after oxygen in the Earth's crust (Ma and Yamaji, 2006), yet it was not considered essential for plants (Arnon & Stout, 1939). In 2015, according to the International Plant Nutrition Institute (IPNI), Si was categorized as a "beneficial substance". The application of silicon-containing products can have several agronomic benefits, including improved plant growth and increased yield (Epstein, 1994, Richmond & Sussman, 2003) and protection from pests and diseases (Massey et al., 2006, Sun et al., 2022). Silicon is absorbed by the plant roots as soluble silicic acid $Si(OH)_4$ and in its ionized form – $Si(OH)_3O^-$, which predominates at high pH of the soil solution (Currie & Perry, 2007). It is deposited in various plant organs and tissues as solid amorphous silica ($SiO_2.nH_2O$), where it interacts with polyphenols and pectin and enhances cell wall strength and rigidity (Jinger et al., 2017). These two compounds are found in soil at concentrations of 0.1 to 0.6 mM and are readily absorbed by plants (Epstein, 1994). Silicon accumulation varies between species, ranging from 0 to about 10% of the plant dry shoot weight, and its deposition is not the same in the different parts of the plant (Shwethakumari & Prakashand, 2018). The most significant amounts of Si are accumulated in the plants of the *Poaceae*, *Equisetaceae* and *Cyperaceae* families ($Si > 4\%$) followed by the species belonging to the *Cucurbitacea*, *Urticaceae* and *Camelinaceae* families which accumulate medium amounts of Si ($2\% < Si < 4\%$) (Currie & Perry, 2007). Most of the other plant species accumulate low quantities of Si. Depending on the ability to absorb Si, plants are divided into three groups: active accumulators, passive accumulators, and excluders (Guntzer et al., 2012, Hernandez-Apaolaza, 2014). McNaughton et al. (1985) suggested that silicon may be crucial in controlling pests. Until nowadays, Si has been shown to improve plant resistance and decrease plant damage caused by pathogens, insects, and non-insect pests. In the last decades, many researchers have proposed that silicon can, to some extent, mitigate the adverse effects of variable biotic and abiotic stresses. A significant number of studies were carried out with monocot plants, including rice (Yang et al., 2018, Roy et al., 2023, Tenguri et al., 2023), wheat (Singh et al., 2022, Ashfaq et al., 2023), barley (Sakr, 2021) and maize (Nascimento et al., 2018, Acevedo et al., 2021, Haq et al., 2022). Other articles investigate the Si effect in dicot plants belonging to various families, namely *Cucurbitaceae* (Savvas et al., 2009), *Solanaceae* (Liu et al., 2009, Dos Santos et al., 2015, Somapala et al., 2016), *Fabaceae* (Shwethakumari & Prakashand, 2018) and many others. Almost all of the studies declared reduced pest and disease severity. Still, not all of them explain the mechanism by which silicon reduces the adverse effects of stress.

Forms of silicon applied for biotic stress alleviation

Silicon is absorbed from the soil by the roots, but it can also be applied to the shoots via foliar spray. The forms of available silicon used in the field or in glasshouses are various (Table 1), including potassium silicate K_2SiO_3 (Schuerger & Hammer, 2003, 2006, 2007, Liu et al., 2020), sodium silicate Na_2SiO_3 (Li et al., 2009, Sun et al. 2022), calcium silicate $CaSiO_3$ (Resende et al., 2013, Alves et al., 2015), silicic acid H_4SiO_4 (Shwethakumari & Prakash, 2018), silica gel (SiO_2) (De Oliveira et al., 2020), and Si-rich straw or hulls (Somapala et al., 2016, Bakhat et al., 2020) (Table 1).

Table 1. Forms of silicon applied for biotic stress alleviation

Form of Si	Plant	Reference
Potassium silicate (K_2SiO_3)	strawberry	Abd-El-Kareem et al. (2019), Kanto et al. (2007), Liu et al. (2020)
	cucumber	Schuerger & Hammer (2003)
	zinnia	Ranger et al. (2009)
	lettuce	Garibaldi et al. (2012)
Sodium silicate (Na_2SiO_3)	wheat	Basagli et al. (2003)
	potato	Li et al. (2009)
	strawberry	Abd-El-Kareem et al. (2019)
	cucumber	Sun et al. (2022)
Calcium silicate ($CaSiO_3$)	sorghum	Resende et al. (2013)
	sweet pepper	Alves et al. (2015)
	rice	Linger et al. (2017)
	strawberry	Abd-El-Kareem et al. (2019)
Silicic acid (H_4SiO_4)	soybean	Shwethakumari & Prakash (2018)
Silica gel (SiO_2)	vine	Parrilli et al. (2019)
	wheat	De Oliveira et al. (2020)
Silicon-rich biochar (rice husk)	tomato	Somapala et al. (2016)
	wheat	Otitodun et al. (2017)
	eggplant	Bakhat et al. (2020)

The beneficial effects of Si are associated with the mechanical and physiological modification of plants, depending on whether it is applied to the roots or to the shoots of *Podosphaera aphanis*-infested strawberry plants (Liu et al., 2020).

The protective role of Si application to the root system was attributed to Si accumulation in leaves, which hinders cuticle penetration by pathogens (Seal et al., 2018). According to several studies, the application of Si to the root system is promising in the protection against pathogens, but when supplied to the leaves, the protective effects are lower (Gomez et al., 2017).

According to other researchers, the mode of action of the foliar-applied K_2SiO_3 on powdery mildew could be attributed to the formation of physical barriers and osmotic effects on leaf surfaces (Rodrigues et al., 2009). Another cheap and natural source of Si is the Si-rich plant material such as the rice hull (husk) (Otitodun et al., 2017). It is organic, rich in silicon and contains about 8% of Si in its dry weight (Somapala et al., 2016).

Stress responses in plants

During the process of evolution, plants have developed various specific mechanisms to overcome the adverse effects of different stressful factors (Rejeb et al., 2014). Exposure to biotic and abiotic stress causes a disruption in plant metabolism, which leads to physiological damage (Bolton, 2009) and a decrease in plant health and productivity. Abiotic stress is one of the most essential characteristics of growth and has a significant impact on it. Therefore, it is responsible for severe losses in the field. The resulting reduction in growth can reach > 50% in most plant species. Biotic stress is an additional obstacle inducing intense pressure on plants (Mordecai, 2011).

During plant-pathogen co-evolution, plants have developed a variety of defense mechanisms to prevent invasion and colonization by pathogens, belonging to diverse species including fungi, oomycetes, bacteria, viruses, and animals. A plant defense is successful when it ensures an early and fast restriction of the pathogen infestation and subsequent induction and mobilization of structural and biochemical protective mechanisms (Voigt, 2014).

Silicon-induced physical amendment of plant cells tissues

Plants can react to the attack directly and indirectly. Direct protections related to the morphological characteristics of the plant such as wax layer, trichomes (hairs), lignification of cell walls, affect the enemy feeding process (Dos Santos et al., 2015, Massey & Hartley, 2009). These plant features represent a physical (mechanical) barrier and are the first line of defense. Plant cell walls are the front line of defense against pests and pathogens (Swaminathan et al., 2022). One of the hypotheses about the silicon mode of action is related to the mechanical changes in the plant cell and tissues that increase their strength and abrasiveness. The physical defenses against herbivores consist of structures such as raphides (needle like crystals), trichomes (hairy structures), thorns, rough and tough epidermal cells, spines, hard shells and pods (Vicari & Bazely, 1993). Many studies report a decrease in the pathogen population due to a reduced penetration of pathogens in strawberry (Kanto et al. 2007, Liu et al. (2020), cucumber (Menzies et al., 1991), potato (Liu et al., 2009) and many others (Table 2 and Table 3).

The formation of a mechanical barrier in the cuticle and in the cell walls, caused by the polymerization of silicon was the first hypothesis about the Si mode of action in relation to reduction in plant disease severity (Samuels et al., 1994, Song et al., 2021). Silicon prevents the physical penetration of pathogens as it forms a thick layer under the leaf cuticle making the plant cell wall less susceptible to enzymatic degradation (Yoshida et al., 1962).

Table 2. Potential mechanisms of the silicon-induced protection against diseases (fungal diseases)

Disease/pathogen	**Plant host**	**Mode of action**	**Reference**
Fungi			
Powdery mildew	wheat	Synthesis of phenolics and phytoalexins	Rémus-Borel et al. (2005)
	strawberry	Physical barrier	Kanto et al. (2007)
	strawberry	Physical barrier, biochemical amendment	Liu et al. (2020)
	cucumber	Physical barrier, papillae, phenolic synthesis	Menzies et al. (1991), Samuels et al. (1994)
	cucumber	Flavonoid phytoalexins synthesis	Fawe et al. (1998)
Fusarium oxysporum f. sp. cucumerinum	cucumber	Antioxidant defense, activation, photosynthesis increase, Calvin cycle related to the gene expression	Sun et al. (2022)
Dry rot of potato tubers (*Fusarium sulphureum* Schltdl.)	potato	Thickening of the hyphal cell walls, cell distortion, and the deposition of electron-dense material in hyphal cells	Liu et al. (2009)
Leaf blight (*Phomopsis obscurans*)	strawberry	Activation of peroxydase, polyphenol oxydase and chitinase	Abd-El-Kareem et al. (2019)
Early blight (*Alternaria solani)*	Tomato	Expression of defense-related genes and antioxidant enzymes	Gulzar et al. (2021)
Anthracnose	Tomato	Thicker cuticle and increased fruit firmness	Somapala et al. (2016)

Table 3. Potential mechanisms of the silicon-induced protection against diseases (bacteria and viruses)

Disease/pathogen	**Plant host**	**Mode of action**	**Reference**
Bacteria			
Bacterial blight (*Xanthomonas oryzae* pv. *oryza*)	rice	Activation of β-1,3-glucanase, endochitinase and exochitinase	Xue et al. (2010)
		Increased synthesis of total soluble phenolics and lignin, activities of PAL and PPO	Song et al. (2016)
Bacterial wilt (*Ralstonia solanacearum*)	sweet pepper	Increased production of chitinase, superoxide dismutase, ascorbate, peroxidase, β-1,3-glucanase, lignin and total protein	Alves et al. (2015)
Bacterial wilt (*Ralstonia solanacearum*)	tomato	Priming effect, triggering the expression of JA, ET, and/or ROS dependent genes	Ghareeb et al. (2011)
Viruses			
Tobacco ring spot virus (TRSV)	tobacco	Delay of TRSV systemic symptom formation	Zellner et al. (2011)

Outside the cells, Si is accumulated in the subcuticular layer, the cell wall and intercellular spaces (Datnoff et al., 2007). The silicon-induced pathogen resistance is associated with a delayed incubation period, a reduced colony size, a decreased lesion size and number, and a suppressed inoculum production of fungi (Debona et al., 2017).

According to many authors, the plant resistance to pests could be enhanced by antixenosis (reducing pest colonization) and antibiosis (reducing the reproductive period and the fecundity of pests such as aphids) after Si fertilizer application (Ranger et al., 2009, Dias et al., 2014, Boer et al., 2019). In the research of de Oliveira et al. (2023), the soil application of silicon led to a linear increase in the productivity of wheat and to a reduction in *Sitobion avenae* number. Both wheat genotypes (susceptible and constitutive resistant) demonstrated enhanced productivity and decreased aphid numbers, indicating that the Si treatment is compatible with the use of resistant plants. The authors couldn`t explain whether the observed resistance was caused by antibiosis, antixenosis, or both, but the Si applications demonstrated the potential of using *S. avenae* in wheat in integrated management.

Silicon reduces the digestibility of tissues (Calandra et al., 2016, Massey et al., 2006). Silicification occurs in macro-hairs and typical rectangular epidermal cells (Hodson et al., 1984), which is common for many grasses. Many authors suggested that the reason for the silicon-induced reduction in the pest numbers was the physical amendment of the plant tissues (Acevedo et al., 2021, Dos Santos et al., 2015, Haq et al., 2022, Massey & Hartley, 2009, Roy et al., 2023, Sidhu et al., 2013, Tenguri et al., 2023, Vilela et al., 2014, White & White 2013, Xue et al., 2022, Yang et al. 2018). The silicon deposits were clearly located under the Scanning Electron Microscope at different doses of the silicon treatment, indicating that the increase in the silica dose enhanced its deposits, confirming its role in the defense mechanism (Roy et al., 2023).

Regarding the anatomy of their mouth parts, insect and noninsect pests are divided into piercing-sucking (like leafhoppers, aphids, whiteflies, thrips and mites) and chewing (like moths, butterflies, and beetles) (Kumar & Rathor, 2020). Both groups could be effectively suppressed after feeding on Si-treated plants (Table 4 and Table 5).

Table 4. Potential mechanisms of the silicon-induced protection against insect pests (chewing insects)

Insect Pest	Host plant	Mode of action	Reference
Chewing pests			
Brown plant hopper (*Nilaparvata lugens* (Stål)	rice	Physical barrier	Yang et al. (2018), Roy et al., (2023), Tenguri et al. (2023)
Rice leaf folder *Cnaphalocrocis medinalis* (Guenee)	rice	HIPVs production	Han et al. (2016)
Stalk borer *Diatraea saccharalis* (F.)	sugarcane	Physical barrier	White & White (2013), (Sidhu et al., 2013), Vilela et al. (2014)
Fall armyworm *Spodoptera frugiperda* (Smith)	maize	Physical barrier	Nascimento et al. (2018), Acevedo et al. (2021), Haq et al. (2022)
African armyworm *Spodoptera exempta* (Walker)	ryegrass	Physical barrier	Massey & Hartley, (2009)
Tomato leaf miner *Tuta absoluta* (Meyrick)	tomato	Physical barrier	Dos Santos et al. (2015)

According to Massey & Hartley, (2009) the high content of silicon in tissues leads to a reduced leaf digestibility and causes mandible wear, which is probably crucial for the herbivore performance. The authors reported that the Si-rich diet was responsible for the extremely rapid insect mandibles wear, occurring within a single instar. The damage of the mandibles correlated with the decreased absorption of nitrogen and reduced growth rates. Herbivores, fed on Si-rich leaves, cannot completely recover after switching diets. This demonstrates the strong deterrent effect of the silica-based defenses. These defenses, in contrast to many chemical defenses, cannot be compensated or overcome with a dietary change: the adverse effects remain even when the insects start feeding on plants with low silica (Massey & Hartley, 2009).

The silicon microstructures slow down insects' penetration into plants, reducing the susceptibility of plants to pathogen damage (Bakhat et al., 2018).

Table 5. Potential mechanisms of the silicon-induced protection against piercing-sucking insect and non-insect pests

Insect Pest	Host plant	Mode of action	Reference
Piercing-sucking pests			
Spider mites	strawberry	Physical barrier, metabolism amendment	Liu et al. (2020)
Whitefly (*Bemisia tabaci*)	cucumber	Metabolism amendment	Correa et al. (2005)
	eggplant	Metabolism amendment, increased growth and Ca intake	Bakhat et al. (2020)
Aphids *Myzus persicae* (Sulzer), *Sitobion avenae* (F.)	wheat	Antibiosis	Dias et al. (2014), Jiang et al. (2023), Ranger et al. (2009)
Bird cherry-oat aphid *Rhopalosiphum padi* (Linnaeus)	wheat	Emission of HIPVs	De Oliveira et al. (2020), Liu et al. (2017)
Corn leaf aphid, *Rhopalosiphum maidis* (Fitch)	maize	Antibiosis and non-preference	Boer et al. (2019)

Phytoliths

The physical defense induced by the Si deposition in plant parts in the form of phytoliths (largely composed of SiO_2) was one of the first theories proposed for studying the stress tolerance to pests (Song et al., 2021). The monosilicic acid polymerizes and forms the so called phytoliths, which are accumulated within the plant (Epsteian, 1994). Phytoliths play a structural protective role in plants (Xu et al., 2023). In leaves phytoliths reduce the digestibility of plant tissues and weaken the mouth parts of the pests (Bakhat et al., 2018). The silicon deposition enhances the number of phytoliths on the surface of stems, which increases the cell wall thickness of the stem sclerenchyma (Miyake & Takahashi 1983). A large number of closely arranged phytoliths protects the vascular tissue of leaves and significantly enhances their resistance (Reynolds et al., 2009).

Papillae

According to Voigt (2014), the papillae are complex structures that are established between the plasma membrane and the inner site of the plant cell wall. The papillae formation is reported as a possible mechanism of the Si-induced defense in plants under biotic stress (Pozza et al., 2015, Verma et al., 2021). These structures could have variable biochemical compositions in the different plant species, but some compounds such as phenolics, reactive oxygen species, cell wall proteins, and cell wall polymers are commonly present.

Callose

Callose is an important linear form of polysaccharide which is synthesized in the plant cell walls. It is mainly build of β-1, 3-linked glucose residues with a small amount of β-1, 6-linked branches (Li et al., 2024). Callose deposition is a process that is coordinated through the expression of the genes encoding callose synthase (OsGSL1) and hydrolase (Gns5) (Hao et al., 2008). Callose not only plays an important role in plant development but also participates in the plant defense against environmental stresses (Swaminathan et al., 2022). Other researchers analyze the feeding behavior of phloem-sucking pests and report about the Si induced callose accumulation (Tenguri et al., 2023, Yang et al., 2018). The most intensely silicified tissues are usually the leaf epidermis, root endodermis, and abaxial epidermis of inflorescence bracts (Kumar et al., 2017).

Effect of Si on plant metabolism under biotic stress

The second line of plant defense includes secondary metabolites (such as phenols, lignin) (Alves et al., 2015, Emam et al., 2014, Xue et al., 2022), along with various enzymes (phytohormones) such as polyphenol oxidase (PPO), phenylalanine ammonia lyase (PAL) (Xue et al., 2022) and peroxidase (POD) (Alves et al., 2015), which are involved in their synthesis. One of the mechanisms by which Si is proposed to act and alleviate biotic stress is the production of reactive oxygen species (ROS) and the activation of the antioxidant metabolism (similar to the abiotic stress mitigation) (Van Bockhaven et al., 2013). The generation of ROS and incresed oxidative metabolism help to reduce plants oxidative damage (Domiciano et al, 2015, Yang et al., 2017). These mechanisms have been related to stress due to a pathogen (bacterial and fungal) infection, as well as damage to the plant from chewing and piercing-sucking insects (Domiciano et al, 2015, Yang et al., 2017, Debona et al., 2014). The reactive oxygen species are involved in several signaling actions in different defense signaling pathways with plant hormones, such as JA and SA (Glazebrook, 2005, Ramputh et al., 2002, Torres, 2010, Gulzar et al., 2021). Last but not least, ROS may affect the plant defense genes, resulting in the accumulation of protective metabolic substances such as phytoalexins and allelochemicals in plants (Thoma et al., 2003).

Phenolic and phytoalexin synthesis

The role of phytoalexins in the plant resistance is well established (Dakora & Phillips, 1996, Daniel, 2017, Fawe et al., 1998). Phytoalexins are antimicrobial biomolecules with a low molecular weight that are synthesized in plants as a response to biotic and abiotic stresses (Jeandet, 2015). Silicon can induce the formation of such antimicrobial compounds (Rémus-Borel et al., 2005). Microscopic analyses of the leaf cells of the Si-supplied cucumber plants demonstrated a rapid accumulation of phenolics in response to *Podosphaera xanthii* infection (Menzies et al., 1991). The high concentrations of flavonoids and phenolic acids in the leaf extracts of the Si-treated cucumber plants reduced powdery mildew symptoms (Emam et al., 2014). The hardness and brittleness of the wounds of *Trichothecium roseum*-infested muskmelon plants increased during the postharvest period due to lignin, suberin polyphenolic and silicon deposition in the wounded tissue, and the activation of phenylalanine ammonia-lyase (PAL), and the increased content of five phenolic acids (Xue et al., 2022).

Salicylic acid, jasmonic acid, and ethylene synthesis

According to several researchers, Si plays a significant role in the multiple phytohormone signaling pathways to mitigate plant biotic stress (Frew et al., 2018, Manivannan & Ahn, 2017, Coscun et al., 2016). Silicon acts as an emitter of systemic stress signals, leading to the efficient synthesis of protective compounds. The phytohormones salicylic acid (SA), jasmonic acid (JA) and ethylene play a major role in organizing the protective reactions of plants. Jasmonic acid is thought to regulate protection against both chewing insects and piercing-sucking insects, while SA is associated with protection against piercing-sucking insects, feeding on phloem. There is evidence of a strong interaction between Si and JA against insects, which is considered a possible mechanism by which Si increases plant resistance to insect pests.

According to Grant et al. (2013), to protect themselves from microbial pathogen infections, plants have created a multilayer immune system, relaying on constitutive and inducible defense mechanisms, where plant hormones play key roles.

The signaling pathways that allow rice plants to establish resistance to the rice leaf folder (*Cnaphalocrocis medinalis*) are dependent on JA (Liu et al. 2017). Silicon and JA are strongly associated with the different aspects of the rice defense system, as increased levels of transcripts encoding protective genes, the activity of defense-related enzymes (PPO, POD and trypsin protease inhibitor), in addition to the change in the so called herbivore induced plant induced volatiles HIPV (Ye et al., 2013).

Silicon increases the tolerance against the necrotrophic fungal pathogen (*Cochliobolus miyabeanus*), but according to Van Bockhaven et al. (2015) this effect was not dependent on JA and SA pathways. The authors proposed that the Si mode of action is based on the deactivation of the pathogen ethylene production. They suggested that photorespiration and the development of ROS played a vital role in the Si-induced defense against pathogens.

Photosynthesis and enzymatic defense system activation

Photosynthesis is among the most important phenomena, which is responsible for biomass production and overall growth and development in plant (Rastogi et al., 2021). Photosynthesis-related factors play a key role in plant metabolism and are involved in the defense against pathogens (Letousey et al., 2010). There are several studies that investigated the effect of Si in case of pest or disease attacks and proposed that the positive effect of Si was due to the photosynthesis enhancement (Bueno et al., 2017, Sun et al., 2022) and activation of the stress-related enzymes from the antioxidant defense system (Gulzar et al., 2021, Manivannan & Ahn, 2017, Rahman et al. 2015). Silicon pretreatment increased the net photosynthetic rate, and the leaf gas exchange parameters stomatal conductance and transpiration rate in *Fusarium oxisporum*-infected cucumber (Sun et al., 2022). According to Meunier et al. (2017) one of the reasons for the increased photosynthetic ability of plants is that phytoliths are responsible for the leaf erectness and hence provide large surface area to absorb more sunlight. Si supplementation enhanced the early blight resistance in tomato by modulating the expression of defense-related genes and antioxidant enzymes (Gulzar et al., 2021). Such activation of the antioxidant defense system was observed also in ryegrass against infection by *Magnaporthe oryzae* in rice (Rahman et al. 2015).

Tritrophic level of silicon-mediated plant defense via HIPVs emission

It is observed that Si is able to influence both bitrophic (plant-herbivore), as well as tritrophic (plant-herbivore–natural enemy) interactions, which, according to Kvedaras et al.

(2010) and Reynolds et al. (2016), may provide another mechanism for pest control. The secondary metabolites are essential in the interactions of plants with insects and other natural enemies. The plant volatile emissions are constitutive or inducible in response to stress and are involved in the protective reactions elicited by grazing animals (Dicke & Baldwin, 2010). In tritrophic systems, the chemical substances are emitted from plants in response to insect induced damage in the form of HIPVs (herbivore induced plant volatiles). These compounds, regardless of their chemical nature, may act either as direct repellents or attractants for the insects and could be used as host signals from entomophagous predators and insect pest parasites (Van Oudenhove, 2017).

Silicon can provoke different plant species to emit, enhance and/ or alter HIPVs (Kvedaras et al. 2010, Alhousari & Greger, 2018). Wild-type rice plants treated with silicon, established a strong indirect protection as a response of the rice leaf folder (*Cnaphalocrocis medinalis*) feeding, based on HIPVs production (Han et al., 2016, Liu et al., 2017). The volatiles emitted included hexanal 2-ethyl, α-bergamoten, β-sesquiophelandrene, and cedrol, produced in significantly smaller amounts in infected Si-treated plants. Their emission significantly enhanced the attraction of adult female parasitoids *Trathala flavo-orbitalis* and *Microplitis mediator* to Si-treated plants attacked by *C. medinalis* (Liu et al. 2017). According to De Oliveira et al. (2020), the silicon-induced changes in the wheat volatile blend mediate the non-preference behavior of the bird cherry-oat aphid (*Rhopalosiphum padi*) and the attraction of the aphid parasitoid *Lysiphlebus testaceipes*. It was also reported that the Si treatment is able to alter the grapevine volatile profile of the grapevine moth-infested plants (*Phalaenoides glycinae* Lewin) (Connick, 2011). The authors observed an enhanced production of n-heptadecane, but a decreased synthesis of Cis-thio rose oxide in the Si-supplied plants compared to the controls.

CONCLUSION

Silicon plays an unexpectedly vital role in enhancing the direct and indirect protection of plants against many pests and pathogenes via two closely related mechanisms that, in many cases, act in combination: strengthened physical or mechanical barriers and biochemical mechanisms trigger protective responses in plants. We could speculate that the soil application of silicon may offer a combined physical and chemical protection from diseases and pests, while the foliar application contributes only to the physical defense against enemy penetration. In some cases, the physical amendment ensures more sustainable protection as it is irreversible, and the permanent damages to the pest's digestive system cannot be alleviated via dietary change. Probably, the physical mode of protection is more often observed against chewing pests or fungi. On the other hand, the phloem-feeding piercing-sucking pests and bacteria are restricted mostly via the amendment of the plant metabolism. It is hard to judge which protection approach is more reliable and effective. Still, with the development of science and technologies, we could declare that all these mechanisms act synergistically rather than separately, relying on a combination of physical and biochemical amendments to reduce pest and pathogen damage or to attract their natural enemies (Figure 1).

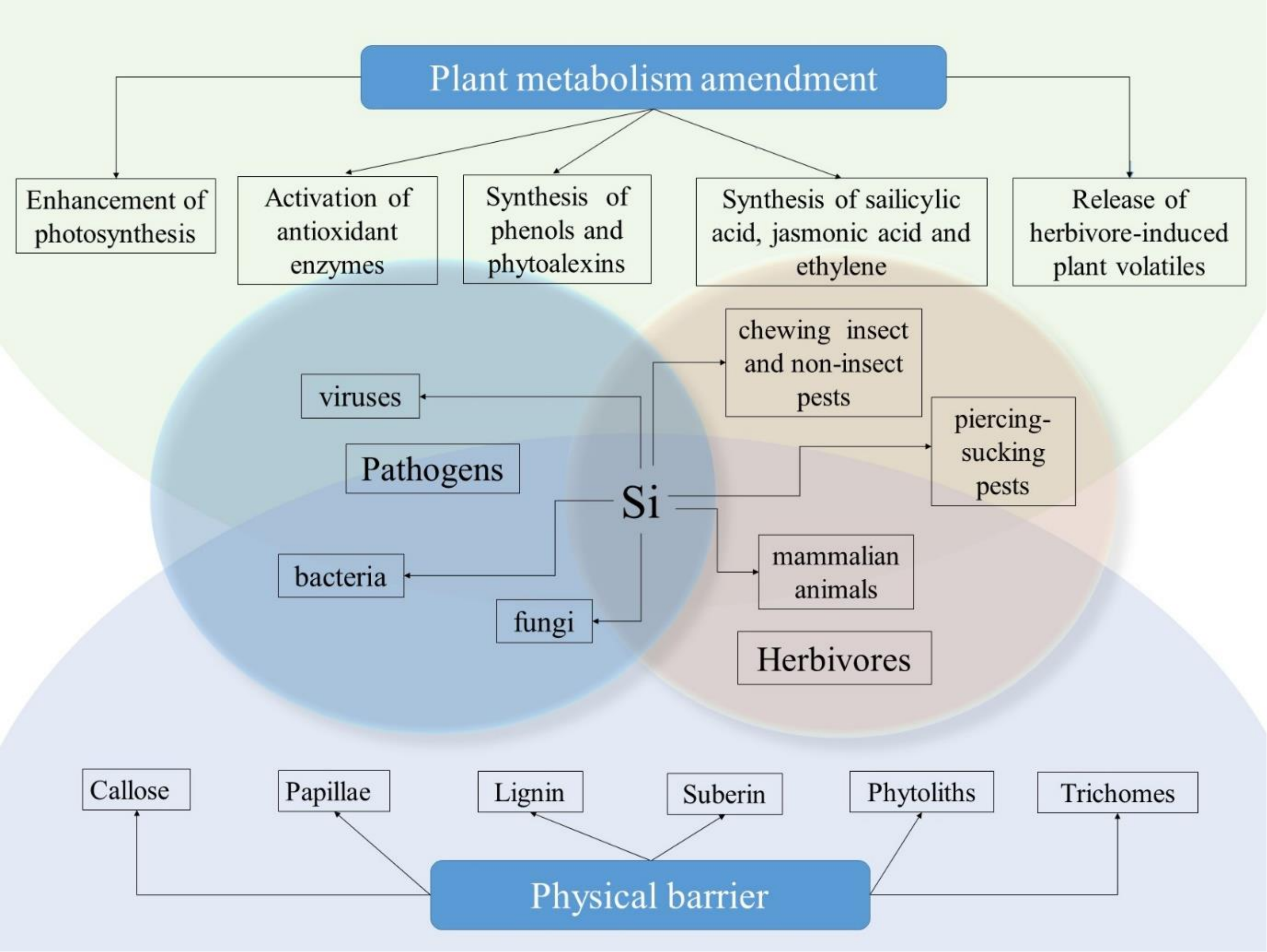

Figure 1. Mechanisms of the silicon-induced defense in plants against pathogenes and herbivores pests

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