

Interaction Between Nanoparticles and Phytopathogens



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1 Introduction

Phyto-diseases may evoke extensive deterioration in the plant community. It is crucial that phyto-diseases are rapidly identified and treated rationally. As per the current projections, the production demand for food globally needs to be doubled by 2050 (Tilman et al. 2011). With the anticipation that the changes in climate may contribute to disrupt the cycle of food production, such concerning prediction becomes more distressful. The plant pathogens are often greatly responsible for the annual loss of economically important plants and crops. In order to overcome this dire situation, nanotechnology extends its opportunities as a new edge weapon to improve and maintain plant health. With its diversified applications, the field of nanotechnology, specially nano-agriculture holds promise to provide us new avenues and streamline the utility of nanomaterials in crop production as well as protection of plants. Although the use of nanotechnology for phyto-disease management or diagnosis is at infancy, still it has tremendous potential in improving already existing as well as future crop production via plant protection techniques that will resist pests and diseases, help in phytopathogen monitoring, and plant diseases detection. However, there is still a lack of awareness and appropriate knowledge on how to bridge nanotechnology with agriculture and plant physiology and utilize it

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directly or indirectly in plant disease management. Thus, in this chapter we will discuss in detail the plant pathology and intertwined mechanisms along with the microbial organisms associated with it. Successively, new advancements and achievements acquired by utilizing nanotechnology in the field of phytopathology and agriculture will also be discussed for readers to gain insights into the role of nanomaterials in plant pathology.

2 Phytopathogens

A plant or phyto-disease can be broadly defined as any circumstance that evokes cascade of responses in plant cells and hinders the plant to perform its activity in highest potential. These diseases can be both biotic or abiotic in nature and the science of deciphering various phyto-diseases along with their causes is known as *plant pathology*. Plant pathology is closely related to bacteriology, virology, mycology, entomology, and weed science owing to the derogatory consequences of bacteria, virus, fungus, insects, and weeds, respectively, upon plants. Classification of plant diseases can be based on several criteria such as infected organs, disease symptoms, types of infected plants, or the causative phytopathogens. However, the phytopathogenic-based classification is considered to be more rational as it helps in easy determination of plant disease causes, related complications and probable measures of control (Cramer 1967). Following this criterion, phyto-diseases can be of two broad types: namely, biotic or infectious disease caused by microorganisms and abiotic or non-infectious disease which is the outcome of extreme environmental conditions (Horsfall and Cowling 1980). The diseases caused by abiotic factors, although being common, do not spread from plants to plants. Abiotic stresses include conditions such as excessive or deficient nutrients and moisture, soil compaction, presence of toxic chemicals in soil or air, salt injury, ice-attack, sun-scorch, etc. (Horsfall and Cowling 1980).

On the other hand, pathogenic microorganisms are the causative agents for biotic stress. The pioneering research indicating *Erwinia amylovora* for causing blight in pear and apple served as the foundation of plant pathology (Glawe 1992). With progress in time, several plant diseases due to bacteria, viruses, fungi, nematodes have been documented till then (Fang and Ramasamy 2015). Plant disease epidemics (epiphytotics) are also known to occur in many plants worldwide (Agrios 1997). The infectious disease occurs due to the phytopathogens' capability to get transferred from an infected to healthy plant resulting in identical disease as well as symptoms. While the internal plant environment is preferred for inhabitation by many phytopathogens, certain other microorganisms like bacteria and fungi live on the surface of plants. Some phyto-diseases also develop due to parasitic higher plants that grow upon attachment to other plants contributing to no mutual benefit but depriving the host plant of essential nutrients. This abnormal alliance leads to fragility of the healthy host plants. Examples of such plants are dodder, mistletoe, and witchweed broomrape.

2.1 Broad Classification of Phytopathogens

As discussed earlier, pathogens affecting plant health may vary from fungi, viruses, bacteria, parasitic higher plants, mollicutes, parasitic green algae, nematodes, protozoa, and viroids. Owing to their effective penetrating ability in plant tissues, these parasites can also tolerate diverse host conditions which enable them to feed and thus proliferate in plant tissues. Such pathogens which depend on living hosts for survival are known as obligatory parasites. On the contrary, the non-obligate parasites like fungi and bacteria can survive on both living and non-living hosts and utilize different nutrient media. Among the non-obligatory parasites, those who can grow/develop on organic dead matter saprophytically are called facultative saprophytes (semi-biotrophs) (Ellingboe 1968). Another variety of facultative parasites (necrotrophs) which grow saprophytically in general can attack and cause disease in living plants but under certain circumstances. It has to be noted that severity in phyto-disease is not often dependent on the parasitism type or degree. For instance, weak parasitic pathogens are often responsible for greater derogatory outcomes in plants with respect to those caused by other obligate parasites. In most cases, the non-obligatory parasites use lysozymes for degrading plant cellular wall that allows progressive invasion as well as infection (Dollet 1984). The most common variants of pathogenic microorganisms that are responsible for diversified plant disease along with their characteristic features have been enlisted in Table 1.

The parasitic phytopathogens also possess negative impact on host metabolic processes. Vascular pathogens attack the xylem and phloem vessel tissues of host plants for their growth and multiplication processes that impede sugar and water transportation in host plant cells (Abdulkhair and Alghuthaymi 2016a). Phytopathogens (e.g., *Fusarium oxysporum f. sp lycopersici*, *Verticillium albo-atrum*, *Verticillium dahliae*, *Xanthomonas oryzae pv. oryzae*, *Ralstonia solanacearum*, *Xylella fastidiosa*, *Xanthomonas campestris pv. campestris*, *Erwinia amylovora*, *Clavibacter michiganensis ssp. michiganensis*) categorized as vascular wilt pathogens are responsible for overwintering soil along with plant debris (Yadeta and Thomma 2013). While most bacteria and fungi belong to groups of soil-borne microscopical pathogens, foliar pathogens are constituted of phyllosphere viruses, bacteria, and fungi. Spots, cankers, blights, overgrowth of plants, tissue rots, root branching, stunting, and leaf epinasty are some of the well-known and familiar plant disease symptoms (Martins et al. 2018).

Table 1 Common phytopathogens and associated plant diseases

Sr. No	Types of phytopathogens	Characteristic features	Top 10 economically important phytopathogens	Few common Plant Disease
1.	Bacteria	Microscopic (single-celled) organisms possessing cell walls. Mode of reproduce involves binary fission. phytopathogenic bacteria Most of the phytopathogenic bacteria among the 200 variants either grow as parasites within or on the surface of the plant or in plant debris or soil like saprophytes	<i>Pseudomonas syringae</i> , <i>Ralstonia solanacearum</i> , <i>Agrobacterium tumefaciens</i> , <i>Xanthomonas oryzae</i> , <i>Xanthomonas axonopodis</i> , <i>Xanthomonas campestris</i> , <i>Erwinia amylovora</i> , <i>Xylella fastidiosa</i> , <i>Dickeya (dadantii and solani)</i> , <i>Pectobacterium carotovorum</i> (Khater et al. 2017)	Aster yellows, bacterial wilt, blight fire blight, rice bacterial blight, canker, crown gall, basal rot, scab
2	Fungi and fungal like organism	These pathogenic species lack chlorophyll and thus are incapable of making their own food. They exhibit filamentous growth and reproduction may be dependent or independent on spores. These microorganisms are classified as necrotrophic, hemibiotrophic, and biotrophic based on their living styles or mechanism of interaction with host plants	<i>Magnaporthe oryzae</i> , <i>Botrytis cinerea</i> , <i>Puccinia</i> spp., <i>Fusarium graminearum</i> , <i>Fusarium oxysporum</i> , <i>Blumeria graminis</i> , <i>Mycosphaerella graminicola</i> , <i>Colletotrichum</i> spp., <i>Ustilago maydis</i> , <i>Melampsora lini</i> , <i>Phakopsora pachyrhizi</i> , <i>Rhizoctonia solani</i> (Dean et al. 2012)	Anthraxnose, black knot, blight (chestnut blight, late blight), canker clubroot, damping-off, Dutch elm disease, ergot, Fusarium wilt, leaf blister, downy mildew, powdery mildew, oak wilt, etc.
	Virus and viroids	Viruses are characterized as intracellular particles bearing nucleic acid and are known to possess a protein coat that contributes in their different replication processes in the target living host cells. Virus-like particles devoid of protein coat are called viroids	<i>Tobacco mosaic virus</i> , <i>tomato spotted wilt virus</i> , <i>tomato yellow leaf curl virus</i> , <i>cucumber mosaic virus</i> , <i>potato virus Y</i> , <i>cauliflower mosaic virus</i> , <i>African cassava mosaic virus</i> , <i>plum pox virus</i> , <i>brome mosaic virus</i> , <i>potato virus X</i> (Scholthof et al. 2011)	Curly top, mosaic psorosis, spotted wilt
	<i>Nematodes</i> , <i>Phytoplasmas</i>	The microscopical worm like animals	—	—

(continued)

Table 1 (continued)

Sr. No	Types of phytopathogens	Characteristic features	Top 10 economically important phytopathogens	Few common Plant Disease
	<i>and Parasitic higher plants</i>	that are majorly characterized as soil dwellers are known as nematodes. Phytoplasmas are on the other hand bacteria like filamentous microscopic living organisms without cell walls. Parasitic high plants are chlorophyll containing plants that lack the ability to synthesize their own food and thus show parasitic activity on other host plants to collect water and nutrients		

3 Plant–Pathogen Interactions

3.1 *The Disease Triangle of Host, Environment, and Pathogen*

One of the most common models for studying plant pathology is represented by a triangle comprised of 3 major participants—host, environment, and pathogen (Fig. 1a). This model is based on the concept that a susceptible host can be attacked by a biotic agent, that is, any virulent pathogenic microorganisms that give rise to disease. Thereby, elimination in any one of the factors may prevent disease development (Francl 2001). Such conditions can further promote the infection-inducing properties of opportunistic fungi and bacteria (Abdullah et al. 2017). As discussed earlier, phytopathogens possess the aptness for epiphytic survival or growth within tissues of host plants, soil and/or separate plants. Physical injury or weakness caused in plants by the hostile abiotic (environmental) factors further assists pathogenic entry into host cells. For instance, factors like temperature, excess or scarcity of nutrients, moisture, humidity, torrential rain, and imbalance in salinity help the pathogens to multiply as well as propagate within the host plant escalating the disease and thereby affecting the plant health adversely (Agrios 1997). It has been observed that favorable climate during the monsoon triggers disease epidemics such as pomegranate blight caused by bacteria expands exponentially under conditions of elevated humidity common in rainy season (Chikte et al. 2019). Moreover, both epiphytic and endophytic phases have been documented in life cycle of

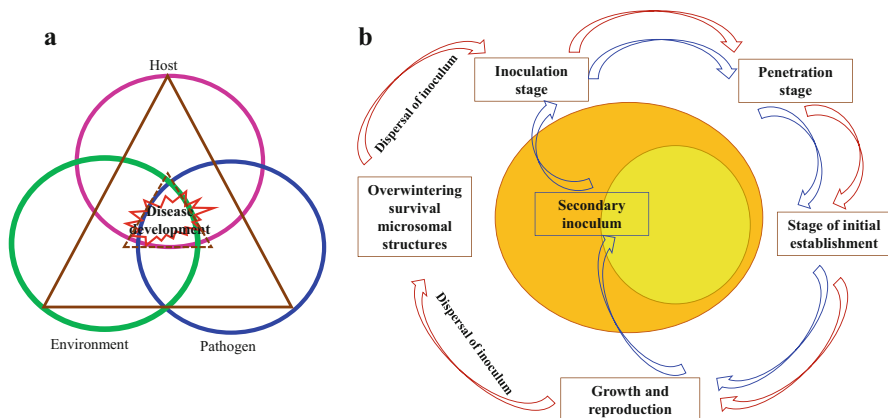


Fig. 1 (a) The vicious disease triangle of host, environment and pathogen: the phytopathogenesis only develops when each factor coincided with each other. (b) the cycle of disease development: the monocyclic virulent pathogens complete their cycle following the red arrows, while the polycyclic pathogenic microorganisms normally follows the blue arrows to complete their cycle for most of the seasons but shifts to the red arrows at the end

gram-negative pathogenic bacteria (Agrios 1997). The capability of phylogenetically rare species to elude disease pressure is well known and the host's phylogenetic structure also modulates pathogens' potency to spread, thereby affecting disease severity (Gilbert and Parker 2016). Thus, knowhow of phylogenetic connection in host and also virulent pathogens serve in predicting disease risk in multi-cropping system, which may help to avoid probable economic loss. However, it is important to note that there are multiple variables within the three components of disease triangle that may alter both disease incidence and severity. Life cycle, genetic diversities, and biology of both plants and pathogens as well as environmental conditions are a few of such variables.

3.2 Disease Cycle

For disease development, the tissue or cell of host plant should be successfully invaded by a virulent pathogen. Fig. 1b depicts the series of events involved in development of phyto-diseases. A disease cycle can be monocyclic or polycyclic. The various stages of the disease cycle are being briefly discussed below (Abdulkhair and Alghuthaymi 2016b):

Inoculation This step involves the phytopathogen introduction into host. Different pathogenic microorganisms deploy different modes of inoculation and are also equipped with diversified specialized mechanisms that promote inoculation. While some pathogenic fungi use spores that are airborne for inoculation in addition to sclerotia of mycelium fragments, intact cells also represent the inoculum in cases of

bacteria, protozoa, mollicutes, viruses, and viroids. The inoculum categorized as primary and secondary causes respective phyto-infections.

Penetration While certain plant pathogens utilize wound or injury sites and naturally occurring plant openings (stomata and hydathodes) to enter the host plant tissues, other pathogens employ unique modes to penetrate directly. Under optimum temperature, moisture and other favorable environmental conditions, fungi and nematodes undergo active penetration in tissues and cells of host plant.

Infection After invading the plant tissues, the phytopathogens develop a parasitic relation with the plant. Being unable for active penetration into the host plant tissues, phytoplasmas, bacteria, and viruses depend on alternative methods for infecting tissues and cells in plants. The virulent pathogens rely on insects as vectors that assist inoculation as well as dispersal.

Incubation After entering the plants, the pathogenic microorganisms enter the incubation stage and stay in latent condition for a specific period of time before initiation of the phyto-diseases.

Reproduction Depending on the type of phytopathogens, the mode of reproduction may be sexual or asexual.

Survival The evolution process of phytopathogens has enabled them for prolonged survival by tolerating hostile environmental conditions. The dark brown colored spores produced by fungal pathogen are an example which lower the light penetration and thereby prevent cell death. Another example of survival strategy may be the habit of soybean cyst nematode laying its eggs in a cuticle case. Such casing is very rigid that prohibits penetration of harmful chemicals or microbes which kill the eggs prior to hatching.

As discussed above, disruption in one or more steps of the cycle will either curb the disease severity or may even prevent its promotion or development in host plants. Thus, the knowledge of disease cycle may help to manage various phyto-diseases.

4 Phyto-pathogenesis-Linked Molecular Mechanisms Mediated by Bacteria, Viruses, and Fungi

Phyto-pathogenesis exhibits a critical and complicated process (Fig. 2a). As a pathogenic virulent microorganism encounters a plant, it should be capable enough for adapting to the living conditions in epiphytic surfaces as well as survive for adequate time period necessary for initiating infection. Thus, throughout the process of infection, the response toward environmental conditions plays a pivotal role. The correlation of signaling pathways (both intracellular and community level) with that of environmental signals triggers responses critical for phytopathogen populations. The ultimate goal of phytopathogens is to migrate from surface of the epiphytes into

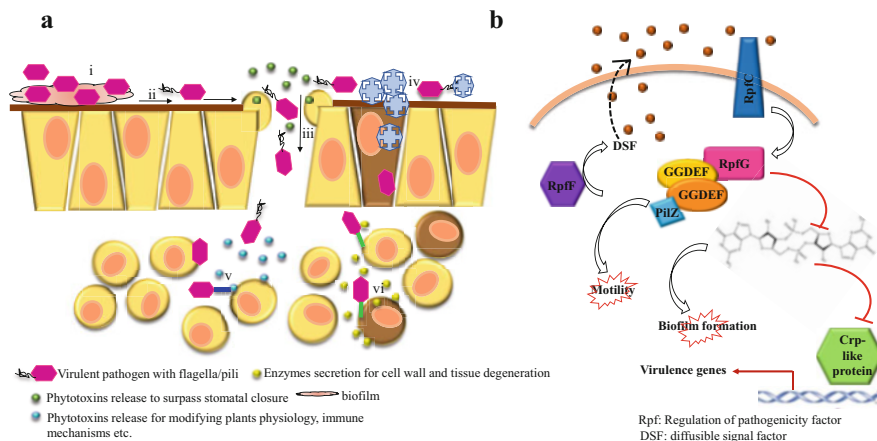


Fig. 2 (a) Basic mechanism of phytoinfection by pathogenic microbes: The common steps include (1) surface infestation and adaptation of microbes along with formation of biofilm, (2) surface migration of the pathogens mediated by flagella/ pili to gain access through the apoplasts, (3) phytotoxin mediated stomatal entry, (4) damage of plant surface through ice nucleating agents (INA), (5) toxins mediated alterations of plant physiology essential functions and even immune responsiveness, (6) plant tissue degradation and disruption of cell wall through secreted enzymes. (b) Rpf conjugated QS/cdG signaling system in pseudomonas species: The sensor kinase, RpfC upon sensing QS signal (DSF) produced by RpfF, causes phosphorylation and activation of RpfG. RpfG in turn via its phosphodiesterase activity degrades cdG thus reducing biofilm formation and Clp protein release repression. Subsequently, virulent genes undergo Clp mediated transcription. Additionally, interaction of RpfG with other GGDEF domain comprising proteins, is responsible for controlling bacterial motility. Rpf regulation of pathogenicity factor, *QS/cdG* quorum sensing/ cyclic di-guanosine monophosphate, *Clp* Crp-like protein

the host plant tissues mediated by motility or chemotactic pathways. This migration involves introduction into plant apoplast after surpassing the physical along with chemical barriers. Following their introduction in plant tissues/cells, phytopathogens utilize an array of effectors (proteins) and phytotoxins produced by different secretory systems that co-ordinate various pathogenic functionalities (Melotto and Kunkel 2013).

4.1 Bacterial Phyto-pathogenesis

4.1.1 Surpassing Stress on Epiphytic Plant Surface

The surface of leaves presents a hostile environment for virulent pathogens. Bacteria have to face regular exposure to desiccation, adverse alteration in temperature, UV radiation, and mechanical abnormalities like strong wind. Despite these hindrances, epiphytic bacteria possess certain virulence strategies that promote their microbial persistence on the surface of most plants. The epiphytic survival is materially

regulated by metabolic responsiveness to shock, cold, stress, and desiccation (Djonovic et al. 2013; Freeman et al. 2013). In *Pseudomonas syringae* (*P. syringae*), trehalose (osmo-protectant) has been indicated for benefiting its survival and also maintain its required population in phyllosphere (Freeman et al. 2010). It has also been suggested to potentiate nitrogen requirement and enhance proliferation in leaf apoplast thus contributing to plant disease development by *P. aeruginosa* (Djonovic et al. 2013). Various literatures have pointed out the pivotal contribution of exopolysaccharides (EPS) like alginate, xanthan, levan (Freeman et al. 2013; Dunger et al. 2007) in the epiphytic survival of various plant-related microbiomes such as *xanthomonas species* (Dunger et al. 2007) and *P. syringae* (Yu et al. 1999). The EPS molecules are closely correlated with epiphytic survival and contribute to enhance the pathogenic capability for resisting freeze-thaw process (Wu et al. 2012), tolerate stress due to osmosis and dryness (Freeman et al. 2013), and also maintain adequate microbial population (Dunger et al. 2007). Various phytopathogens possess the EPS molecules that mediate Ca^{2+} signaling quenching at the time of phyto-immune response and thereby allow the microbes to evade the immune system (Aslam et al. 2008). Relative to surface of leaves, literature points out strong upregulation of biosynthetic locus of levan in *P. syringae* pv. *syringae* (Pss) B728a in the apoplast that indicates its role in post-infection virulence (Yu et al. 1999). Moreover, the pathogenic trait of EPS molecules has also been observed in case of biofilm formation by Psa NZ V-13 (Renzi et al. 2012). On the other hand, Wss (acetylated cellulose) molecules not only foster the root colony formation of *Pseudomonas fluorescens*, but also facilitates *P. syringae* pv. *tomato* (Pto) DC3000 (Gal et al. 2003).

4.1.2 Signaling Cascades Regulated by Phytopathogens

The virulent phytopathogenic bacteria demonstrated evolved and efficient cell-to-cell signal transduction system which exhibits diversified and overlapping parallel input signals along with gene (non-linear) co-ordination. Moreover, the plant surface also reveals various bacterial species to be closely interlinked with various signaling systems. Among the wide variety of signaling systems QS (quorum sensing) and cdG (cyclic guanosine 3',5'-monophosphate) signaling (second messenger pathway) are considered to perform major roles in plant pathogens.

4.1.2.1 Quorum Sensing (QS) in Phytopathogenic Bacteria

QS is utilized by ultraviolet bacteria for communicating as well as assessing cellular density via the products of autoinducers which are tiny signaling molecules. The major signals in bacteria are acyl-homoserine lactones (AHLs), DSF(diffusible signal factor), and Ax21.

QS molecules are majorly constituted by AHLs. AHL itself plays as pivotal role in positively regulating synthase gene transcription. *P. syringae* is known to produce

3-oxo-C6-HSL (homoserine lactone), an AHL molecule. In *Pss*, both synthesis of EPS and motility are controlled by *ahlI/ahlR* system which are essential for maintaining virulence of pathogenic bacteria as well as plant colonization (Quinones et al. 2004, 2005). While *Agrobacterium tumefaciens* (crown gall bacteria) control virulence by producing 3-oxo-C8-HSL that stimulates Ti plasmid copy numbers, secretion of phytotoxin and flagellum assembly coordinated motility in *Burkholderia glumae* (rice pathogen) is regulated by C8-HSL production (Kim et al. 2004). *LasI/LasR*, *OscR* (orphan regulator), and *RhII-RhIR* are 3 AHL pathways which are employed by *P. aeruginosa* for producing 3-oxoC12-HSL along with C4-HSL that are known for affecting more than 300 gene expressions among which many are associated with restriction of toxins, biofilm formation, and also motility (Schuster et al. 2003). Another QS molecule called PQS (Pseudomonas quinolone signal), chemically known as 2-heptyl-3-hydroxyl-4-quinolone, is also reported to be synthesized by *P. aeruginosa* which control both formation of biofilm and virulence factors production (Allesen-Holm et al. 2006). Moreover, PQS, *las*, and *rhl* (complete and semi-independent) QS systems also mediate *LasB* expression encoding a secreted (type II) protease.

Recently, another QS signal known as Ax21 has gained quite interest. *Xanthomonas oryzae pv. oryzae* produces the Ax21 which is a sulfated small protein in nature and performs the role of QS molecule necessary for expressing virulence genes (Han et al. 2011). *X. oryzae pv. oryzicola* (Qian et al. 2013) and *Stenotrophomonas maltophilia* (McCarthy et al. 2011) have been documented to possess similar proteins that are interrelated with EPS and biofilm formation enhancing motility and virulence.

Another essential QS molecule termed as DSF is composed of fatty acids (unsaturated). *cis*11-methyl-dodecenoic acid is a DSF signal that is recognized by pathovar Xcc responsible for causing crucifer black rot (Wang et al. 2004) and is involved in modulating virulence as well as synthesis of xanthan and protease (Barber et al. 1997). DSF has also been reported to be used by *Xy. fastidiosa*, *X. oryzae pv. Oryzae*, and other *Xanthomonas* species. DSF signaling pathway which is synchronized by components of the gene cluster Rpf (regulation of pathogenicity factor) present in Xcc upon mutation reduces virulence (Barber et al. 1997). DSF upon synthesis is readily detected RpfC, a component of RpfC/RpfG (hybrid sensor kinase) which is also known for negatively regulating DSF synthesis (Slater et al. 2000). Following activation of RpfC/RpfG system and signal transduction through it, *cdG* is degraded with subsequent repression of Clp (Crp-like protein) transcription regulator release that finally leads to activation of virulence gene expression (Fig. 2b) (Chin et al. 2010). Xcc also consists of another DSF sensor, RpfS apart from RpfC which has been proven to be essential for virulence in Chinese radish (An et al. 2014a). On the other hand, mutation of RpfF in *Xylella fastidiosa* increases colonization and virulence in grape xylem tissues. *Xy. fastidiosa* engage DSF signal transduction in a multifaceted fashion for regulating its colonization, virulence as well as adhesion potential (Chatterjee et al. 2008a, b).

4.1.1.2.2 cdG Signal Transduction Pathway

Cyclic adenosine monophosphate (cAMP) and cdG (cyclic-di-GMP) like nucleotides that serve as secondary messengers, function as signaling molecules with pleomorphic roles for controlling and regulating virulence of bacteria. Apart from regulating virulence, cdG the secondary messenger participates in coordinating a wide range of functions including motility, biofilm formation. PDE (Phosphodiesterase) and DGCs (diguanylate cyclase) are known for regulating intracellular levels of cdG. While DGCs utilize 2 GTP (Guanosine triphosphate) molecules for synthesizing cdG, PDEs cause degradation of the same. Often additional domains such as GAF, REC, or PAS present in DGC/PDEs are also associated with signaling. cdG interacts with a wide variety of binding domains for exerting its action, some of them being PilZ domain containing protein, DGCs, and PDEs which are enzymatically inactive, transcriptional regulators such as Clp, RNA riboswitches, and FleO (regulator of pseudomonas motility and/or EPS) (Romling et al. 2013). cdG in DSF/rpf signaling system undergoes interaction with Clp preventing its promoter binding and subsequent related target genes transcription (Fig. 2b). Clp in *Xanthomonas* species controls gene expressions that encode extracellular enzymes (Chin et al. 2010). Similar Clp/cdG interaction is evident in *Xanthomonas axonopodis* pv. *Citri* (Leduc and Roberts 2009). On the other hand, Xcc also exhibits a different dual component RavS/RavR system which is associated with cdG and found to be important for bacterial virulence. This RavR protein is involved in alteration of cdG levels mediated by activity of PDE via its EAL domain and also modulates expression of virulence factors through Clp, the transcriptional regulator (He et al. 2009). The regulatory effect of cdG systems in controlling multiple and essential behavioral facets of phytopathogenic *Pseudomonas* species along with regulating the virulence of various other pathogenic species and pathovars is well documented (Pfeilmeier et al. 2016). Previous literatures also indicate its role in managing activity of T3SS (type III secretion system) and flagellum with simultaneous regulation of proteome composition by modifying ribosomes (Trampari et al. 2015; Little et al. 2016). It has been suggested that Gac/Rsm nexus that is responsible for controlling quantum signaling, biofilm formation, secretor systems, toxin, and siderophore production, manipulates productions of PDE/DGC thereby subsequently affecting cdG levels (Moscoso et al. 2011, 2014). While expression of T6SS (type IV secretion system) is interlinked with GacA (sensor kinase) in *P. syringae* (Records and Gross 2010), RsmA, the post-transcriptional regulator (RNA binding), when trans-overexpressed results in repression of secretion of various virulence factors (Kong et al. 2012). The key functionalities of cdG signal transduction in *Ralstonia solanacearum*, *Serratia*, and *Erwinia* genera need to be elaboratively explored apart from *Xanthomonas* and *Pseudomonas* and species. Recently researches have revealed two new targets for cdG binding in XCC and *P. syringae*, which are XC_3703 (YajQ family protein) (An et al. 2014b) and injectisome (type III) ATPase HrcN, respectively (Trampari et al. 2015).

4.1.3 Adapting Skills of Pathogenic Bacteria to Phyto-environment

The interaction and cross talk between different components of plant microbe are known to largely affect phytopathogenic bacterial behavior in natural environment. Epiphytic endurance and phyto-infections are affected prominently by both commensal and antagonistic interactions (Delmotte et al. 2009; Ritpitakphong et al. 2016). Downstream of the signal transducing nexus, pathogenic responses are integrated to environment by transcriptional alterations related with life on phyto-surfaces. It has been documented that in Pss B728a (*P. syringae* strains) affecting the bean plants' surface, there is marked upregulation of genes associated with nutrient attainment, virulence, intracellular signaling as well as membrane transport (Marco et al. 2005). On the other hand, epiphytic survival of Pss B728a on surface of the leaves is promoted by active and strong induction of osmotolerance coupled with T6SS and alginate synthesis. Another phyto-environment identifying regulatory pathway in *Ag. tumefaciens* involves low pH, plant-related sugars, and phenolics (acetosyringone) mediated evocation of virulent gene expression (Peng et al. 1998). In *Agrobacterium*, certain chemical signals-mediated induction of virulence gene at the site of plant wounds are modulated by VirAG/ChvE pathway that finally results in effective crown gall tumor formation (Peng et al. 1998).

4.1.4 Apoplastic and Plant Surface Motility of Bacteria

Motility or migration plays an important role in phyto-infections. Recently, regulation of motility as well as pili, surfactant or flagella loci expression at proper time during phyto-infection phases are being considered as one of the salient factors in pathogenicity of plant. When in contact with surface of leaves, many phytopathogenic bacteria express traits that assist in promoting bacterial persistence until apoplastic penetration is allowed by environmental conditions. Under favorable conditions, pathogens utilize different motility systems that enable their migration from surface of the leave to interior of the plants through different access sites like wounds and stomata. Flagellar motility confers epiphytic competence benefit in *P. syringae* and plays an important role in plant virulence and surface colony formation (Tans-Kersten et al. 2001). It has been observed that chemotaxis along with formation and utilization of surfactant molecules in bacteria are closely intertwined with expression of flagellar genes that allow bacteria for migration through leaf surfaces (Yu et al. 2013; Burch et al. 2012). Signaling genes like rpfS (in Xcc) (An et al. 2014a), rimK (in *P. syringae*) (Little et al. 2016), and xbmR (from *X. citri* ssp. *Citri*) (Yaryura et al. 2015) upon deletion contribute in defective bacterial virulence. Also, in *P. syringae*, *R. solanacearum* and in several other pathogens, type IV pili are found to be necessary for producing and attachment of biofilm, twitched motility, and pathogenic virulence (Nguyen et al. 2012; Kang et al. 2002).

During the plant infections, the formation as well as expression of flagella should be closely controlled for directed bacterial migration toward the apoplast and also prevent from being detected by PRRs (plasma membrane-localized pattern recognition receptors) which would then lead to initiation of pattern triggered immunity (PTI) (Macho and Zipfel 2014). The excess of flagellin monomers is known to be degraded by Apr A (alkaline protease A) (Pel et al. 2014).

4.1.5 Bacterial Invasion of Plant Tissue Mediated by Hijacking Stomatal Entry and Cell Wall Degeneration Enzymes

The plants as a part of their immune (innate) system keep their stomatal pores closed to inhibit ingress of bacteria (Melotto et al. 2006). But this defensive mechanism needs to be surpassed by phytopathogenic bacteria for gaining apoplastic access. It has been noted that Xcc (Gudesblat et al. 2009), *P. syringae* species (Melotto et al. 2006), and many other pathovars perturb stomatal immune system through secretion of phytotoxins. Virulent pathogens secrete varied molecules including toxins like syringolin and coronatine that enact as antistomate defense components (Melotto and Kunkel 2013) where they impede NRPI (non-expressor of pathogenesis related 1) regulated SA (salicylic acid) signaling (Xin and He 2013). On the other hand, other pathogens secrete enzymes and specific proteins that degenerate the cell wall allowing them to enter plant tissues. Other literatures indicate another mechanism of overcoming phyto-defense systems through production of ice nucleating agents (INAs) which have been identified in *P. syringae* (Gagnard and Luisetti 1993), *X. campestris* (Gurian-Sherman and Lindow 1993), and *Pantoea ananatis* (Sauer et al. 2014). Water molecules are transformed by INAs into clathrin lattices identical to ice that elevate temperature allowing nucleation of ice with corresponding freezing of water at higher sub-zero temperatures (Garnham et al. 2011). Through this mechanism of ice-nucleation, the phytopathogens cause frost damage and thus gain access for entering into plants. Epiphytic bacteria also possess genes-rendering resistance to “freeze-thaw” that foster their survival irrespective of both environmental and biotic factors evoked frost conditions (Wu et al. 2012).

Additionally, phytopathogens also deploy certain secretion systems (mainly type II) through which wide arrays of enzymes are released (Korotkov et al. 2012). These contribute in degeneration of the structural molecules constituting cell walls of plants and also cause hydrolysis of the lamellae connecting individual plant cells which supply the pathogens with a source of carbon that promotes pathogens' propagation through apoplast and get distributed throughout the host plant tissues. *Xy. Fastidiosa* attributes in damaging the xylem's inter-vessel pit membranes in grapevine that facilitates pathogenic propagation (Sun et al. 2011). Extracellular enzymes like pectinases, proteases, xylanases, and cellulases are categorized as cell wall damaging enzymes that are critically related with *Xanthomonas spp.*, Phytoplasma, and Xylella along with Erwinia and Pectobacterium genera (soft-rot pathogens) (Dejean et al. 2013; Lee et al. 2014; Toth et al. 2003).

4.1.6 Maneuvering Various Plant Protective Systems by Phytopathogenic Bacteria

The virulent microbes are also capable of synthesizing and secreting small phytotoxins that are responsible for potentiating bacterial virulence by suppressing host plant defensive mechanisms with subsequent enhancement of necrosis in tissues and chlorosis. While phytotoxins like syringopeptins and syringomycins directly deteriorate the plant cells, other toxins manipulate and interfere with different signaling pathways and metabolic activities that succor the invasion by the phytopathogens. *P. syringae* species synthesize toxins (modified peptides) such as mangotoxin, phaseolotoxin, and tabtoxin which trigger both tissue chlorosis as well as necrosis. The above-mentioned toxins primarily disrupt nitrogen metabolism by inhibiting the activity of targeted enzymes involved in biosynthesis of amino acids. The resultant nitrogen-rich intermediates are then successively utilized by the phytopathogens as a source of nutrition and food (Arrebola et al. 2011).

It has been observed that on release of hydrolysis-mediated toxic component of tabtoxin inside plant cell, glutamine synthetase is irreversibly inhibited and chlorophyll is degraded that consequently cause yellowing of tissues and chlorosis (Langston-Unkefer et al. 1987). On the other hand, another enzyme carbamoyl transferase is inhibited by Phaseolotoxin that also leads to similar consequences of host plant as an outcome of metabolic imbalance within plant cells (Bender et al. 1999).

The mechanisms of bacterial plant pathogens are not only restricted to these but are extensive in which they also disturb hormonal physiology in host plants and manipulate internal signal transduction cascades that exponentiate bacterial virulence and potentiate the pathogenic outcome. Structural as well as functional parallelism of most phytotoxic components with that of phytohormones like auxin has been observed. For example, coronatine which resembles the plant hormone Polyketide is involved in stimulating proliferation of apoplast, opening of stomata which finally confer to aggravated symptomatic development of phyto-diseases (Zeng and He 2010). The phyto-receptor complex COI1/JAZ (coronatine insensitive1/jasmonate ZIM-domain) senses coronatine that results in stimulation of JA (jasmonic acid) transduction in plants with simultaneous suppression of defense mechanisms arbitrated by SA (salicylic acid) signaling (Xin and He 2013).

Phytopathogens may also directly manipulate plant hormonal signaling pathways by encoding enzymes that are involved in synthesis of plant hormones. Several bacterial strains like *P. syringae*, *Ag. tumefaciens*, *Pantoea agglomerans*, and *Pseudomonas savastanoi* have been correlated with synthesis of abscisic acid (ABA), JA, indole acetic acid (auxin), cytokinins, and ethylene (Robert-Seilaniantz et al. 2011). The phytopathogens owing to their ability to produce or suppress various hormones directly exploit the critical crosstalk existing among the hormone transduction pathways that provide them the opportunity to subvert plant defensive mechanism and metabolism for their own benefit (Robert-Seilaniantz et al. 2011).

4.1.7 Effector Proteins-Mediated Bacterial Virulence

The phytopathogenic microorganisms are linked with secretion and release of miscellaneous virulent factors like phyto-toxins, enzymes, and other molecules for circumventing host plant defenses either directly into host plant's cytosolic environment or in the extracellular locale. *Xanthomonas* spp., *P. syringae*, and other hemi-biotrophic bacteria employ amalgamation of different secretory systems for effectively exporting and delivering secreted proteins called effectors responsible for maintaining structural and functional integrity of host plant's components to relevant locations to further potentiate the degree of infection. Co-ordinated secretory systems show prominent effect on the versatility of phytopathogens (Fig. 3a).

RsmA, in *P. aeruginosa*, functions as a molecular switch to coordinate between acute and chronic phases of infection causing translational suppression of T6SS, pel (pectate lyase), and psl mRNAs with corresponding upregulation in transcription of flagellar, T3SS, and T4SS genes (Moscoso et al. 2011). In Pss B728a, these T6SS and T3SS are negatively regulated by RetS and LadS (sensor kinases) (Records and Gross 2010). In *Xanthomonas*, previous reports indicate the regulatory role of QS over T2SS (Jha et al. 2005). Also, extensive researches are being conducted on modulation of hypersensitive response and pathogenicity (hrp) regulon which constitutes T3SS-related structural genes, T3SS regulators, and multiple T3ES (Buttner and Bonas 2010). During the infection phase, pathogenic bacteria keep tight control to deliver T3E hierarchically and temporally with the help of post-translational techniques (Galan et al. 2014). While *salmonella enterica* shows orderly recruitment and secretion of T3Es effectuated by chaperone-facilitated cytoplasmic cell sorting platform (Lara-Tejero et al. 2011), other bacterial pathogens deliver T3Es inside host cells by deploying chaperons, export control, and other hrp-associated (hpa) proteins (Lohou et al. 2013). Interaction between HpaB (global chaperone for T3E export) and HpaA in *R. solanacearum* causes selection of T3ES and guides them to HrcN (T3SS related ATPase) effectuating translocation (Buttner et al. 2006). Currently, the allosteric role of cdG in regulating HrcN action is also being explored that suggests its crosstalk with the dynamics of T3E translocation. In case of Pss B728a, regulated T3Es secretion is found to be essential during the phase of epiphytic growth which is marked by the prominent role of HopAA1 and HopZ3in promoting definitive leaf surface colonization (Lee et al. 2012).

Complex transportation mechanisms are required for translocating proteins and other molecules coordinately (Fig. 3a). Type I-VI transportation systems are engaged by gram-negative bacteria for delivering proteins into the extracellular milieu or inside the host cellular components (Gerlach and Hensel 2007). While T3SS plays a pivotal role in pathogenicity, T2SS is also widely used by different pathogens such as members of *Ralstonia*, *Pseudomonas*, *Xanthomonas*, and *Erwinia* genera for extracellular delivery of proteins (Jha et al. 2005; Johnson et al. 2006). T2ES mostly comprising of different virulence factors like cell-wall degeneration enzymes, toxins, and also proteases potentiate the virulence in plants. Gram-negative bacteria and members of *Xanthomonas* species are known to carry a lipA

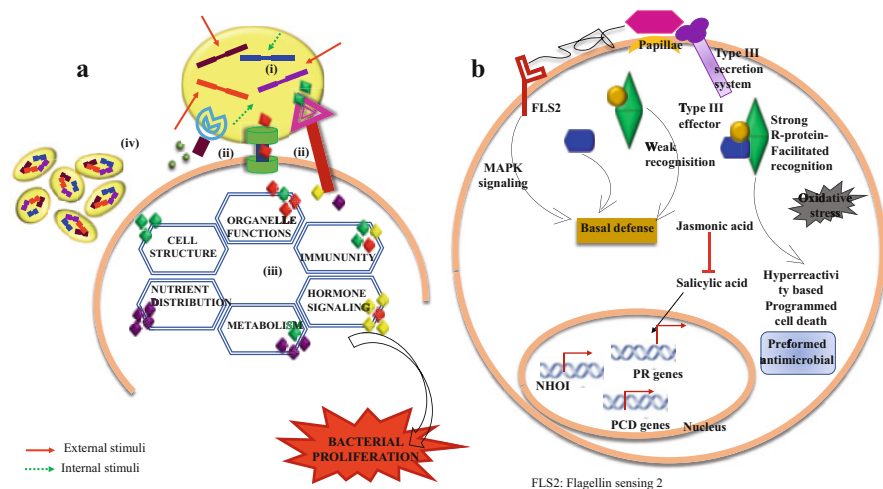


Fig. 3 (a) Bacterial effectors mediated mechanisms of phytopathogenesis: (1) extracellular and intracellular stimuli coordinated the expression of virulence genes (2) different secretion systems mediated effector translocation such as by type III secretion system (T3SS, T4SS, T2SS etc.), (3) Essential functions of host plants like immunity, metabolism, cellular structure, hormonal signals, distribution of nutrients etc, are all targeted and compromised by the effectors, (4) Host-pathogen interactions exponentially increases and diversifies virulent pathogenic gene families. (b) Phytopathogens targeted defense mechanism to promote disease development: Pathogenic avirulent factors upon strong recognition activate hyperreactivity (HR) dependent programmed cell death (PCD) which is a rapid response arresting the development of pathogenic infection. On the other hand, avirulent factors upon feeble recognition as well as flagellin or chitin through FLS2 also promotes basal defenses via different pathways including MAPK. Basal defenses subsequently stimulate expression of defense genes or induces late onset of pathogenic cell death. Formation of papillae at the site of nascent colonization of bacteria or site of fungal penetration corresponds to defense mechanism associated to cell wall. Jasmonic acid (JA) signaling pathway upon activation induces suppression of salicylic acid (SA) transduction pathway leading to repressed expression of specific pathogen related gene. Reactive oxygen species triggered oxidative stress is direct bactericidal in nature. Moreover, already existing antimicrobials help in repulsion of pathogenic activity. As a counter response to pathogen attack, signaling through programmed cell death facilitates cell death. The expression of the *NHO1* gene expression triggered by nonhost and/or avirulent bacterial pathogens is necessary in certain cases of non-host resistance. *PR* pathogen related gene, *PCD* programmed cell death, *NHO1* non-host resistance 1

gene that encodes for a secreted lipase (type II) essential for imposing complete virulence by *X. oryzae pv. oryzae* (Aparna et al. 2009) and also *X. campestris pv. vesicatoria* (Tamir-Ariel et al. 2012). Additionally, it has been discovered that T4SS which is generally associated with translocation of DNA and protein to the extracellular locale or inside host cells, mediates the transfer of T-DNA in *Ag. Tumefaciens* inside plant cells that confers in altered metabolic functions and morphology leading to tumor development (Bhatty et al. 2013; Gohlke and Deeken 2014).

These effectors improve microbial competence in the plant environment by interfering with essential phyto-processes. T3Es are reported to majorly suppress

plant immune responses (Macho and Zipfel 2015). *Xanthomonas* and *Ralstonia* spp. members encode TAL effectors (transcription activator-like) which are phyto-transcription factors and are interlinked with promotion of plant virulence as well as providing a bacterial growth compatible environment (Bogdanove et al. 2010). *X. oryzae* pv. *oryzae* (rice pathogen) utilizes various TAL effectors to modify the gene expressions encoding sugar transporters (SWEET). The resulting sugar in apoplast, effluxed from the plant cells may be accompanied with release of water for maintenance of tissue osmotic balance that further alters the milieu of intracellular spaces thus providing advantage for bacterial infection (Streubel et al. 2013; Macho 2016). In *X. campestris*, AvrBs3 (TAL effector) upregulates UPA20 expression which regulates the size of plant cells and thereby causes enlargement of mesophyll cells leading to increased bacterial dissemination and growth (Kay et al. 2007). *P. syringae* associated T3ES like AvrPtoB, AvrRpt2, and HopX1 modulate the respective activities of ABA (Abscisic acid), auxin, and JA signal transducing pathways (Cui et al. 2013; Gimenez-Ibanez et al. 2014). Phyto-metabolic activities are also found to be directly modified by T3Es as they intrude secondary metabolites forming biosynthetic pathways. Perturbance of metabolism of phenylpropanoid by T3E belonging to the AvrF family secreted by *Pantoea stewartii* enhances the virulence of phytopathogens (Asselin et al. 2015). Similarly, mitochondrial activities are curbed by HopG1 that impedes plant development and may also increase the virulence (Block et al. 2010).

4.1.8 Subduing Plant Defense Mechanisms by Phytopathogenic Bacteria

To circumvent the defense mechanisms of plants, pathogenic bacteria utilize diversified strategies to target and modulate core constituents of phyto-immunity including JA signal transducing pathway, HR (hypersensitive response)-dependent programmed cell death (PCD), defensive and basal gene expressions as well as cellular wall-related defense mechanisms. Table 2 and Fig. 3b represent certain host phyto-defenses that are commonly targeted by the virulent bacteria.

4.2 Viral Phyto-pathogenesis

Plant pathogenic viruses must expropriate host survival factors. The viral-encoded multifunctional proteins should strategically be involved in different phases of life cycle and elicit defensive responsiveness. Thus, most viral encoding protein usually performs the role of determinants of pathogens. The viral proteins regulating replication, encapsidation, transmission, and motility may play prominent role in directly or indirectly modulating pathogenesis.

Table 2 Few phytopathogen-mediated subversion of various plant defense mechanisms

Sr. No.	Phytopathogens	Particular defense targets	Probable mechanism to surpass the plant defense system
1	<i>P. syringae</i> pv. <i>tomato</i> DC3000	Various pathogenic DC3000 effectors like AvrPtoB, HopPtoD2, AvrPto, AvrRpt2 target hypersensitive response dependent programmed cell death, pathogenesis related gene expression, cellular wall mediated and basal defenses (Abramovitch et al. 2003; Espinosa et al. 2003; Bretz et al. 2003; Jamir et al. 2004; Hauck et al. 2003; Lim and Kunkel 2004)	Programmed cell death is restrained along with increased susceptibility toward infection. Often their functions are dependent on tyrosine phosphatase or cysteine protease enzymes activity. May also prevent formation of papillae while inducing alterations or downregulation of cell wall related and pathogenesis related genes expression. Basal defense mechanisms are attacked by targeting RIN4
		Effectors of type III secretion system (TTSS) target expression of non-host resistance (NHO1) gene or programmed cell death gene expression (Kang et al. 2003; Liang et al. 2003)	NHO1 resisting non-host pathogens is generally downregulated by coronatine insensitive 1 (COI1) dependent fashion. Moreover, the pathogen may also trigger expression of ACD5 (a ceramide kinase), which acts as a negatively regulates cell death
		Effectors of type III secretion system in association with coronatine toxin attack defense mechanisms controlled by jasmonic acid signal transduction pathway (He et al. 2004)	Activation of coronatine insensitive 1 (COI1) and Jasmonic acid insensitive 1 (JAI1) signaling pathways with simultaneous suppression of salicylic acid-based defense system
2	<i>X. campestris</i> pv. <i>vesicatoria</i>	Effectors of type III secretion system targets the cell wall associated defense system (Brown et al. 1995)	The virulent pathogens act by inhibiting papillae formation
3	<i>Rhizobium</i> sp. <i>NGR234</i>	The effector NopL targets expression of pathogen related genes (Bartsev et al. 2004)	The pathogen causes suppression of the pathogen related gene
4	<i>B. graminis</i> f. sp. <i>hordei</i>	Hypersensitive response dependent programmed cell death is targeted in addition to cell-wall mediated defense (Piffanelli et al. 2002)	Negative cell-death regulators MLO and BL1 genes are activated by the virulent pathogen that allows pathogenic invasion
5	<i>S. lycopersici</i>	The enzyme tomatinase targets already synthesized antimicrobials and hypersensitive reaction-based programmed cell death (Bouarab et al. 2002)	Tomatinase enzymes leads to degradation of saponins that provide plant defense. The degeneration of saponins results in formation of by products that contributes in repression of hypersensitive reaction-based programmed cell death
6	<i>P. infestans</i>	Soluble forms of glucans target hypersensitive reaction-based	

(continued)

Table 2 (continued)

Sr. No.	Phytopathogens	Particular defense targets	Probable mechanism to surpass the plant defense system
		plant defense mechanism and also generation of ROS (Doke 1975)	The ROS burst is inhibited with hypersensitive reaction suppression
7	<i>M. pinodes</i>	Suppression (Glycopeptide) targets pathogen related gene expression and hypersensitive reaction-based plant defense mechanism (Yoshioka et al. 1990)	plasma-membrane regulated ATPase activity is modulated to defense mechanism suppression

4.2.1 RNA-replicase-Associated Viral Proteins and Their Role in Phyto-pathogenicity

Viral RNA replicase (i.e., RNA dependent RNA polymerase) through modulation of viral replication process and consequent accumulation of virus, indirectly affects phyto-pathogenesis. Reports reveal that in both *Tobacco mosaic* (TMV) (Lewandowski and Dawson 1993; Chen et al. 1996) and *Pepper mild mottle* (PMMoV) (Yoon et al. 2006) viruses, mutation of p126/p183 proteins (RNA replicase-related proteins) resulted in truncated accumulation of virus along with attenuated symptoms. Similar observations were concluded in case of 2a protein mutation in *Cucumber mosaic virus* (CMV). The molecular mechanism of RNA replicase in development of the phyto-disease involves auxin (Aux) responsive pathway reprogramming. It is interconnected with TMV126/183K replicase crosstalk with IAA (indole acetic acid)/Aux that confers in corresponding enhancement in viral accumulation (Padmanabhan et al. 2008). RNA replicases function as elicitors of ETI (effector triggered immunity) operated by R-gene resulting in hypersensitive response. They may influence either localized lesions due to necrosis or systemic symptoms that are viral specific. These viral polymerases may also perform the role of breaking determinants of different resistance sources thereby modulating pathogenesis. It has been seen that *Tomato mosaic virus* replication proteins can subvert inhibitory interplay with resistance Tm-1 gene products via point mutation (Ishibashi et al. 2007). Alteration of single amino acid in methyltransferase domain of Potato virus X replicase assists disruption of JAX1 (jacalin-type lectin required for potexvirus resistance 1)-mediated resistance in *N. benthamiana* (transgenic) system (Sugawara et al. 2013).

4.2.2 Viral Coat Proteins-Mediated Pathogenicity

These are prototypical and multifunctional viral proteins that are associated with multifaceted functions such as encapsidation, replication, motility, translations, and even host defense responsive system (Ni and Cheng 2013). The expression of symptoms in concerned host plants is significantly affected when the coat proteins

of respective CMV (Shintaku et al. 1992), TMV (Dawson and Bubrick 1988), Turnip crinkle virus (TCV) (Heaton et al. 1991), and Brome mosaic virus (Rao and Grantham 1996) undergo point mutations. The coat proteins of Tomato mosaic virus (TMV), CMV, Potato virus X(PVX), TCV, and PMMoV (Moffett 2009; Gilardi et al. 1998) act as avirulent factors eliciting resistance coordinated by the R gene (dominant). The coat proteins of TCV promote hypersensitive response development in resistant strain of *Arabidopsis* ecotype Dijon. The HRT and RRT host genes as well as SA signaling control such types of responses (Kachroo et al. 2000). The transcription factor TIP belonging to the NAC family interacts with coat proteins which stimulates the action of HRT gene and also inhibits TIP localization in nucleus (Ren et al. 2000, 2005). Photosystem II electron transport is prevented by tobamovirus-mediated infection which disrupts oxygen-evolving complex (OEC) (Rahoutei et al. 2000). Infected host plants revealed that the levels of OECpsbP and PsbQ (photosystem II proteins) are decreased in comparison to healthy plants. It has been recently demonstrated that while the interaction of PspB with Alfalfa mosaic virus's (AMV) coat protein results in inhibition of viral replication (Balasubramaniam et al. 2014), mutation of amino acid on the other hand renders virulence to the coat protein of CMV pepo strain that represses genes associated with chloroplast and photosynthesis thus causing chlorosis in tobacco plants infected with CMV (Mochizuki et al. 2014).

Similarly, interaction of coat protein of ToMV with IP-L (specific tobacco protein) causes localization of thylakoid membranes (Zhang et al. 2008). Also, the outer capsid P2 protein of phyto-reovirus upon interacting with the biosynthetic mediator of gibberellins known as entkaurene oxidase promotes dwarf symptoms (Zhu et al. 2005).

4.2.3 Viral Protein Interrelated with Movement and Their Role in Phyto-infections

The phyto-viruses are translocated into the cells of host plant with the help of movement proteins (Pallas et al. 2011; Lucas 2006) as these play an essential role in determining specificity of host (Mise et al. 1993). Various endogenous host factors are manipulated by the movement proteins facilitating the transportation of viral genome finally leading to alterations in physiology of plants with directly affecting the symptoms. The interaction of host plant factors with movement protein may facilitate or impede the viral movement as seen in case of the interplay between the crucial hydrogen peroxide decomposing enzyme tomato catalase (CAT) 1 and TGBp1 (triple gene block protein 1) of PepMV (Mathioudakis et al. 2013). This interaction leads to excessive peroxide scavenging and thus aid in development of PepMV infections by negatively regulating plant defense system. Movement protein also gives rise to hypersensitive reaction upon interaction with R gene. The avirulent determinant that potentiates Sw-5 (tomato gene)-induced resistance against tomato spotted wilt virus is suggested to be dependent on movement protein NSm (Peiro et al. 2014). The Potato virus X triple gene block protein 3 (TGBp3) promotes

programmed cell death as well as unfolded protein response during the course of infections caused by PVX (Ye et al. 2013). The movement proteins also contribute in enhancing viral RNA silencing thus manipulating susceptibility of host plants mediated by stimulating silencing among cells (Amari et al. 2012).

4.2.4 Viral Suppressors of RNA Silencing

Certain viral proteins cause disruption of phyto-homeostasis counteracting with antiviral silencing and lead to development of disease symptomatology (Wang et al. 2012; Pallas and Garcia 2011). Transgenic expression of RSSs (RNA silencing suppressors) leads to development of abnormalities that mimics disease symptoms (Chellappan et al. 2005; Dunoyer et al. 2004). These RSSs employ different mechanisms to interrupt the silencing processes, mainly at post transcriptional phase and sometimes also during transcription (Incarbone and Dunoyer 2013) that results in phyto-disease (Wang et al. 2012). miR167 upon being inactivated by RSSs like potyviral HCPro, tombusviral P19, and pecluviral P15 causes dysregulation of auxin response factor 8 which majorly contributes in development of abnormalities (Jay et al. 2011). It has also been suggested that inactivation of miRNAs regulating (negatively) NBS-LRR-R genes involved in autoimmune response induction by the RSSs may result in overexpression of these R genes conferring in lethal necrosis and other deleterious effect (Wang et al. 2012; Li et al. 2012; Shivaprasad et al. 2012). Similarly, the strategies of RSSs to inactivate AGO1 (Argonaute-1) and other effector proteins lead to inhibition of antiviral silencing and evoke developmental abnormalities as observed in cases of 2b and TGBp1 proteins of CMV and PIAMV respectively (Zhang et al. 2006; Okano et al. 2014). Additionally, the ability of RSSs to induce pathogenic symptoms without blocking gene silencing directly has also been implied (Du et al. 2014). While the Cauliflower mosaic virus-associated RSS P6 interacts with ethylene signaling (Geri et al. 2004), CMV-related RSS 2b manipulates catalase of host plant (Inaba et al. 2011) and Potato virus A-associated HCPro RSS usurps microtubule-related protein (Haikonen et al. 2013). HCpro interactions are also responsible for precipitating proteasomal dysfunctions that contribute in pathogenicity (Pacheco et al. 2012). Performing the role of elicitors for ETI (effector triggered immunity), acting as second phyto-defensive layer, RSS can also cause developmental disease symptoms (Wang et al. 2012). For example, RSS P19 associated to tomato bushy stunt virus (TBSV) is known to induce hypersensitivity response (Chu et al. 2000).

4.2.5 Other Phytopathogenic Viral Factors

Together with the above-mentioned viral protein, certain addition proteins have also been researched that contribute to viral pathogenicity. P1 (Chiang et al. 2007), P3-6K1, CI (Desbiez et al. 2003), P3N-PIPO (Hisa et al. 2014), and 6K2 (Spetz and Valkonen 2004) proteins of potyviruses, p25 (Klein et al. 2007) and p31 (Rahim

et al. 2007) of Beet necrotic yellow vein virus, are some of the examples of such viral determinants of pathogenicity. But the molecular mechanistic strategies of these proteins need to be thoroughly explored. Moreover, the nucleic acid of virus can also be function as direct determinants of viral pathogenicity. In case of defective interfering RNA (DI) of tombusvirus, DI-specific siRNA gets accumulated due to interference thereby saturating the capacity of silencing suppressor P19 to bind siRNA (Havelda et al. 2005).

4.3 Fungal Phyto-pathogenesis (Vadlapudi and Naidu 2011; Yang et al. 2017)

In case of fungal pathogenesis, well-conserved proteins are said to be used by fungal pathogens to induce infection. The fungal pathogens are known for deploying novel mechanisms to promote infections such as formation of appressoria, which are special infection structures that allow penetration of host plant cells.

The complete function of virulence protein is primarily facilitated by peroxisomes during this process of infection as in case of *Magnaporthe oryzae* (rice blast fungus). *Colletotrichum higginsianum* causes anthracnose disease in cruciferous plants via ChSTE7 gene that contributes in forming appressoria, vegetative and invasive growth in plant host tissue. Acetylation and other modes of histone modifications like methylation control regulation of transcription and structural chromatin organization to induce functional response. The genetic expression profiles are strategically transferred by the process of histone modification. The growth and fungal development are suggested to be controlled by SET-domain comprising proteins. It has been observed that Ash1like histone modification protein MoKMT2H essentially participates to induce pathogenesis of *M. oryzae*.

5 Conventional Strategic Approach for Phyto-infections and Disease Management

Epiphytotics (plants disease epidemics) transpires in crops every year and is a common phenomenon in different parts of the world. Plant pathogens negatively impact the both quality and quantity of the marketable agricultural yield that adversely affect the economy (Agrios 1997). Globally, phyto-diseases are responsible for 14% crop loss, while yield losses may account to 20–40% in the cultivates varieties (Baker et al. 1997). The pathogenic dissemination possesses a serious threat to the sustainable supply of food chain as it is responsible for enhancing the severity as well as the incidence of disease development (Savary et al. 2012). Although eradicating the phytopathogens completely still remains a challenge, extensive

research is going on to explore new avenues for management of these infections in plants.

Among the various approaches that are associated in managing the plant infections, the conventional strategies include (1) implementing good and proper farming techniques that can resist infections, (2) destroying physically that is by plucking uprooting, etc. the affected or infected plant parts and tissues such as wilted roots, or stems, diseased fruits and other parts to hinder pathogen transmission from the infected to healthy parts, (3) control of pathogens through different measure which might involve insecticides or broad spectrum pesticides (e.g., copper) to check insect vectors, antibiotic to suppress infections precipitated by bacteria. These strategies mainly emphasize in preventing the plant disease to spread to healthy parts rather than on the cure of phyto-infections. Multi-integrated disease management practices are generally preferred. In cropping system and also in horticulture, use of disease-resistant plant and hybrid varieties is widely practiced. On the other hand, to minimize the use of hazardous and toxic chemical in environment, development of genetically modified plants is also being used that have the capacity of resisting development of pest and pathogens. However, such plants have limited cultivations due to their associated risk and low consumer acceptance (Hails 2000). Producers also take care and use sanitized and disinfected, certified virus/bacteria free tools and farming equipment to curb the growth of pathogens. Crop rotation techniques are followed and care is taken to prevent development of wound on plant surface that serves as an entry point for virulent pathogens. Additionally, bacteriophages are also used to control bacterial pathogenesis specifically to prevent bacterial infections. Phage-coded endolysins are also being attempted to be successfully incorporated in plants. As an alternative to use antimicrobial in agriculture, host-specific phages are being widely researched to reduce the environmental risks and concerns (Frampton et al. 2012). However, all these methods are associated with their individual shortcoming and thus require integrative approach of implementing two or more strategies to prevent crop loss to diseases. Although several countries witnessed evident abundancy in agricultural output as a consequence of green revolution (Pingali 2012), but this food and crop prosperity is gradually becoming disturbed due to pathogenic attack of food and plants, climatic changes, deterioration of soil quality, scarcity of arable lands, extensive increase in population, and many other associated factors.

In order to reinstate the food security, complementary strategies that are both efficacious and environmentally safe are need of the hour. In this context, the field of nanotechnology with its diversified applications and benefits may serve as an exciting opportunity to establish nano-weapons that may prove advantageous in phyto-disease management.

6 Nanotechnology and Its Impact on Agricultural Produce

For the past decades, extensive research on nanoscience and its associated technologies are constantly evolving in the fields of agriculture and also food system (Nair et al. 2010). Development of novel nanoparticles is being implemented to improve the chain of food supply with sustainable intensification and also by managing soil and water conditions. With at least one dimension having a size range of 1–100 nm, the nanomaterials are characterized by unique size-dependent properties, which include higher surface: volume ratio, better conductance ability, optical properties. Such varied features allow these nano-systems to be used not only to protect plants but also to provide them with nutrition (Ghormade et al. 2011). Nanomaterials are also being used for biotechnological purposes (Mukhopadhyay 2014; Dapkekar et al. 2018; Silva et al. 2010) which include amelioration of complications-associated soil structure providing stability against soil erosion and maintain salinity balance, increasing availability of nutrient and mobility, for identifying moisture content, availability of macronutrients, pH of soil, etc. and controlling environmental pollution, and finally as nano-cargoes for delivery of herbicides, pesticides, siRNAs, micronutrients, DNA, etc. The utilization of nanotechnology is not only restricted to the biotechnological advancements but is also extensively implemented in agriculture (Mohmood et al. 2013; Khiyami et al. 2014; Paknikar et al. 2005) where it is used for removing water or soil contamination, antimicrobial advanced food packing, nano-barcoding, biosensors, agro-commodities shelf life indicators, nanoparticles (clay-based)-mediated water management, bioremediation, etc. Figure 4 depicts the diversified application of nanotechnology in different fields of agriculture. For the past few decades, there has been steady increase in integrating nanotechnologies with agricultural practices. However, every avenue of

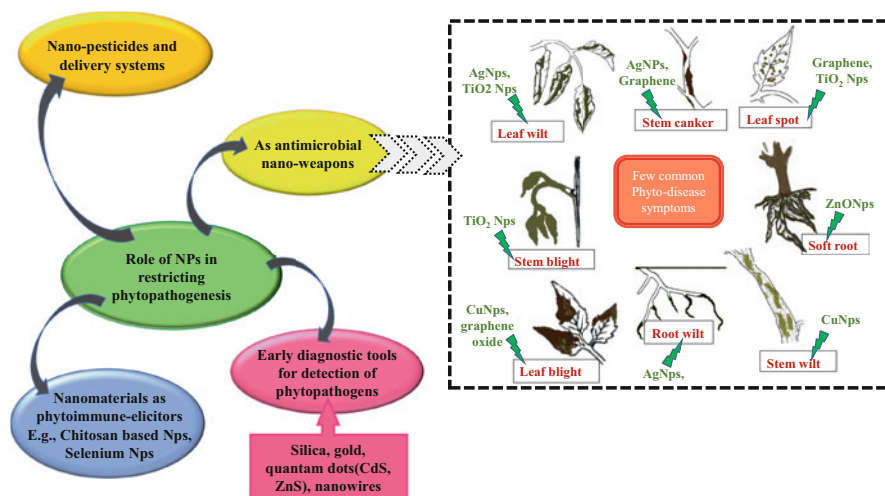


Fig. 4 Nanotechnology and their diversified role in management of plant diseases

nanotechnology and its advantages should be explored to the fullest and implemented strategically to maintain quality, sufficiency, and security of food supply, along with prevention of phyto-infections, diagnosis of plant disease, and genetic transformations.

7 Types of Nanoparticle and Their Role in Phytopathogen Suppression

7.1 Silver Nanoparticles (AgNps)

AgNps are well known for their broad spectrum and potent antibacterial activities and based on these properties, they were first investigated for management for phyto-diseases. Numerous studies have pointed out the efficacy in plant disease management. Prior application of nano-formulation containing silver and silica with a hydrophilic polymer (0.3 mg/L) on the cucumber leaves has been reported to show protective effect against *Podosphaera xanthii* (Park et al. 2006). Similarly, colloidal silver nano-formulation restricted the growth of *Sphaerotheca pannosa* and thus prevented the occurrence of rose powdery mildew (Kim et al. 2008). Similar studies were further substantiated with more detailed investigations in which silver nanoparticles (10–100 mg/L) were sprayed on cucumber and pumpkin leaves before and after the plants were infected with powdery mildew. The results indicated that at both stages of application, highest concentration of AgNps formulation was associated with only 20% disease incidence. Such results also indicated the rationale use of AgNps for rescue treatment as the nanoparticles produced comparable outcomes with that of a few commercially available fungicides (Lamsal et al. 2011a). Another study pointed out the efficacy of NanoAg formulation (100 mg/L) in suppressing anthracnose disease outbreak when applied to peppers prior to the infection (Lamsal et al. 2011b). It was also found that the postharvest disease severity in banana caused by *Colletotrichum musae* was significantly reduced when applied at a concentration of 2000 mg/L (Jagana et al. 2017). Silver nano-formulations are found to be effective in controlling various phytopathogens belonging to fungal and bacterial species like *Xanthomonas*, *Bacillus* sp., *Acidovorax*, *Pseudomonas*, and *Azotobacter* sp., (Fayaz et al. 2009; Krishnaraj et al. 2012; Mala et al. 2012). AgNps are also found to act synergistically with other Nps of Titanium dioxide (TiO₂), graphene oxide, silicon-aluminum carbide, and copper for providing protection against infections such as scabs, wilts, and molds caused to economically important agricultural crops like tomatoes, potatoes, and rice (Ocsoy et al. 2013; Boxi et al. 2016; Strayer et al. 2016; Aleksandrowicz-Trzcińska et al. 2018; Bhargava et al. 2018). Studies have pointed out AgNps stabilized by mucin derived from bovine submaxillary show potent action against seedling infections caused by both gram-negative and gram-positive bacteria such as *Acidovorax*, *Xanthomonas*, and *Clavibacter*, respectively (Makarovsky et al. 2018). On the other hand, bile salt sequestered AgNps were

found to be effective against anthracnose disease (Shanmugam et al. 2015). While Ag-chitosan nanocomposites were found to prevent infections in strawberry caused by molds (Moussa et al. 2013), potent antifungal efficacy of amphopolyglycinate-stabilized silver nano-dispersions has been observed against phytopathogenic fungi like *Phytophthora infestans* isolated from pathogen infected potatoes (Krutyakov et al. 2016). AgNps are also being considered as alternative to pesticides owing to their wide range of antimicrobial potency.

7.2 Copper Nanoparticles (CuNps)

The crucial role of redox active transition element copper in plant biology is well accepted. This trace element is an integral component of most metalloenzymes that participate in different plant metabolic processes like photosynthesis respiration (Elmer and White 2018). Copper and its associated compounds comprised the first metal containing fungicides that were used to check pathogenic invasions and since then their wide-ranging antimicrobial activity has been utilized for antipathogenic management for centuries (Lamichhane et al. 2018). In order to resist bacterial blight copper hydroxide, Bordeaux mixture, copper oxychloride, etc. are still being used in pomegranate (Ruparelia et al. 2008). In the recent years, copper nanoparticles are being investigated for their anti-pathogenic activities and also being manufactured in large-scale industrial level. Various factors like of copper concentration, pH, temperature, and also pathogenic concentration affect the bioactivity of copper Nps (Ruparelia et al. 2008). Studies have pointed out CuNps treatment (0.2 mg/L) inhibited the growth of *X. axonopodis* pv. *punicae*, suppressing water-soaked lesion and thus protecting pomegranate leaves (Mondal and Mani 2012). On the other hand, CuNps formulation in conjugation with MBPF-01 (*Pseudomonas fluorescens* strain, antagonist strain of bacteria) conferred in 70% reduction in incidence of leaf blight infection in rice plants mediated by *X. oryzae* pv. *Oryzae* (Mondal et al. 2010). CuNps also manifest significant protective action against mungbean blight caused by *X. axonopodis* pv. *phaseoli* (Mondal and Mani 2012; Mondal et al. 2010) while wilt disease in tomato caused by *Fusarium* and *Verticillium* was markedly reduced on application of foliar nanoformulations of copper oxide, manganese oxide, and zinc oxide (Elmer and White 2016). Its destructive effects toward pathogens such as *Alternaria alternata*, *Phoma*, and *Curvularia lunata* are also well known (Kanhed et al. 2014). Recently, reports exhibited inhibitory efficacy of Cu-copper oxychloride (Cu-CoC) nano-formulation (50 mg/L) against *Phytophthora cinnamon*. Mycelial development as well as sporulation were suppressed by their synergistic effect when used against the phytopathogen *Alternaria alternata*. When used against *Pseudomonas syringae*, CuNps showed inhibitory action at 200 mg/L concentration. Studies have also pointed out the biocompatibility of these Nps as they do not adversely affect microorganisms beneficial for plants such as *Rhizobium* spp. and *Trichoderma harzianum* (Banik and Luque 2017). Novel nano-compounds such as fixed quaternary ammonium compounds, core shell copper composites, multivalent copper

nanoparticles evaluated for their protective effects against tomato bacterial spot demonstrated bactericidal activity against causative agent *Xanthomonas perforans* (copper-resistant strain). Such copper nanoparticles have manifested evident control of phyto-diseases under greenhouse environmental conditions without negatively affecting the yield of tomatoes (Strayer-Scherer et al. 2018). They also efficiently inhibit *Phytophthora infestans* infections in tomatoes (Giannousi et al. 2013). When used against species belonging to fusarium genera, CuNps showed potent activity in resisting the phytopathogens *Fusarium equiseti*, *F. oxysporum*, and *F. culmorum* (Bramhanwade et al. 2016). Green synthesis of copper nanoparticles with leaf extract of papaya demonstrated significant inhibitory effect on soil-borne *Ralstonia solanacearum*, causing wilt under both normal and green house conditions (Chen et al. 2019). Additionally, CuO nanoparticles in the form foliar spray also showed bactericidal effect against *Fusarium oxysporum* f. sp. *niveum* in watermelons thereby preventing wilt. Under greenhouse surroundings also these nanoparticles evinced bactericidal actions with simultaneous increment in yield (Elmer and White 2018). Copper nano-formulations, synthesized using *Streptomyces zaomyceticus* Oc-5 and *Streptomyces pseudogriseolus* Acv-11, were found to be efficient antifungal activities against a number of phytopathogenic fungal strains like *Aspergillus niger*, *Pythium ultimum*, *Alternaria alternata*, and *Fusarium oxysporum* (Hassan et al. 2019).

7.3 Zinc Oxide (ZnO)-Based Nanoparticles

Inorganic zinc oxide possesses unique photocatalytic, optical, electrical as well as magnetic characteristics (Wang 2004). In addition to the wide-ranging usage in ceramics, pharmaceuticals, rubber industry, ZnO-Nps are also being extensively used in the agricultural industry. Apart from its function as micronutrient fertilizer, recent studies also document the antimicrobial efficacy of these Nps (Kołodziejczak-Radzimska and Jesionowski 2014; Dizaj et al. 2014). Zinkicide SG4 & 6 formulated as zinc oxide-based nano-formulations when tested against *X. citri subsp. citri* and *C. paradisi* exhibited potent bactericidal effect when applied in foliar spray and thus decreased the developmental incidence of citrus canker in sweet orange and prevented grape fruit (ruby red) rot (Graham et al. 2016). Zinkicide exhibited broad spectrum activities against disease caused by phytopathogenic fungi such as *Elsinoe fawcetti* and *Diaporthe citri*, lowering the incidence of citrus scab and melanose on grapefruit. The zinc oxide nanoparticles are also reported to resist the phytopathogenic effects of bacteria species like *Xanthomonas citri subsp. citri*, *E. coli*, and *X. alfalfa subsp. citrumelonis*. Moreover, their potential actions against *Botrytis cinerea* and *Penicillium expansum* causing postharvest disease are also documented. Conidiophores along with conidia development in *P. expansum* are restrained by the zinc-based nanoparticles that gradually lead to degeneration of the hyphae of pathogenic fungus thereby losing their ability to cause infection (He et al. 2011). In another studies ZnO Nps when used in broth of mung bean broth and also in

sand, resulted in significant repression of *F. graminearum* growth (Dimkpa et al. 2013a). It also inhibits the mycelial growth of pathogenic *Sclerotinia homoeocarpa* and thus prevents the appearance of dollar spots in cool season turfgrasses (Li et al. 2017). Nanocomposites of silica and zinc oxide were found to be toxic against *Cercospora beticola* Sacc and thus prevented sugar beet from the disease CLS (*Cercospora beticola* Sacc) (Derbalah et al. 2012). The inhibitory potency of these Nps against *Aspergillus fumigatus* and *A. flavus* has also been documented (Navale et al. 2015).

7.4 Titanium Dioxide (TiO₂) Nanoparticles

Owing to the chemical stability and nontoxic nature of titanium dioxide, their nano-formulations are widely being explored for environmental and agricultural applications. Having a long shelf life, TiO₂ has been reported to have antibacterial effect. It has been seen that titanium oxide Nps enhance the photosynthetic rate and promote growth of plants with simultaneous increment in yield and truncated disease severity (Chao and Choi 2005). In a field trial, titanium nanoparticle in the form of foliar spray manifested high protection against the phyto-diseases brown blotch as well as cercospora leaf spot in *Vigna unguiculata* Walp (Owolade et al. 2008). On the other hand, lesions in geranium plants and leaf spot disease in poinsettia plants caused by *Xanthomonas hortorum* pv. *pelargonii* and *Xanthomonas axonopodis* pv. *poinsettiicola* respectively were evidently reduced by the application of TiO₂ nano-formulations (Norman and Chen 2011). The TiO₂ nanoparticles are also known of imparting photocatalysis (Paret et al. 2013a). Studies have also revealed the potency of titanium hollow nanoparticles with or without silver doping as potent antifungal agents resisting the development of tomato or potato wilt caused by *Fusarium solani* and apple scab infection by *Venturia inaequalis*. Owing to the photocatalytic property, the significant antimicrobial efficacy was found in visible light. The titanium nano-formulations at low dose is also found to arrest the formation of fungal pathogenicity imparting naphthoquinone pigment in *Fusarium solani* (Boxi et al. 2016). When combined with zinc, the TiO₂-Zn nanocomposites revealed reduction in severity bacterial spot in tomatoes with resisting the growth of *Xanthomonas perforans* without any adverse effect on the yield (Paret et al. 2013b). Colonization of *Hypocrea lixii circinelloides* and *Mucor circinelloides* is also significantly arrested by titanium oxide Nps thus preventing decay in wood (De Filpo et al. 2013). The oxidizing capability of titanium nanoparticles renders their antimicrobial efficacy. These Nps degrade the cellular membrane in bacteria leading to cellular components leakage that succumbs to impediments essential cellular activities (Frazer 2001). TiO₂ is often used as nanocarriers for silver nanoparticle that allows them not to get aggregated.

7.5 Other Nano-formulations Preventing Phyto-pathogenesis

In addition to all the nanoparticles discussed individually earlier, many of them are used in combination which may impart improved antimicrobial activities. Studies have indicated the potency of silver-silicon dioxide in preventing infections caused by *Phytophthora capsici*, *Fusarium oxysporum* as well as *Rhizoctonia solani* (pathogenic soyabean crop fungi) mediated by generation of reactive oxygen species in association with the released silver ions from the nanoparticles' surface. Such results imply promising role of Ag-SiO₂ nanocomposites in soyabean farming (Nguyen et al. 2016). The essential functions of sulfur in plant biology is well known and it is used as one of the primary components in many formulations used for commercially managing plant infections. Recently the efficacy of sulfur nanoparticles in organic farming is also being explored to protect crops and plants like apple, tomato grapes, and potatoes (Rao and Paria 2013). Sulfur nanoformulation (1000 mg/L) has been found to significantly reduce the invasion of *Erysiphe cichoracearum* in okra (Gogoi et al. 2013) and requires lower concentration than that of available commercial products to prevent the powdery mildew infection. While *Aspergillus niger* is efficiently restricted by sulfur Nps, early blight in tomatoes and apple-scab caused by *F. solani* and *V. inaequalis* is also decreased evidently by the small-sized nanoparticles (Rao and Paria 2013). As the nanoparticles deposit on the fungal cell wall, they contribute in its digestion leading to leakage of cytoplasmic components and subsequent fungicidal activity.

Other nanoparticles possessing antibacterial potency are the graphene oxide ones. The graphene oxide (GO) Nps have shown to inactivate *X. oryzae pv. oryzae* strain resistant to copper, *Aspergillus oryzae*, *A. niger*, and *F. oxysporum* (Chen et al. 2013). GONps demonstrated 90% cell death when applied against *Pseudomonas syringae*, *X. campestris pv. undulosa* and also are being used in treating macroconidia caused by *F. graminearum* and *oxysporum* (Chen et al. 2014). Thus, they can efficiently protect against various diseases like bacterial leaf blight and leaf streak, fungal head blight. Studies have also indicated silver graphene nanocomposites to show antipathogenic efficacy against *X. perforans* therefore reducing the incidence bacterial spot in tomato plant (Ocsoy et al. 2013). On the other hand, silver graphene composites containing dsDNA have prominent effect in reducing severity of phyto-disease as they accumulate on the pathogenic cells destroying them (Ocsoy et al. 2013). These nanocomposites in another study were found to show potent inhibitory action against both Cu-tolerant and sensitive *X. perforans* strain causing tomato bacterial spots (Strayer et al. 2016). Bactericidal activity was also observed against other pathogenic strains like *X. vesicatoria*, and *X. gardneri*. Another recent study has revealed the enhanced protective effect of GO-Ag nanoparticles against the rice pathogen *X. oryzae pv. oryzae* in comparison to silver nanoparticles alone (Liang et al. 2017). In floriculture, and specifically during the stages of growth as well as post-harvest, the fullerene nanoparticles can render protection against rose plants infection by resisting the growth of *B. cinerea* (Hao et al. 2017). Zinc oxide and magnesium oxide nanoparticles and also their

combination nanocomposites (ZnO-MgO) and ZnO-Mg(OH)₂ are reported to possess potent bioactivity against the fungal phytopathogen *Colletotrichum gloeosporioides* responsible for causing anthracnose in economically important crops like *Persea americana* and *Carica papaya*. These nanoparticles cause structural degradation of conidia thereby preventing its germination and thus can prevent anthracnose disease commonly occurring in tropical fruits (De la Rosa-García et al. 2018). MgO nanoparticles when used for treating roots of tomato seedlings depicted efficacy in protecting them against the incidence of infection caused by *Ralstonia solanacearum* while another study revealed their efficacy in inhibiting the Cu-resistant strain of *X. perforan* (Imada et al. 2016; Liao et al. 2019).

7.6 Suppression of Phytopathogens by Green-synthesized Nanoparticles

In the recent years, researchers have concentrated in the field related to green synthesis and its rationale utilization to resist phytopathogens and their adverse effects. Ag, Cu, gold (Au), Zn, and other metallic nanoparticles formulated as biosynthetic preparations are known to exhibit broad spectrum antipathogenic activities with potent antibacterial efficacy against both gram-positive and -negative bacteria including *Bacillus subtilis*, *S. aureus*, and *E. coli* and also against certain virulent fungi like *Aspergillus niger*, *F. oxysporum* (Nisar et al. 2019). While green synthesized silver nanoparticles using *Streptomyces* exhibited strong antifungal activity against *A. niger*, *Alternaria alternata*, *Pythium ultimum*, and *F. oxysporum*, zinc oxide and titanium oxide nanoparticles formulated using extract of lemon fruit resisted the incidence of stem and root infection of sweet potato caused by *Dickeya dadantii* (Hossain et al. 2019). On the other hand, chamomile flower extract used as reducing agent in formulating magnesium oxide and manganese dioxide nanoparticles resisted the growth of *Acidovorax oryzae*, the bacterial strain responsible for brown stripe infection in rice.

8 The Nanoparticles and Their Mechanisms to Prevent Phytopathogenesis

8.1 Metallic Nanoparticles

The probable mechanisms of the metallic nanoparticles in imparting antipathogenic activity are documented in Table 3.

Table 3 Mechanism of antipathogenic action of few metallic nanoparticles

Sr. No.	Metallic nanoparticles	Probable mechanistic action
1	Silver nanoparticles (Lamsal et al. 2011a, b; Jo et al. 2009; Mishra et al. 2014)	Triggers contact inhibition against formation of pathogenic spores as well as fungal hyphae. Hyphal wall degradation in turn leads to suppression of conidial germination. The silver nanoparticles also prevent germination of spores and promote deposition in vascular bundles
2	Silver-chitosan nanocomposites (Moussa et al. 2013)	Contribute in lysing the pathogenic hyphae
3	Silver quenched hollow titanium dioxide nanoparticles (Boxi et al. 2016)	Stimulates the formation of disulfide bonds and bond between silver and sulfur with microbial cell-proteins leading to cell degeneration and the free radical burden causes cell death
4	Copper nanoparticles (Palza 2015; Hajipour et al. 2012)	Nanoparticles after entering the cells produce soluble ions contributing to “Trojan horse effect” and also disrupts bacterial cell membranes
5	Cupric oxide nanoparticles (Elmer and White 2018; Chen et al. 2019)	Stimulates the expression of pathogen-resistant 1 gene and polyphenol oxidase. As the nanoparticles are absorbed through the cytomembrane they induce nanomechanical damage to the microbial cells and also impede the activities motility and pathogenesis related genes
6	Magnesium oxide nanoparticles (Imada et al. 2016)	Superoxide radicals are generated by the nanoparticles in polyphenolic presence. Also upregulate the expression of salicylic acid governed pathogen related gene 1, jasmonic acid governed Lipoxygenase A, ethylene mediated Osm, and systemic resistance inducible GluA. These nano-formulations also cause b-1,3-glucanase as well as tyloses accumulation promoting systemic resistance. These Nps also ensure cell membrane damage and leakage of intracellular damage leading to cell death
7	Zinc nanoparticles (Jin et al. 2009)	The bacterial cell membrane is degraded by these Nps leading to leakage of intracellular components and subsequent cell death
8	Zinc oxide NPs (He et al. 2011; Dimkpa et al. 2013a; Gordon et al. 2011)	Triggers oxidative stress through formation of free radicals such as hydrogen peroxide causing cell damage. The released ions also promote acidification and damage to hyphae with restricted growth of conidiophores and conidia
9	Silver and zinc oxide nanocomposites (Li et al. 2017)	These nanocomposites upregulate stress response genes expressions, viz., glutathione S-transferase and superoxide dismutase 2 and also elevate the amount of nucleic acid in fungal hyphae. Zinc transporter (Shzrt1) are also overly expressed

(continued)

Table 3 (continued)

Sr. No.	Metallic nanoparticles	Probable mechanistic action
10	Graphene oxide nanoparticles (Chen et al. 2013, 2014; Liang et al. 2017)	As the nanoparticles directly interacts with bacterial cell, they mediate membrane disruption with consequent disturbance in membrane potential promoting lysis of the bacterial cells. On the other hand, sporic wall damage instigates leakage of intracellular components. Graphene oxide Nps mediated oxidative stress also plays a major role in their antipathogenic activity
11	Titanium dioxide nanoparticles (Linsebigler et al. 1995)	ROS mediated oxidative stress guide pathogenic cell wall and membrane degradation. They also oxidize organic matter and exhibit photocatalytic activity

8.2 Green Synthesized Biocompatible Nanoparticles

Although metallic Nps being formulated following green synthesis exhibit potent antipathogenic effect, however, the exact mechanism by which they exert their action is still not completely known. The Nps have been documented to disrupt the normal protein functions by either oxidizing cystine in the iron binding site or degrading iron–sulfur cluster or by exchanging catalytic or structural metals. They may also cater to depletion of cell membrane potential or membrane degradation leading to impairment in cell-membrane or functions cause oxidative stress through generation of ROS. The oxidant and antioxidant balance is disturbed as the Nps deplete antioxidants and also inhibit expression of iron (III) transporter gene thus interfering with uptake of nutrients. Moreover, the nanoparticles also precipitate genotoxicity. Some or all of these mechanisms function simultaneously and contribute in the antipathogenic action (Lemire et al. 2013). The positive or very low negative charge bearing nanoparticles adheres to the microbial membranes that are negatively charged through electrostatic attraction and disrupts the morphological components and structures. These alterations depolarize the membrane and interferes with permeability of cellular membrane as well as respiration that confers in cell structures degeneration and final cell death. The degeneration of cellular structure causes the exudation of DNA, proteins, enzymes, metabolites, and other internal contents. Additionally, irregular pits produced by nanoparticles on the cell wall of the pathogens allow them to penetrate into the periplasmic tissues and intracellular spaces of the microbial cells (Gahlawat and Choudhury 2019). AgNps formulated through green synthesis technique promoted rupturing of cell wall with subsequent release of cytoplasmic as well as nuclear constituents and cellular swelling which resulted into bacterial cell death of *Acidovorax oryzae* strain (RS-2) (Elbeshehy et al. 2015). Similarly, according to another report, on application of another biosynthesized silver nano-formulation against *Fusarium graminearum*, it distorted hyphae and degenerated cell wall inducing antifungal activity (Ibrahim et al. 2020).

Corresponding outcomes were also observed in case of application of such AgNps against various pathogenic microbes such as *A. alternata*, *Botrytis cinerea*, and *Trichosporon asahii* (Xia et al. 2016). The cytotoxicity of these Nps can also be imparted through the generation of oxidative stress mediated by accumulation of ROS (Vankar and Shukla 2012). As a consequence of the release of free radicals, microbial cell wall as well as other integral components such as DNA, proteins, and lipids are degraded. ROS may impart mutation of DNA, its deletion, double or single stranded breakage, protein crosslinking, etc. (Soenen et al. 2011) and all these have synergistic antibacterial effect.

8.3 Nanoparticles and Their Role as Immune Elicitors

The natural co-polymers, chitosan, and chitin are together available in nature. Chitosan being a biocompatible polymer has several advantages like lesser toxicity, and biodegradability and has been used as drug delivery system for years (Rodrigues et al. 2012). Studies have revealed immunomodulatory function of chitosan in plant systems. Chitosan Nps promote growth and protects plants and also have biocide actions (Sathiyabama and Parthasarathy 2016). Foliar application of chitosan Nps results in augmentation of innate immunity mediated by various mechanism such as enhancement of activities of defensive enzymes, upregulated expression of genes related to defense system, and increment in total phenolic content. Biocompatible chitosan Nps are also used as phytosanitary agents (Chandra et al. 2015). Reports have pointed out the antifungal potency of chitosan Nps to protect finger millet leaves from blast disease symptoms caused by the invasion of *Pyricularia grisea*. These nanoparticles trigger ROS formation and elevate peroxidase enzyme activity in the leaves thereby leading to the antifungal action (Sathiyabama and Manikandan 2016). Yet another study depicted the ability of chitosan Nps in evoking nitric oxide that induced innate defense activities and protected tea plants from symptoms of blister blight infection (Chandra et al. 2017). Chitosan nano-formulations were also found to exhibit protective effects against *F. oxysporum*, *P. capsici*, *X. campestris* pv. *vesicatoria*, and also *Erwinia carotovora* causing infections in tomatoes. When used in maize to protect it from Curvularia leaf spot disease, biocompatible copper-chitosan nanocomposites showed potent antimicrobial action and also promoted plant growth. These nanocomposites aggravated activities of antioxidant enzymes like superoxide dismutase, peroxidase, polyphenol oxidase, and phenylalanine ammonia-lyase thus inducing a defense response (Choudhary et al. 2017). Harpin is known for eliciting death of hypersensitive cells, incite plant to be disease as well as insect-resistant, and effectuate plant growth. Through activation of PAMP (pathogen-associated molecular pattern)-induced immunity, harpin renders plant disease-resistant. Despite such biological activities, its use as biopesticide is limited because of poor assimilation. To overcome this hurdle, chitosan is used as biocarrier of harpin and when harpinPss (an elicitor derived from *P. syringae* pv. *syringae*) incorporated chitosan Nps were used, they promoted peroxidase and phenylalanine

ammonia lyase functions thereby resisting *Rhizoctonia solani* disease (Nadendla et al. 2018).

Selenium nanoparticles are also documented to produce resistance against root-knot nematode and thereby protect tomato plants from infection. Expression of PR-6 gene by selenium Nps results in upsurge of proteinase inhibitors activity and thus shields the roots and leaves from microbial invasion (Udalova et al. 2018). Similarly, when synthesized using *Trichoderma asperellum*, these selenium Nps restricted the incidence of downy mildew disease in pearl millets through truncated growth, viability of zoospore and sporulation of *Sclerospora graminicola* (Nandini et al. 2017). Moreover, selenium Nps are also found to arrest biofilm formation and viability of *Clavibacter michiganensis* subsp. *sepedonicus* (Perfileva et al. 2018).

9 Multifaceted Roles of Nanoparticles to Limit Plant–Pathogen Interactions

9.1 Nanomaterial-Based Diagnostic Tools for Phytopathogenic Detection

In order to efficiently manage plant disease, accurate and timely detection of the virulent pathogens with simultaneous applications of pesticides is of utmost importance. Nanoparticles may also be employed as biomarkers for detection of virulent phytopathogens (Chartuprayoon et al. 2013; Yao et al. 2009). They are either formulated for directly detecting the disease evoking pathogens or may sense certain conditions or signals that are associated with the phytopathogenic diseases. Nanochips comprise of oligoprobes (fluorescent) that are highly sensitive and specific in detection of even a single bacterial or viral nucleotide mutation. Various nanochips are being efficiently employed for pathogenic detection including antibodies conjugated silica (fluorescent) nanochips that can sense *Xanthomonas axonopodis* pv. *vesicatoria* (Yao et al. 2009) and gold nanoparticles acting as immunosensors for detecting *Tilletia indica*, the causative agent for karnal bunt disease in wheat (Singh et al. 2010). If utilized in certification of seed as well as in plant quarantine, these nano-sensors can provide an effective platform for detection of pathogenic diseases of plants. It is also known that stress conditions trigger various physiological changes in plants (Khan and Rizvi 2014). Stress-mediated stimulation of plant defense system coordinated majorly by salicylic and jasmonic acid and methyl jasmonate is one of such primary examples (Khan and Haque 2013). Copper (Cu) nanoparticles in combination with Au modified electrode is reported to be successfully used for identifying changes in level of ascorbic acid, salicylic acid, etc. in plants as well as seed which may help in detection of pathogen invasion (Wang et al. 2010). Advancements in such sensing technologies, which can identify alterations in physiological and/or biochemical parameters or directly monitor the

pathogenic invasion may prove to be beneficial for management of phyto-diseases and protect economically important crops.

9.2 *Nano-Pesticides and Efficient Carrier System*

As nano-formulations act as efficient carrier systems allowing release of chemicals in controlled fashion, thus they can significantly reduce the quantity of pesticides that are generally required and its associated toxic outcome. The use of nano-pesticides will not only curb the conventional application rate of pesticides but will also exponentiate their effectivity owing to the timely and controlled release of chemicals as and when requires at the time of phyto-infection. The improved stability, lower viscosity, nanosize, and optical transparency confer nano-emulsions as better delivery cargoes for pesticides which may enhance the solubility of the active chemical ingredients and hence their bioavailability (Xu et al. 2010). Imidacloprid (1-(6-chloro-3-pyridinyl methyl)-N-nitroimidazolidin-2-ylideneamine) formulated as controlled release nano-pesticides using PEG (polyethylene glycol) and other aliphatic diacids has shown significant potency in pest control for different crops (Adak et al. 2012). While polyhydroxyl alkanate is used as a biodegradable polymer to achieves sustainable release of pesticides (Pepperman et al. 1991), Intelimer, the thermosensitive polymer on the other hand controls pesticide release based on the temperature variations in different seasons which prevent undesired leaching. The suitability of different polymers like those from natural sources like proteins and polysaccharides, or polyacrylamide, and polystyrene categorized as synthetic polymers or even inorganic materials such as zeolites, glass beads, ceramics, etc. is being extensively researched for the production of nano-pesticides (Chuan et al. 2013). SDS (sodium dodecyl sulfate) fabricated silver-titanium dioxide nano-formulation of imidacloprid have shown improved protective efficacy against phytopathogen invasion in cabbages and cucumbers at seedling phase (Guan et al. 2010). On the other hand, studies have indicated encapsulation of zineb or mancozeb, the two common pesticides inside carbon nanotubes graft poly citric acid material helped in nano-fungicide formation which significantly arrested *A. alternata* mediated fungal spot development (Sarлак et al. 2014).

Thus, these nano-formulations, containing active pesticide chemical, increase the efficiency of protecting the crops and plants thereby escalating productivity of food with simultaneous reduction in adverse environmental impact (Chhipa 2017). Such nano-formulations also prevent unnecessary degradation of pesticides due to evaporation and leaching. And thus, with proper eco-toxicological screening they can be used as a promising technique for harnessing plant-pathogen interactions.

10 Nanotechnology and the Threats Imposed

10.1 Environmental Impact of Metallic Nanoparticles

Although the nanoparticles play major role in controlling the plant–pathogen interactions (Elmer and White 2018), but they also impose certain adverse effect on environment (Fig. 5). The nanoparticles which resist the growth of pathogenic microbes in the crops sometimes get dispersed in the surrounding soil, water bodies, and also atmosphere through probable processes like leaching, air current-mediated transfer, and through rainwater as well as transfer trophically (Gardea-Torresdey et al. 2014). It has been indicated that the microbes existing in the roots of plants, soil and sedimental deposits may also absorb these nanoparticles which finally undergo accumulation (Kim et al. 2016). Various organisms like mollusks, arthropods, protozoa, insects, fishes, and birds when consumes or utilize plant products, microbes or even the waste products assist in tropical transferring of the NPs from one level to another (De la Torre et al. 2015). Such process lays concern that the risk and adversities posed by the nanoparticles may be inherently passed to the offspring (Shimizu et al. 2009) which is evident among the marine ecosystem and organisms and also the food chain lining plants with herbivorous and carnivorous animals (De la Torre et al. 2015; Shimizu et al. 2009; Bielmyer-Fraser et al. 2014). Keeping such scenario in mind, the nanoparticle formulations application should be standardized and rationally used to maintain their safety and sustainability in agriculture. The probable risk associated with nanoparticles should be judged carefully and proper

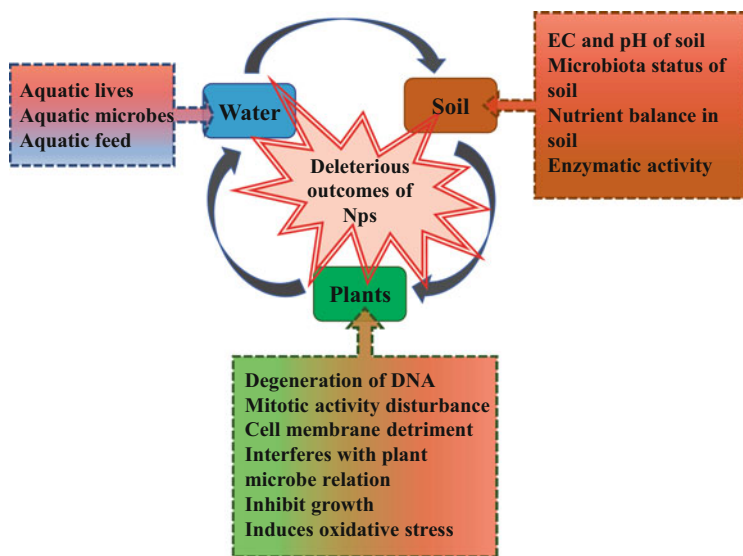


Fig. 5 Metallic nanoparticles and their negative impact on major components of agroecosystems like water soil and plants

knowledge about the nature of interaction of such Nps with the crops and plants along with the ecosystems in which they exist which includes other plants, animals and microbial organism is mandatory before they are being used in large scale field applications.

10.2 Toxic Impact of Nano-formulations on the Favorable Microbial Plant Interrelation

The epiphytic and endophytic association of various microbial organisms with the plants are well known as they exist in bulk soils surrounding rhizosphere and root. The microorganisms participate actively in producing auxins and phytohormones, N₂ fixation, solubilizing phosphate, etc. (Abdallah et al. 2019). Evaluation of respiratory activities as well enzymatic functions in soil allows understanding of the alterations occurring in microbial community in soil (Simonin and Richaume 2015). Reduction in biomass, truncated enzymatic actions of urease, dehydrogenase and phosphatase along with decreased levels of phospholipid (total) fatty acid are observed in the soil microbiota on application of copper oxide and titanium dioxide Nps in flooded field of rice (Xu et al. 2015). Saline and black soils also indicate similar alterations in enzymatic activities (catalase, invertase, etc.) and diversity of soil microbiota when nano-formulations of iron, cerium, zinc, etc. are applied (You et al. 2018). Application of cerium and zinc nanoparticles have exhibited to affect soil enzyme functionalities with reduction in thermogenic metabolic action, number of bacteria enabling phosphate and potassium solubilization, azotobacter, etc. (Chai et al. 2015). Similar reports are also presented for silver and zinc oxide Nps which interferes and diminishes the number of bacteria participating in nitrogen fixation like *Rhizobium leguminosarum* *Azotobacter chroococcum* solubilization of phosphates like *Arthrobacter sp.* MTCC 8160, *Serratia marcescens* MTCC 7642 and also formation biofilm like *Bacillus subtilis* MTCC 441, *Pseudomonas aeruginosa* MTCC 7763 (Chavan and Nadanathangam 2019). While silver Nps demonstrated bactericidal consequence and modified the soil bacterial population, the zinc nanoparticles were accompanied with bacteriostatic outcome (Chavan and Nadanathangam 2019). Studies have also indicated zinc nanocomposites to possess more toxicity than that of cerium nanoparticles (Bandyopadhyay et al. 2012) against the helpful soil microbiota.

10.3 Metallic Nanoparticles and Their Adverse Impact on Plants

The nanosize dimension of the particles allows acts as a dual sword in case of nano-formulations by facilitating the plants to fight against pathogens on one hand and on

the other, adversely affecting beneficial microbes and surrounding plants, animals, fishes, birds, and even humans. The nano-formulations are applied to the plant parts present both above and below the ground and even on seedling stage. These nanoparticles may induce antipathogenic effects locally or undergo translocation all through the plant system and get accumulated in different plant parts thereby contributing to toxicity in different cells or organs (Kurepa et al. 2010). Exact size, surface of particles, and even composition determine the degree of Nps uptake and distribution along with other factors like concentration of nano-formulations and species on plant to which they are applied. As they get accumulated in different plant parts, the physiology of plant gets affected which in turn adversely effects plant growth. Minimal concentration of nanoparticles is reported to have high toxicities even with rare dispersal in environment (Ali and Ali 2019). Excessive nanoparticles when used in cultivation of crops like tomato, zucchini, and wheat disrupt electron transportation chain that subsequently cause oxidative stress. This impedes the processes involved in detoxifying free radicals and causes genotoxic outcome (Dimkpa et al. 2013b; Pakrashi et al. 2014) which in turn interferes with production of plant hormones and secondary metabolites essential for plant growth (Sanzari et al. 2019). The nano-formulation restrains transportation of water in plants, and promotes chromosomal disruption, reduction in growth hormone formation, disorders of metabolic system, alterations in profiles of gene transcription, etc. which makes the plants more susceptible to naturally occurring toxins like arsenic (Morales-Díaz and Ortega-Ortíz 2017).

11 Conclusion

Nanotechnology may serve as a magic bullet for developing multimodal techniques that will contribute to improving plant health either by disease monitoring or through controlling disease or strengthening the plant immune system. Various nanometallic formulation has shown to facilitate disease suppression at much lower concentrations than their counterpart fungicides or other pesticides. However, the associated limitation of such nano-formulation on adversely affecting plant health, soil microbiota, and beneficial soil microbial interactions with plants along with other toxicities imposed on environment and ecosystems should be strategically addressed. Integrating nanotechnology and plant pathology will mark the advent of new era of the use of functionalized metallic nanoparticles as pesticides, insecticides, nutrient fertilizers, etc. and would succor to conquer the impediments of food production globally.

Conflict of Interest The authors declare no conflict of interest.

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