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ORIGINAL RESEARCH ARTICLE

Interplay of plant pathogens and host defenses: Unveiling the mechanisms and strategies for crop protection

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INTRODUCTION

Pathogen is a microorganism that has the ability to cause disease in its host organism by invading and multiplying within a host body. The interaction between pathogens and their hosts is a complex process that not only involves the direct invasion of host tissues but also the evasion of the host's immune response, enabling the pathogen to grow, reproduce, and spread, either through direct contact or via vectors (Jones & Dangl, 2006). The growth and proliferation of pathogens within their hosts are influenced by various factors, including environmental conditions, the genetic resistance of the host, and the specific virulence factors of the pathogen itself (Gerba, 2015). These dynamics are crucial not only in human health but also in agriculture, where pathogen interactions with plants can lead to

significant crop losses and, consequently, economic and food supply impacts (Creissen *et al*., 2016). Over the past decade, the agricultural sector has faced significant challenges due to various pathogen outbreaks affecting plants, emphasizing the urgent need for advanced research and strategic preparedness to combat these threats. Notable among these is the banana Fusarium wilt, caused by *Fusarium oxysporum f. sp. cubense* Tropical Race 4 (TR4), which has threatened global banana production by affecting key producing regions (Ploetz, 2015). Similarly, the advent of wheat blast by the *Magnaporthe oryzae* in Bangladesh in 2016, marked a critical concern for South Asia's food security due to its potential impact on wheat yield (Callaway, 2016). Another devastating disease, citrus greening (Huanglongbing or HLB), caused by a bacterium spread by the Asian *Citrus psyllid*, has wreaked havoc on citrus industries

across the Americas with no known cure, underscoring the dire need for effective management strategies (Li *et al*., 2020). Additionally, olive quick decline syndrome (OQDS) in Italy, triggered by *Xylella fastidiosa*, has led to the mortality of millions of olive trees, significantly impacting olive oil production and prompting research into disease resistance and vector control (Saponari *et al*., 2019). These outbreaks highlight the critical challenges posed by plant pathogens, mirroring the complexities seen in human and animal diseases, and underscore the necessity for a coordinated, global approach to safeguard crops, ecosystems, and economies against such pervasive threats.

The present status of pathogen research, particularly from 2018 to 2023, has seen remarkable advancements in understanding pathogen biology, host-pathogen interactions, and the development of novel therapeutic and preventive measures. Innovations in genomic sequencing, bioinformatics, and molecular biology have propelled the identification of new pathogens, tracking their evolution, and devising targeted interventions (Vashisht *et al*., 2023). This review is written to address a novel aspect of pathogen research that has been underexplored in previous studies: the integration of interdisciplinary approaches combining genomics, environmental science, and socio-economic analysis to predict, prevent, and manage pathogen outbreaks. Despite significant strides in biological sciences, the holistic understanding of pathogens within the context of changing global climates, shifting human behaviors, and economic disparities remains fragmented. By bridging these disciplines, this review aims to shed light on innovative strategies to combat pathogen threats more effectively, emphasizing the need for a global, unified response to infectious diseases.

Identification of host by pathogen

Fungus: Fungal pathogens that live in the soil employ chemical

cues to find and colonize the host plant. Secretion of plant peroxidases (Prx) promotes hyphal chemotropism towards tomato roots. Depending on the host species, some rootcolonizing fungi switch between endophytic and pathogenic behavior, and combinations of effector proteins together shape the fungal lifestyle of a particular plant (Redkar *et al*., 2022). These results identify that the filamentous pathogens directed hyphal development toward the hosts (Nordzieke *et al*., 2019).

Bacteria: Microorganisms in the environment interact with plants. The interactions occur at all stages of development and in almost all their organs. The interaction might be both positive and negative benefits for the plants or harmful depending upon the disease severity. The interaction may be short-term or longterm as well. Microorganisms live inside the cell for an infinite period either endo parasitically or endophytically (Tsai *et al*., 2020). Multicellular organisms are known for their ability to communicate across cells, tissues, and organs to maintain physiological homeostasis. Plants rely on plasmodesmata for intercellular communication (Aung *et al*., 2020).

Nematodes: Most parasitic nematodes are infective during the larval stages and in that phase, they engage in finding the host. Even though host-seeking is one of the complex behaviors, juvenile larval stages get clues like gustation, olfaction, humidity sensation, and thermos sensation (Mkandawire *et al*., 2022).

Virus: The infection shown by the virus can be both direct infection and indirect infection. In most cases, insects and aphids feed on the plant, especially the phloem part. Whiteflies, aphids, thrips, and mealybugs were seen in the community causing the indirect infestation (KC, 2021). These insects might carry the viral particles from one host source to new plant hosts. The infection seems to be similar to that of the wound caused by the beetle.

Figure 2. *Disease triangle.*

Figure 3. *Fungal diseases. Powdery mildew in cucumber (A), Rust in wheat (B), and rot in tomato (C).*

Figure 4. *Bacterial disease in common plants. Canker in citrus (A), Wilts in tomato (B), and Anthracnose in bean (C).*

Figure 5. *Viral disease in tomato (A) and Root knot nematode (B).*

Mode of Entry of Different Pathogens

Fungus: In healthy competent hosts, fungi rarely cause disease. When fungus enters the host, either accidentally or by abnormalities, pathogen growth is promoted, which may lead to disease in the plant. The attachment of the fungus to the surface of the host cell triggers the entry of the pathogen into the host cell. This attachment produces an uptake signal ultimately leading towards cytoplasmic internalization. To develop a successful infection, most pathogens use a range of molecular surfaces to bind to the host's extracellular surface or matrix. Fungal pathogens secrete numerous effector proteins that can enter host cells. These effector proteins are present in the intercellular space which can be taken up by plant cells using restricted recognition motifs and initiate susceptibility in plants (Wu *et al*., 2022). Focal adhesions play a role in the attachment of the fungus to the host plant. The fungus produces adhesions, which are proteins that specifically bind to receptors on the plant cell surface, helping the fungus attach to the plant. The adhesions may interact with integrins or other proteins in the focal adhesions to anchor the fungus to the plant cell (Murphy & Brinkworth, 2021).

Bacteria: Bacterial pathogens, unlike fungi, are incapable of mechanically penetrating the cutinized plant tissues due to the lack of appressoria in them. Active bacterial invasion through the non-cutinized surface is sometimes feasible. Phagocytosis is the common method by which the host cell engulfs and internalizes bacteria (Uribe-Querol & Rosales, 2017). Natural openings of plants like stomata, hydathodes, or lenticels could help suck bacteria into the plant. Pathogens enter through abrasions on openings like leaves, stems, or roots. Pili and fimbria that protrude from the surface of bacteria attach to the surface of the host. Besides these, a plethora of bacterial adhesions recognize many elements of host-cell surfaces. Some pathogenic bacteria have specialized appendages called type III or type IV secretion systems i.e. T3SS, or T4SS, which they use to insert virulence components exactly into the host cell, thus allowing them to enter the cell and cause infection (Ellison *et al*., 2022).

Nematodes: Nematodes, also known as roundworms, are a diverse group of parasitic organisms that can infect plants. The mode of entry of nematodes into plant cells can differ depending on the nematode species and host plant type. One common way that nematodes can enter plant cells is through natural openings in the plant cell wall, such as stomata or root hairs. Some nematodes can move through the soil and penetrate the plant root directly while others may be able to infect the plant through wounds in the plant tissue. Low pH attracts some nematodes, such as the *Meloidogyne* species, which is consistent with the fact that expanding roots provide a low-pH environment (Hua *et al*., 2020). Another way that nematodes can enter plant cells is through a process called stylet penetration. Many plantparasitic nematodes have a needle-like structure called a stylet, which they use to puncture the cell wall and enter the host cell. Once inside the host cell, the nematode can feed on the cell contents, which can cause plants to become stunted or wilted. Some parasitic nematodes also produce enzymes that can dissolve the cell wall allowing the nematode to enter the host cell (Bohlmann & Sobczak, 2014).

Disease triangle: Various sources emphasize the significance of the disease triangle in disease management. It highlights how pathogens, the environment, and societal factors play essential roles in disease development (Scholthof, 2007). The triangle framework provides a structured approach to analyzing the impact of these factors on disease occurrence and spread (Figure 2).

Fungal diseases: Chlorosis is the most common symptom. The common fungal disease includes mildew (powdery, downy), rust (stem, leaf, and stripe), and rot (Sclerotium, Sclerotinia, Fusarium, Rhizoctonia, and Botrytis).

Mildew

Symptoms: It is mainly characterized by white powdery spots on both sides of the leaf. The spots expand quickly and are converted into larger blotches very quickly. At the later stage of infection, fruits start to rot and fall prematurely.

Preventive Measures

Traditional method: Acetic acid from vinegar, neem oil, or

Jojoba oil also helps to prevent disease. Sesame oil has the curative property for the control of *E. chrysanthemi* (Bradshaw, 2015). Baking soda, liquid soap, and milk spray can also be considered effective methods to prevent mildew.

Mechanical method: Plants should remain in a sunny area with good air circulation. Powdery mildew can spread when water droplets land on the leaves of the plant. The best time to irrigate is the morning after sunrise.

Biological method: Serenade (Serade) is a bacterium namely *Bacillus subtilis* which prevents powdery mildew from spreading throughout the plant (Xie *et al*., 2021).

Chemical method: Sulfur is considered an effective action to control the fungus and act as a fungicide, especially for powdery mildew (Ramos *et al*., 2020). Potassium bicarbonate is also used for powdery mildew (Redl *et al*., 2021).

Rust

Symptoms: Rust mostly damages the plant's foliar region. The surface of the leaf looks reddish to orange and occasionally brown. The fruiting bodies and spores that are on the surface of the leaf are what are causing the coloring shift. Spores are commonly known as pustules.

Preventive measures

Cultural method: Infected plants might contain spores of rust. Pruning infected leaves and cleaning the debris and infected plant parts can be the prominent solution for the eradication of rust. Similarly, avoiding overhead sprinklers and splashing water on the leaves also prevent the spreading of rust. Drip irrigation can be implemented to prevent foliar wet limits.

Traditional method: Neem oil, and baking soda with horticultural oil can be used. The baking soda disrupts the fungal spores, preventing them from spreading. Intercropping wheat and other crops break the disease cycle and infestation of stripe and mildew is less observed (Angon *et al*., 2023).

Mechanical method: Rust thrives in humid, stagnant conditions. By improving air circulation around the plants, we can help to reduce humidity and prevent the disease from spreading. Pruning affected parts of the plant can help to remove infected leaves and reduce the spread of the disease.

Biocontrol method: Bacterial endophytes are the potential biocontrol agents for rusts (Kiani *et al*., 2021). Streptomycetes are found to significantly reduce the stripe rust incidence in wheat (Jia *et al*., 2023)**.**

Chemical method: Weekly dusting of sulfur, and calcium sulfamate prevents rust by disabling the fungus within the host tissue (Kurmanbayeva *et al*., 2021). Protectant fungicides like Chlorothalonil, Mancozeb, and Maneb formulation, systemic fungicides like Endura formulations, and Triadimefon, and eradicants like Myclobutanil help to protect the plant from an infestation of the pathogen (Carmona *et al*., 2020).

Rots

Symptoms: The plant is mainly characterized by decomposition and putrefaction. The parts that show decay symptoms are mainly dry and hard, spongy and watery.

Preventive Measures

Cultural method: Legume-rhizobial and plant mycorrhizal interactions can increase the resilience of a root system to stress and strengthen the plant's immune system. Similarly, cover cropping and soil solarization are found useful in the control of rot (Arora *et al*., 2021)**.**

Mechanical method: Minimizing the moisture content reduces the severity caused by rot. This can be done by incorporating compost humus and leaf litter like asuro, ritha and so on (KC, 2021). Maintaining air circulation and ensuring good drainage in the soil helps to prevent the accumulation of water around the plant's roots and reduces infestation.

Biological method: When disease pressures are modest, biological control agents like *Trichoderma harzianum* and *Gliocladium virens* offer protection (Heflish *et al*., 2021). Trichoderma is a beneficial fungus that can suppress the growth of rot pathogens.

Chemical method: Cinnamon acts as a natural fungicide. Using baking soda, soaking the soil with hydrogen peroxide and water mixture, washing the pot or using the new potting soil, and using the fertilizer sparingly helps to reduce the infestation. The fungicide fosetyl-al (Aliette) may be used on a variety of ornamental plant species in conjunction with the proper cultural management to help avoid Phytophthora infestations (Mannai & Boughalleb-M'Hamdi, 2021).

Bacterial diseases

Bacteria are difficult to observe. We can identify the infection from bacteria by the ooze, and water-soaked lesions. The common bacterial diseases include wilt, blight, leaf spot, canker, fruit spot, and canker. This pathogen shows the typical type of symptoms in plants.

Canker

Symptoms: Sunken patches can be seen on the trunk and the branches. Dieback and swollen flattened structure are the common symptoms shown in the plants. We can see the release of the sticky and gummy-like exudates from the sunken patches. The crackers and discoloration can be seen in the plants.

Table 2. Common bacterial diseases with preventive breeding approaches.

Preventive measures

Cultural method: Irrigated water should not hit the canopy of the tree. It should be applied underneath the canopy. The plant should get enough light intensity.

Mechanical method: The damaged parts of the plants should be removed, and all the pruning material should be removed during the dry weather. Enfolding fledgling trees to prevent high infestation of insects and pests and covering the surface by burning nettle helps to avoid the pathogen to some extent (KC *et al*., 2022). Evading congestion, drowning, and mechanical wounds also avoid the cankers. The injured bark and wood should be treated punctually.

Biological method: The microbes that suppress and inhibit quorum sensing in phytopathogenic bacteria act as an antagonist agent. Quorum sensing is considered the modern approach and an effective strategy for prophylactic and therapeutic interventions. The pathogens namely *Staphylococcus pasteuri* and *Staphylococcus warneri* are alternative biocontrol agents for the prevention of citrus canker (Nugroho *et al*., 2022).

Chemical method: Fungicides with phosphoric acids like Agri-Fos that trigger the immune response of plants are efficient in preserving leaves and fruit and avoiding the development of new cankers, monitoring insect and rodent disease carriers (Kharat *et al*., 2020).

Wilt

Leaves show yellowing and the yellowish coloration slowly spreads towards the margin. Yellow coloration slowly progresses and spreads throughout the leaf. Even if the symptoms get highly visualized in the daytime, it gets recovered during the night.

Preventive measures

Cultural method: Rotating crops with cereal and pulses reduces the infestation of bacterial wilt. Wilts in pigeon pea, banana, pea, and wheat can be minimized by organic amendment. Similarly, the application of potassium helps to manage the wilts in cotton (Ju *et al*., 2022).

Mechanical method: Prompt removal of disease trees, Dipping bulbs and corms in hot water helps to kill the pathogen. Turning over the soil can help bury plant debris and reduce the inoculum of the pathogen in the soil which prevents the buildup of pathogens and diminishes the severity of wilt diseases.

Biological method: The bacterial inducer *Bacillus subtilis* effectively helps to control the Fusarium wilt in tomato plants. It acts as the biological agent to control the pathogen (Akram *et al*., 2021). Genes like PR genes, JIN 1, and 26S proteasome are found to have a high defense against pathogens (KC, 2023).

Chemical method: The use of soil fumigants and systemic fungicides to control the wilts is the most common approach. The combination of pesticides suppresses the infestation of pathogens limiting the visualization of symptoms. Fungicide should be administered into the soil at an equidistant point between healthy and recently infected trees. The combination of fertilizers containing low nitrogen and high phosphorus reduces wilting.

Blight

It is a necrotic lesion that is surrounded by a distinct yellow halo at the leaf margin. Acute water-soaked angular spots can be seen in the beginning. The spots are darkened and are surrounded by yellowish-green halos.

Cultural method: Natural mulch like straw, and wood chips around plant bases prevent fungal spores in the soil from spraying on the plant (Tiwari *et al*., 2021). Ensuring the better air circulation reduces the chances of blight.

Traditional method: The essential oil extract in eucalyptus oil functions as an anti-insecticidal property and can be utilized for its curative, scented, flavoring, antimicrobial, and bio-pesticidal characteristics (KC & Ghimire, 2021). A mixture of baking soda, vegetable oil, soap, and water also reduce blight invasion.

Chemical method: Fungicides like Azoxystrobin, Pyraclostrobin, Trifloxystrobin have been effectively used as a control of Anthracnose. Similarly, copper-based fungicides and systemic fungicides like propiconazole, and myclobutanil act as an effective management practice for the fungus. Mycogenic zinc fungicides are also effective against early blight symptoms (Singh *et al*., 2022).

Leaf and Fruit Spot

Water-soaked areas can be seen in older leaves of plants. The lesions observed will be 0.25 inches in diameter. Lesions are angular in shape and are bordered by leaf veins. Lesions turn black in a short period.

Preventive measures

Traditional method: Planting different crops in the same field in different seasons can help break the disease cycle and reduce the buildup of pathogens in the soil. This is an effective method to prevent various plant diseases, including leaf and fruit spots. Application of *Juglans regia*, Ritha, and Asuro in the areas creates an unfavorable environment for the pests and avoids intensive infestation (KC, 2021). Traditional control methods can be effective in preventing and managing leaf and fruit spots, but their efficacy depends on various edaphic and environmental factors along with the severity of the disease.

Mechanical method: Providing proper irrigation, mulching in the cultivated land, and creating physical barriers like row covers and netting helps to reduce the severity of the leaf and fruit spot disease in plants without the use of chemicals.

Biological method: The biological control agents like *Bacillus subtilis, Trichoderma spp., Beauveria bassiana, Pseudomonas fluorescens, Streptomyces spp*., can be applied isolated or in combination with other regulator methods like cultural and chemical control methods helps to reduce the infestation of pest. *Urtica dioica* is used against plants having the resistivity against the infestation of bacteria (K.C. *et al*., 2022).

Chemical method: Potassium and silica help in the disease management of crops. Protectants like sulfur and copper-based compounds can be used to prevent the infestation of the pest and should be applied before the disease appears. Diverse types of bactericides are available, including copper-based compounds, often used in organic farming, and antibiotics, used in conventional farming. Bactericides should be applied according to label instructions and only when necessary to minimize the development of antibiotic-resistant strains of the pathogen.

Viral diseases

In most cases, virus-infected plants show mosaic leaf patterns. Yellow, crinkled leaves can be visualized if the virus infects the plant. The plant growth retards and it is stunted. The infestation of insect pests spreads the majority of viral diseases. Tomato fields attacked by aphids show high viral symptoms.

Preventive measures

Traditional Preventive measures: Traditional herbal remedies have been used to treat and prevent viral diseases in plants. Extracts from plants such as neem, ginger, and garlic have been shown to have antiviral properties and can be applied to plants to prevent viral infections (KC *et al*., 2022).

Cultural method: Traditional farmers have long used crop rotation to prevent viral diseases in plants. By rotating the crops, farmers can disrupt the life cycle of the virus and reduce the likelihood of it infecting the next crop. Intercropping with plants that are susceptible to viral disease can reduce the spread of the virus by creating a physical barrier between infected and uninfected plants.

Biological method: Many viral diseases in plants are spread by insect vectors such as aphids, whiteflies, and leafhoppers. Living -controlling agents like predatory insects and parasitic wasps can be used to control these insect vectors and reduce the spread of viral diseases.

Chemical method: Unlike bacterial or fungal diseases, viral diseases in plants cannot be effectively controlled by chemical methods. There are currently no chemicals available that can directly kill viruses, and most chemical control methods are focused on preventing the spread of the virus rather than curing an infected plant.

Nematode diseases

Mostly nematodes attack the root portion of the plant. If the plant gets ingested by the nematode, we see lesions on the root. Knots/galls are the most common symptoms. The infected plant shows excessive branching of roots. Since the root tips are injured, the symptoms include clustered root systems.

Preventive measures

Cultural method: Rotating the crop frequently such as cereals like wheat barley, forage legumes like alfalfa, and grasses like timothy is widely used by the population of nematodes in the fields. Cover crop, crop rotation and soil amendments also help to reduce nematode infestation (Sasanelli *et al*., 2021).

Traditional method: The application of neem and castor oil can repel and reduce the feeding of nematodes (Djiwanti *et al*., 2024). Soil solarization involves shielding the soil with transparent plastic during the warmest months of the year to increase the soil temperature and kill nematodes and other soil-borne pests. However, it is crucial to note that traditional methods may not always be applicable in controlling nematode infestations, and in some cases, chemical control may be necessary. However, these methods can be effective in preventing nematode infestations from occurring in the first place.

Mechanical method: Deep plowing, disking, or tilling the soil can help reduce nematode populations by exposing them to the elements and making them more vulnerable to predation, desiccation, and other forms of stress.

Biological method: Introducing natural enemies of nematodes, like nematophagous fungi and predatory mites, into the soil helps to reduce nematode populations. The parasitic fungus *Purpureocillium lilacinum* has a synergistic consequence on rootknot nematode control (Panth *et al*., 2020). This method is often more sustainable and environmentally friendly than chemical control methods.

Chemical method: Nematicides like Telone II, Chloropicrin, and Paladin can be effective chemicals to control nematode (Pulavarty *et al*., 2021). They can be applied as a soil treatment, seed treatment, or foliar spray. Chemical control methods can be expensive and may have negative environmental impacts. In addition, repeated use of chemical pesticides can lead to pesticide-resistant nematode populations. Therefore, it is recommended to use chemical control methods only as a last resort and to use them in conjunction with other control methods, such as crop rotation, sanitation, and biological control.

Conclusion

Studying how pathogens enter plants can be a crucial baseline for developing effective preventive measures. This comprehensive review elucidates the intricate dynamics of plant-pathogen interactions, emphasizing the mechanisms of pathogen entry, colonization, and the resultant disease manifestations in plants. It underscores the importance of understanding these interactions for the development of innovative and sustainable strategies to mitigate plant diseases. The paper highlights the necessity for continued research into pathogen biology, host defenses, and environmental influences to enhance crop protection, thereby supporting agricultural productivity and food security. Future studies should focus on integrating multi-disciplinary approaches, leveraging advances in genomics, bioinformatics, and ecological studies, to foster resilient agricultural systems capable of withstanding pathogen challenges. This integrative perspective is pivotal for devising effective management practices that safeguard crops, ensure high yields, and contribute to global food security amidst the challenges posed by an ever-changing pathogen landscape.

Authors contribution

Conceptualization: Poudel, A., and KC, S.; Methodology: Poudel, A., and KC, S.; Investigation: Poudel, A., and KC, S.; Writing original draft preparation: Poudel, A., and KC, S. Writing—review and editing: Poudel, A., and KC, S. All authors have read and agreed to the published version of the manuscript.

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