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ENVIRONMENTAL MICROBIOLOGY - REVIEW

A critical review on bioaerosols—dispersal of crop pathogenic microorganisms and their impact on crop yield

Abdul Zul'Adly Mohaimin[1] · **Sarayu Krishnamoorthy**[1] · **Pooja Shivanand**[1]

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Abstract

Bioaerosols are potential sources of pathogenic microorganisms that can cause devastating outbreaks of global crop diseases. Various microorganisms, insects and viroids are known to cause severe crop diseases impeding global agro-economy. Such losses threaten global food security, as it is estimated that almost 821 million people are underfed due to global crisis in food production. It is estimated that global population would reach 10 billion by 2050. Hence, it is imperative to substantially increase global food production to about 60% more than the existing levels. To meet the increasing demand, it is essential to control crop diseases and increase yield. Better understanding of the dispersive nature of bioaerosols, seasonal variations, regional diversity and load would enable in formulating improved strategies to control disease severity, onset and spread. Further, insights on regional and global bioaerosol composition and dissemination would help in predicting and preventing endemic and epidemic outbreaks of crop diseases. Advanced knowledge of the factors influencing disease onset and progress, mechanism of pathogen attachment and penetration, dispersal of pathogens, life cycle and the mode of infection, aid the development and implementation of species-specific and region-specific preventive strategies to control crop diseases. Intriguingly, development of *R* gene-mediated resistant varieties has shown promising results in controlling crop diseases. Forthcoming studies on the development of an appropriately stacked *R* gene with a wide range of resistance to crop diseases would enable proper management and yield. The article reviews various aspects of pathogenic bioaerosols, pathogen invasion and infestation, crop diseases and yield.

Keywords Bioaerosols · Crop diseases · Yield loss · Source · Global impact · Biotic factors

Introduction and relevance of bioaerosols in crop diseases

Bioaerosols are the subset of atmospheric aerosol particles that are of biological origin and vary from a few nm to 100 µm in size [182]. They are ubiquitous in the lower parts of the atmosphere i.e., the planetary boundary layer (PBL) as they are majorly released from the Earth's surface due to various natural and anthropogenic activities [304]. They use PBL as a medium to enable and enhance their transportation and dissemination, spread and distribution, evolution, mutation, emergence of new variant, adaptation, improved pathogenicity, development of wide host specificity, and drug resistance [112, 180, 181, 400, 479, 610]. Their unique nature to carry the particles to longer distances with the air currents makes them a key factor in the dispersal of reproductive and other units of plants, animals, and pathogenic microbes across the geographical barrier [124, 182]. Bioaerosols are well known for their beneficial role in the climate system [180] and are equally hazardous to ecosystem health including crop health when they harbor pathogenic microbes in them [124, 610]. They act as agents of spread and dispersal of the human and crop pathogenic microbes that could have deleterious effect on the public and agricultural health of a country [4, 65, 66, 124, 137, 167, 183, 206, 286, 624]. Notably, the pristine atmospheric air present in the vegetated regions play a vital role in the dissemination of the beneficial as well as the crop pathogenic microbes to various ecological niches enhancing their colonization on various substrates [120, 251, 462, 466].

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✉ Pooja Shivanand
pooja.shivanand@ubd.edu.bn; poojashivanand@outlook.com

[1] Environmental and Life Sciences Programme, Faculty of Science, Universiti Brunei Darussalam, Jalan Tungku Link, Bandar Seri Begawan BE1410, Brunei Darussalam

Till date, a significant proportion of the particulate matters in the atmospheric air are said to be composed of bioaerosols which could harbor various pathogenic microbes that could hamper the agricultural sector and economy. Accordingly, bioaerosols were found to contribute to about 24% of the total particulate matters and about 5–10% of the suspended particulate matters in the atmospheric air [4, 373]. Further, various researchers worldwide like [26, 66, 82, 345], Burt [73, 194], and [388] have discussed various crop and plant pathogenic diseases namely rust, smut, powdery mildew, downy mildew, etc. that are generally transmitted by the bioaerosols. Hence, it is highly essential and relevant to study the crop pathogenic bioaerosols and their diversity as they could impact the agricultural sector in the local and the global scale [124]. Furthermore, the uncertainties prevailing in the current understanding of the climate change, the role of bioaerosols in the terrestrial interactions, and anthropogenic influence posed by human activities hampering the agricultural production emphasizes the need to have better insight on the crop pathogenic bioaerosols [529, 533, 541]. Manmade activities like land use pattern and thus liberated bioaerosols have always had a negative implication on the climate and precipitation [402]. Such altered precipitation cycle and climate change would affect the vegetation and agricultural sector thus negatively influencing the economy of a country where agriculture plays a vital role in the gross domestic product (GDP). In this perspective, this article will attempt to summarize and highlight the role of bioaerosols in the spread of crop diseases, various microbial pathogens, mechanism of infection, and the possible preventive measures that need to be followed. Moreover, the manuscript will emphasize on the following objectives: (i) in general the role of bioaerosols in crop diseases and yield loss is understudied, therefore the manuscript elaborates their role and importance in crop disease leading to heavy yield losses; (ii) it also ventures the vital role of meteorological and atmospheric factors in the spread and aerosolization of bioaerosols which would help us in understanding the basic information and knowledge on the influence of changing climatic factors over the increased crop diseases worldwide; (iii) it gives the readers an insight on the diverse pathogenic microbes, source and mode of spread of pathogenic bioaerosols and their route of entry in crops which could help farmers and officials in preparing the crop protection strategies. In order to achieve all these objectives, the manuscript carefully attempts to cover most of the details related to the disease caused by biotic and meso-biotic factors using stringent and specific methodologies in data collection especially the literatures based on the generalized and specific search strings like "bioaerosols and crop diseases, sources of bioaerosols, factors influencing aerosolization and dissemination of bioaerosols, fungal crop diseases, bacterial crop diseases, meso-biotic factors, viral crop diseases, invasion of crop pathogens, etc." excluding the details and data related to the crop diseases caused by abiotic factors like spoilage due to extreme temperature or rainfall and other implications of bioaerosols in ecosystem.

Source of bioaerosols- factors influencing their release and dissemination

As already discussed, bioaerosols are the aerosol particles that contain a biological unit in them which could either be a living cell or a dead material [22, 83, 103, 124, 182, 209, 564, 610, 630]. First study on bioaerosols was reported in the early nineteenth century and many other studies addressing various aspects of the bioaerosols were carried out since then [413]. As addressed by various researchers worldwide, they play an imperative role in the dissemination of various biological units, dissemination of disease and infection, helping in the genetic exchange and development of new variants, and in the development and evolution dynamics of the ecosystem [66, 120, 148, 216, 217, 224, 354, 378, 460, 463, 469, 516, 527, 598]. Though bioaerosols transport the microbes to longer distances, their vertical spread across the troposphere or PBL has not yet been addressed properly [124].

Natural activities as source of bioaerosols

Natural activities observed on the land surfaces and the water surfaces act as an important source of bioaerosols emission and spread [227, 337, 401, 551, 552, 623] (Fig. 1). Further, wind movement over the land surface, water surface, and vegetated regions including the cryptogamic covers contribute to large numbers of bioaerosols from the biosphere [29, 62, 65, 149] as leaf surface area contributes to four times the area as compared to the terrestrial ground surface area [604]. Also, [140] has reported that the dry air and strong wind would favor the dissemination of bioaerosols to longer distances. Movement and activities observed in trees, plants, and crops including the leaf movement were also found to contribute tremendous quantities of bioaerosols to the atmospheric air especially the ice nucleating (IN) microbes which are pathogenic to crops and plants [124, 393, 458, 470, 596]. Furthermore, cryptogamic covers that comprise the region blanketed with the growth of fungi, bacteria, cyanobacteria, lichens, algae, and bryophytes play an imperative role in the release and spread of bioaerosols [37, 61, 67, 120, 122, 124, 164, 183, 366, 511, 526]. Bioaerosols liberation is further enhanced when these cryptogamic covers (which approximately covers almost $1/3^{rd}$ of the ground surface

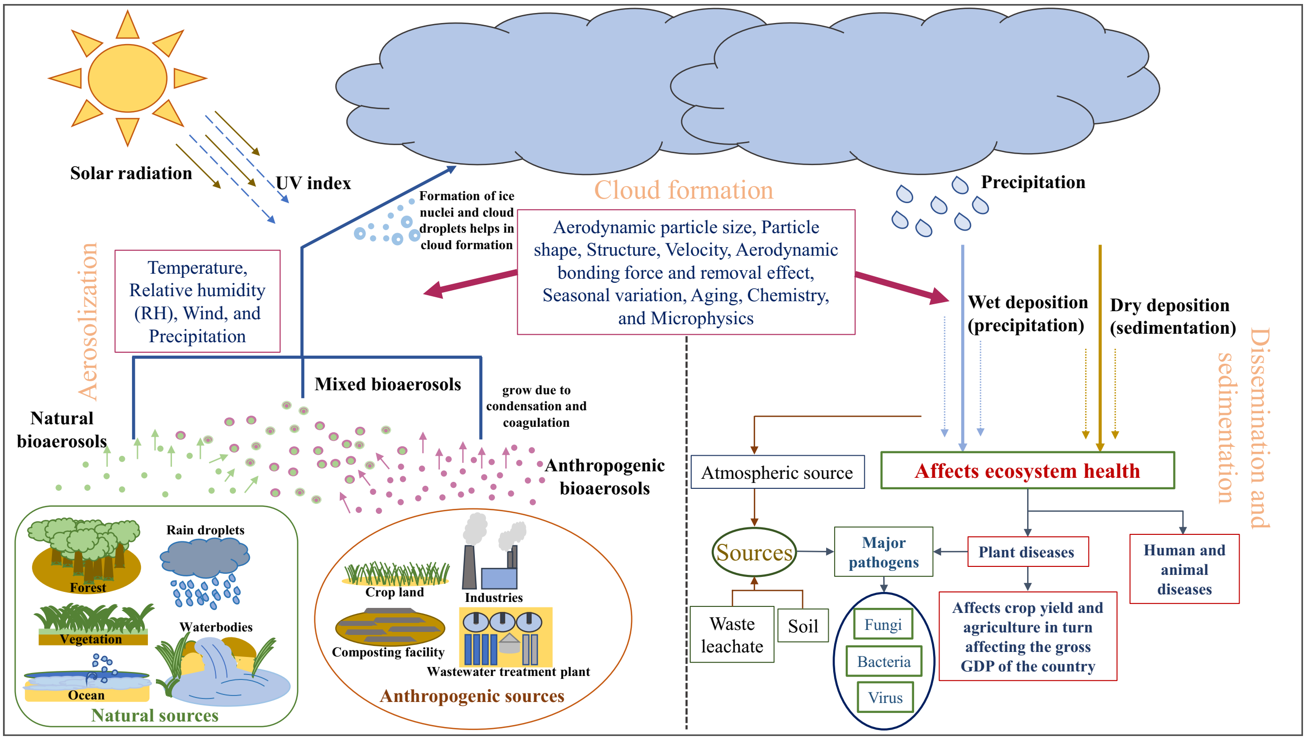

Fig. 1 Schematic representation of the natural and anthropogenic bioaerosols sources, their release from the biosphere along with their role in the ice nuclei formation influencing the climate change, and their role in affecting crop health and ecosystem health through wet and dry deposition

area) are disturbed by the wind, rainfall, and natural activities of human and animals [149, 182]. Such bioaerosols emitted from the vegetated region and cryptogamic covers would mainly comprise of pollen grains, bacterial cells, small seeds, cyanobacteria, fungal spores and segments, plant debris and segments, dead animal units and cells, algae, insects and their segments, etc. [22, 67, 81, 83, 103, 124, 209, 351, 373, 482, 564, 610].

Likewise, virus particles, viroids, cyanobacteria, and bacteria dominate the bioaerosols liberated from the waterbodies and the ocean surfaces along with very sparse presence of archaea, fungi, protozoa, and algae [92, 302, 361, 425, 553]. Splashing, bubble bursting, rain droplets, wave breaking, collapsing of bubble cavity, spume droplets, river water movement and flow are the various activities that are responsible for the release of bioaerosols from the waterbodies (Fig. 1) [12, 16, 92, 120, 124, 160, 254, 280, 323, 463, 493, 593, 608]. Also, Mayol et al. [376] has stated that ocean surfaces can exchange millions of microbes with atmospheric air i.e., millions of microorganisms/square meters of air every day and about 10% of which could thrive in the atmospheric air for longer time of even four days. This shows that meteorological conditions prevailing over ocean surfaces favor the survival of bioaerosols for longer periods compared to terrestrial surfaces.

Role of anthropogenic activities on bioaerosols emission and dissemination

On the other hand, anthropogenic activities, or manmade activities (Fig. 1) like agriculture, solid waste management, wastewater treatment, waste transportation, biomass burning, reuse of solid waste, landfills, road dust, industrial activities, and waste discharge [14, 143, 171, 228, 283, 353, 355, 439] contribute immensely to the release of anthropogenic bioaerosols into the atmospheric air. Human, birds, and animals are said to expel and excrete pathogenic microbes and lots of dead cell debris in the bioaerosols that are released from them [47, 48, 83, 625]. Chen et al. [89] has stated that bacterial bioaerosols dominated the human populated region compared to fungal bioaerosols. Similarly, waste treatment plays an imperative role in the dispersal and dissemination of pathogenic microbes in the bioaerosols, which includes municipal wastewater/sewage treatment, composting, waste dumping yards, landfills, etc. [99, 142, 304]. Further, [99] has stated that actinomycetes and fungal bioaerosols are the majorly released bioaerosols from the composting site as most of bacterial species are killed due to the high temperatures prevailing in the compost. Also, [219] reported the predominance of mesophilic bacteria, psychrophilic bacteria, and microfungi in the bioaerosols collected from a facility containing both wastewater treatment plant and a composting site. This is mainly due to the organic dust released from the composting facility which enables the specific growth of mesophilic and thermophilic species [274, 499]. Hence, wastewater treatment plants, composting facilities, and landfill sites are considered as potential anthropogenic source of pathogenic and non-pathogenic bioaerosols [70, 90, 176, 219, 407, 434]. However, [143] have identified that the animal-feeding operations and animal husbandry release high quantities of pathogenic bioaerosols that could have lethal effects on animals and human. Further, bioaerosols released in the indoor environment are also considered as anthropogenic bioaerosols as they are majorly released from human activities like day-to-day activities and also due to coughing, sneezing, talking, and breathing which could expel human respiratory and oral microbiota[221, 275, 417, 616], the skin microbes as a result of skin aberrations and shedding activities [175, 348, 421], and floor dusts rich in pathogenic microbes [243, 562]. On the other note, [99, 284, 430, 535] and [255] have reported the abundance of bacterial species like *Staphylococcus aureus*, *Pseudomonas aeruginosa*, and *Escherichia coli* in the bioaerosols collected from the industrial sites. Whereas *E. coli* was the predominant species reported in the bioaerosols released from the wastewater and waste treatment site [255]. Study reported by [455] stated that bacterial bioaerosols were the major bioaerosols released during the activity of land spreading of the semi-solid sewage sludge. Also, a study conducted by [138] and [80] explained the presence of bacterial and viral bioaerosols downwind the sewage sludge disposal site. Furthermore, agricultural practices were said to release considerable quantities of bioaerosols to the atmospheric air [333]. Though the bioaerosols released due to anthropogenic activities affect agricultural sector and various aspects of ecosystem, many studies till date elucidate and characterize the diversity and pathogenic properties of human and animal pathogenic bioaerosols. Crop pathogenic bioaerosols and their implication on the crop/agricultural health are less investigated till date.

Influence of meteorological factors and aerodynamic particle size on bioaerosols aerosolization

Globally, many researchers have stated the significant role of meteorological factors and aerodynamic diameter in the prolonged persistence of bioaerosols in the atmospheric air [191, 287, 490, 558, 611]. Concurrently, the concentration of bioaerosols in the atmospheric air decides the transportation capacity of bioaerosols across continents and plays a pivotal role in microbial migration and colonization [124, 182]. Further, [276] have reported that meteorological factors greatly influence the aerosolization properties of bioaerosols. In specific, meteorological factors like relative humidity (RH), temperature, wind direction and speed, and precipitation are said to have major impact on the bacterial bioaerosols release and concentration in the atmospheric air and are reported to vary with seasons [124, 134, 140, 192, 193, 222, 304]. Accordingly, Miquel [391] has stated that fungal spore concentration and emission in the atmospheric air was also guided by seasonal variations and wind direction. Furthermore, it was observed that the movement of bioaerosols and their dispersal is majorly governed by the particle size (aerodynamic diameter) and the flux density [611]. These factors decide the dry and wet deposition properties of bioaerosol particles and influence their spread and transport over longer distances. It is also reported that the particles of high aerodynamic diameter settle down rapidly compared to a smaller particle [124]. Researchers worldwide have estimated that the aerodynamic particle size diameter of pollen grains could range between 17 and 58 μm [312, 539], fungal spores could range from 1 to 30 μm in diameter [213], bacteria could range from 1.25 to 8 μm [512, 567], viruses ranges ≤ 0.3 μm [563] and all other biological particles like fungal segments, bacterial clusters, plant and animal segments could be present in varying size ranges [276].

The other two major factors influencing aerosolization of particles are bonding force and removal effect [276]. The balance maintained between these two forces acts as the driving force for the efficient aerosolization of any particle from the surface. Bonding force can be further defined as the electrostatic force created especially when the surface and the particles are differently charged which are mainly dependent on or influenced by the factors like temperature, moisture content, and the radiation balance [544]. On the other hand, it is the removal effect which is mainly guided by the aerodynamic force or drag developed due to the air movement, electric charge, particle impaction, inertia, and movement of surface away from the particles which are influenced by wind force, raindrop impaction, and physical agitations [542]. Further, the shape and structure of organisms present in the bioaerosols also decide the sedimentation, settlement, and dispersion rate of the bioaerosols [124, 125]. All these uncertainties like the seasonality, type of biological particles in the bioaerosols, life cycle of the biological particle, seasonal variations, aging, chemistry, and microphysics of the particles govern the dispersal and dissemination of bioaerosols in the atmospheric air [72].

Microbe specific aerosolization and dissemination properties

Microbiota comprises of a variety of diverse microbial communities categorized into different taxonomic groups namely the algae, protozoa, slime molds, fungi, bacteria, archaea, and viruses with the major taxonomic levels classified being

Kingdom, Division, Class, Order, Family, Genus, and Species [457]. Each group of which has their own characteristic physical, chemical, and genomic properties that differentiate them from each other [32, 457]. Aerosolization efficiency of these organisms are further dependent on and decided by their physical properties like shape, size, velocity in air etc. [124, 126, 130, 152, 285, 410, 414]. Bioaerosols containing these microorganisms and the number of microbes present in the bioaerosols are dependent on the surrounding environment and the meteorological factors and could even contribute to huge concentration per unit of surface area measured [337, 401, 622]. Archaea, being primitive organisms known till date are reported to be less observed in the bioaerosols as they are majorly present in extreme environments [501]. Nevertheless, the fact that they play a pivotal role in the Earth's biogeochemical cycles, their aerosolization properties are understudied due to the limitations existing in the efficient characterization of archaea. The only report available till date is their presence in the bioaerosols collected from composting sites as stated by [29, 395], and [568]. Similarly, algae and cyanobacteria were reported to get aerosolized from both the terrestrial and marine environments [124, 374, 375], but studies on their airborne quantitative measurements show that they are present in very low concentrations of ~ 300–500 cells/m^3 of the sampled air [478]. Globally, various researchers like [320, 468], Dubovik [141], Reisser [478, 514], and [416] have stated that *Chlorophycean* and *Xanthophycean* are the major species of algae that were observed in the bioaerosols and have also stated that their aerodynamic diameter ranged ≤ 10 µm which favor their rapid aerosolization. Cyanobacteria being one of the successful groups of the microorganisms in the terrestrial habitat, are abundantly available in the marine surface contributing to the global carbon and nitrogen availability and exchange [124, 540]. *Chroococcus limenticus, Lyngbya lagerheimii,* and *Schizothrix purpurascens* are the well know species of cyanobacteria that were reported to be airborne [147]. Similarly, *Phormidium fragile* and *Nostoc muscorum* were reported in the Cairo, Egypt [147, 197].

Bacteria being one of the most abundant microorganisms present in the bioaerosols were reported to be emitted at the rate of 0.7–2.58 Tg yr^{-1} [71, 242, 264]. The characteristic size range of the bacterial cells enable their easy aerosolization and they are often found as single cell as well as in agglomerates and clusters in association with other particles like soil, plant segments, dust, and other debris [59, 334]. Bacterial bioaerosols contain many bacterial pathogens that are lethal to human, plants, and animals and in addition to that they can act as biomarkers indicating the atmospheric, climatic, and environmental changes and anthropogenic influences [218, 356, 403, 404]. Further, [304, 309, 448, 610], and [356] have stated that meteorological factors, type of anthropogenic activities observed, seasonality, and the source materials present could highly influence the aerosolization properties, concentration, and diversity of bacterial species observed in the bioaerosols of the atmospheric air. [127], reported that bacterial concentration in the atmospheric air were found to increase with the increased temperature and wind speed. Release and aerosolization of bacterial particles can occur due to various activities like wind aerosolizing the bacterial particles from the substrates, sedimentation and settlement of particles from different layers of atmospheric air with higher concentration, aerosolization from plant surfaces, and sunlight shifting the electrostatic charge of the particles [276, 334, 570]. *Firmicutes, proteobacteria* (including *alpha, beta, gamma, delta,* and *epsilonproteobacteria*), *Verrucomicrobia, Cyanobacteria, Acidobacteria, Planctomycetes* and *Chloroflexi* are the major bacterial phyla reported till date in the atmospheric bioaerosols [163, 230, 304, 512]. Also, [125, 163], and [159] observed that the concentration and diversity of bacterial bioaerosols varied among the urban and rural regions with high concentrations of bacterial bioaerosols in the urban region. Further, [63], have reported that different land-use activities like agricultural fields, suburban areas, and forests release very high concentrations of bacterial bioaerosols of up to 10^5 to 10^6 cells/m^3 of air. Among the waterbodies, bubble bursting and sea sprays are the activities that liberate the bacterial bioaerosols from the marine environment to the atmospheric air [12, 324, 364] and it is also reported that bacterial bioaerosols liberated from the ocean surface has shorter life span compared to the one liberated from the land surface [71].

Likewise, the most predominant microorganism of all in the bioaerosols are the fungi, fungal spores, and the fungal segments which contribute to a load of about 8–186 Tg yr^{-1} [148, 235, 242, 264, 511]. Fungal concentration in the atmospheric air and their aerosolization are highly dependent on meteorological conditions and maximum aerosolization of fungal particles are favored by temperature of 25–30 ºC, relative humidity of 60–70%, and wind speed ≤ 1 m/second. Further, it was observed that fungal concentration in the atmospheric air reduces with increased wind speed of ≥ 5 m/second [335]. [75] has reported that the maximum release of fungal spores in atmospheric air is high during the dry conditions i.e., during afternoon time when the temperature and wind speed are favorable for the spore release from the conidial chains. Similarly, some wet air spora like *Nigrospora* sp. are reported to release spores favorably during high humid conditions like mid-morning [557] and it was also reported that their spore concentration reduces with increased altitude. Further, [260, 313], and [467] have reported that the spore releasing mechanism of fungi is highly dependent on the surface tension and osmotic pressure. [351], stated that the plant pathogens like *Cladosporium, Alternaria, Penicillium, Aspergillus*, and *Epicoccum* sp. that could cause smut and rust disease of plants are the major species found in the atmospheric bioaerosols. Similarly, *Ascomycota* and *Basidiomycota* were found to be the dominant phyla observed in the bioaerosols and *Basidiomycota* to dominate marine environments [180, 183, 610]. Consecutively, viruses are the tiny airborne microbes in the bioaerosols that are as small as ~ 20 nm in size and are reported to be always attached to other suspended particles in the atmospheric air [135, 627]. Only limited studies are available on the virus bioaerosols persistence and existence in the atmospheric air. It was observed that the environmental factors like altered temperature, humidity, solar radiation, and UV index inactivate the virus particles present in the bioaerosols [124, 461]. Further, Hugh-Jones and Wright in 1970 [252], have stated that wind speed and humidity (over 60%) play a pivotal role in the dispersion and spread of foot and mouth viral disease. Similarly, spread of Aujeszky's disease (a rabies like disease of pigs) was found to be high during winter especially when the temperatures were 2–3 ℃ higher than the normally recorded temperature [96, 97]. Further, it has been reported that sprays from waterbodies acted as source of virus containing bioaerosols, their liberation, and dissemination [38–40]. Moreover, virus bioaerosols were also liberated from infected animals, humans, and birds [276, 634]. Likewise, high concentrations of virus bioaerosols were found to aerosolize from sewage treatment plant, sludge dumping site or treatment plants, and marine environment [79, 124, 182, 319, 517, 543]. However, the virus bioaerosols mass concentration in the particulate matter (PM) was always found to be in negligible quantities, though the concentration of virus bioaerosols were found to be high in certain conditions and activities as mentioned above.

Major crop pathogenic bioaerosols and their implications in crop health and yield

Bioaerosols transmits several plant and crop pathogens causing various crop diseases hampering the agricultural production and yield creating significant economic losses worldwide [66, 73, 194]. Pathogenic bioaerosols gets sedimented and deposited as wet and dry deposition on the plants and crop surfaces during various stages of crop growth causing severe diseases and infections. Further, pathogenic bioaerosols settled and colonized on the soil acts as a vital source of seedling and crop infections. Fungi being the predominant crop pathogens by nature were reported to cause severe infections to a variety of crops worldwide. Bacteria being the second predominant microbial community causing various crop infection are followed by viruses, nematodes, etc. Phyllosphere of plants acts as an important niche for microbial colonization with a diverse lifestyle as epiphytes, saprophytes, and pathogens [41, 337]. Epiphytes are generally found to be present in the leaf surface and the pathogens like the foliar pathogens tend to ingress into the leaf tissues i.e., the intercellular space causing infections.

Fungal crop pathogens- their mechanism of invasion and disease onset

About 19,000 fungal species have been identified till date to cause various crop diseases like leaf spot, rust, anthracnose, blight, wilt, scab, galls, coils, damping-off, mildew, cankers, rots, die-back, smut, warts, etc. [182, 265]. Spore dispersal in the environment is dependent on two major dispersal mechanisms like active [574] and passive dispersal [259] where active dispersal is enabled by forcible dispersion of the spores by fungi itself as a part of their life cycle and passive dispersal is through the bioaerosols, animals, insects, etc. As illustrated in Fig. 2a, the fungal spores settle on the leaf or plant surface by the dry and wet deposition of the fungal bioaerosols and starts invading the plants and crops causing various diseases. Fungal spores are generally categorized into two types i.e., non-motile and motile spores. Where in non-motile spores like the ascospores (sexual spores), urediniospores of rust fungi, sclerotia, conidiospores, oospores, and sporangiospores proliferate at the settlement site whereas the motile spores like the zoospores of chytrid fungi with flagella tend to move to a favourable location after sedimentation on to the leaf surface [215].

Survival of a plant pathogenic microbe is majorly dependent upon the proliferation, growth, and reproductive strategies adopted to exploit nutrient and environmental condition available in the host [20]. Fungal spore invasion into the plant tissue is facilitated by a sequence of proliferation stages that guides the process of germination and formation of appressorium which enables the development of the penetration hyphae that penetrates across the cuticle into the epidermis layer (Fig. 2a) [385]. After sedimentation on the leaf surface, the spores adhere to the plant surface with the help of the adhesion molecules present on the spore surface [7]. Apparently, a germination tube emerges from the spore utilizing the polyols like glycogens, trehalose, and sugar alcohols that are present in the fungal spores as energy source [328, 371]. Further the formation of the melanized appressoria enables the penetration of the appressorium peg into the cuticle with the turgor pressure developed in the appressorium [94, 214, 225, 229, 556, 585]. Penetrated hyphae grow between the epithelial cells (intracellular hyphae) in the intercellular space causing the infection utilizing the host nutrients [453] with the formation of various infective structures like hyphopodia [139, 432, 545], haustorium in the epithelial cells [384, 605] and infection cushions [123, 385] severing the infection.

Similarly, the notorious necrotrophic fungi which follows various phytopathogenic strategies for infecting and killing the crops by absorbing the nutrients available in the plant cells with the production of various cell wall toxins and degradation enzymes leading to various diseases like root rots, hypersensitive reactions, and alteration of the plant metabolism [226, 380]. They also suppress the host plant defence

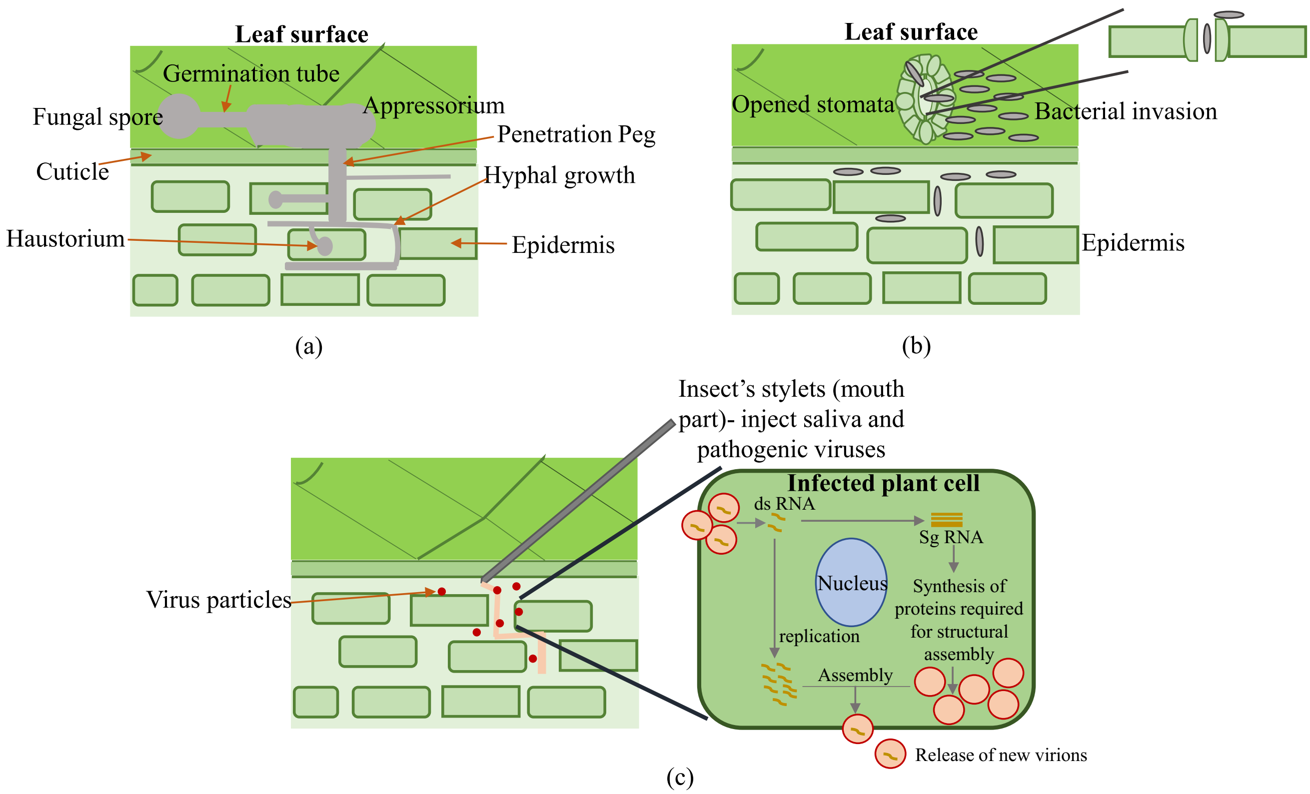

Fig. 2 Illustration of the various modes of invasion by the disease-causing crop pathogens: **a** fungal invasion of the leaf tissues; **b** bacterial invasion of the leaves; **c** viral invasion of the leaf tissues

mechanisms by manipulating the machinery, altering the plant gene regulating the membrane permeability, and by utilizing the amino acid present in the plant cell [549] aiding the fungal infection and disease progression.

Mechanism of bacterial invasion into plant tissues

Numerous bacterial pathogens causing various plant diseases have been discussed by various researchers worldwide [360]. They are mostly passive invaders and enter the plant tissues through all the possible opening on the plant surface like the stomata, rhizoplane (expanding root points), base of trichomes, grooves along the veins, hydathodes, nectarthodes, lenticles in stem and roots, and through cut wounds and scars [34, 247, 322, 336, 337]. Among all the discussed passive openings in the plants, bacterial phytopathogens use stomata as their common entry point as stomata provides access to substomatal chamber and into the mesophyll [371] (Fig. 2b).

Stomatal movement (opening and closing) in the plants are majorly controlled by the plant's immune system by developing a turgor pressure in the guard cells [441]. Further, environmental factors like draught, stress, light intensity, UV intensity, relative humidity, and the concentration of carbon dioxide in the atmospheric air influence the activity of guard cells affecting the stomatal movement [161, 405, 502]. In order to overcome all these barriers, bacterial pathogens alter the plant immune system with the secretion of hormones like jasmonic acid, coronatine (secreted by *Pseudomonas syringae*) promoting the stomatal opening favouring bacterial entry and colonization in the intercellular region [172, 202, 383]. Apparently, they develop various mechanisms to adopt to the relatively unfavourable conditions prevailing in the leaf surface and intercellular spaces with the development of a microenvironment favouring their survival in the area of colonization [69, 257]. Additionally, bacterial pathogens exist in aggregates and biofilms to resist and overcome the unfavourable conditions prevailing during their colonization in the leaf surface and intercellular space as well [110, 396, 397]. They also secrete various enzymes and proteins to adsorb the nutrients available in the plant tissues causing infections [121].

Invasion of viral phytopathogens

Unlike other phytopathogens, viral phytopathogens spread through insect vectors, nematodes, and also through bioaerosols especially the pollen grains play a vital role in carrying the viruses [195, 372]. Insect bite, bioaerosols transmitting the infected plant sap and debris, carry over from generation to generation, and the invasion of nematodes carrying the virions are the major entry routes of virus into plant tissues [68, 78, 253, 497]. Similarly, contaminated seeds and soil are also among the potential sources of phytopathogenic viral transmission and infection [371]. Generally, viruses alter the host mechanisms by upregulating or downregulating the host proteins in order to select the host cells in the plant tissues which favours their infection, replication, and pathogenicity [509]. Viruses use the plants cells as their replication factories by further altering the inner membrane and mechanisms of the host cell. Figure 2c elaborates the viral invasion and replication inside the plant cells. The infected cells generate multiple copies of viruses by promoting the replication of sub-genomic viral RNAs, and the replication of the whole genomic viral RNAs which are then packed into the capsid synthesized by the expression of the sub-genomic RNAs [272, 301]. Generally, viral infection spread form cell to cell transmission of the viruses, and also by the transmission of the infected sap and debris by the insects and bioaerosols. Further, infected soil and the invasion of nematodes carrying the viruses from the infected soil also play a vital role in spreading the viral infection.

Further, the evolutionary factors like the genetic drift, gene flow, natural selection, mutation, and recombination enabling the evolution of resistant and virulent variants makes it a vital pathogen hampering the crop yield and growth [187, 190, 300]. Henceforth, the disease management strategies are majorly focused on the prevention of phytopathogenic viral infections by restricting the entry of viruses into plants and development of resistant varieties rather than its post-infection cure [488].

Pests and vectors using air as a medium to infect crops

Nematodes as pest of crops

Nematodes are the microscopic organisms that can spread through air and water, especially their eggs have the tendency to get aerosolized in air. They are the most devastating pests of crops causing a global loss in agricultural sectors to about 80 billion USD [278, 419]. Researchers have identified about 4100 different species of plant pathogenic nematodes worldwide [118]. These nematodes also act as carriers of various crop pathogenic microorganisms especially the viruses and help in spreading the infections to crops [371].

Nematodes are categorized into three types namely ectoparasites, semi-endoparasites, and endoparasites. Generally, ectoparasitic nematodes dwell outside the host and benefit from the host with the long feeding style inserted into the plants which enables their nutrient absorption. Whereas the semi-endoparasitic nematodes partially enter the roots of the crops for feeding and the posterior end of their body is kept intact in the soil. Endoparasitic nematodes completely dwell inside the roots and other parts of the crops feeding on the internal tissues following a migratory or sedentary lifestyle. Migratory endoparasites feed on the root cells immediately after entering the roots and migrate to other parts of the crops causing a severe damage to the plant tissues and cell death [154, 531, 566]. Similarly, sedentary endoparasites enter the vascular cylinder of the plants and causes redifferentiation of the host cells into multinucleate cells for reproduction and the hypertrophic feeding cells [119, 278, 440, 525]. Researchers like [113, 199, 207, 236, 525], and [381] have reported that endoparasitic infections are initiated with the entry of juveniles near the root tips. Further, they migrate intercellularly to the vascular cylinder to enable the formation of feeding cells by the degradation of the cell walls of the plant cells, inhibiting the anti-nematode enzymes secreted by the plants, suppressing the immune system, and enhancing the secretion of the proteins required for the formation of the feeding cells. They also induce the formation of the multinucleate giant cells by the repeated nuclear division at the favourable locations where the cytoplasmic division is almost absent [1, 157]. However, many parasitic nematodes are reported to have complex interaction with their host plants to receive a rich and continuous food source [584]. Root nematodes feed exclusively on the root tissues whereas, the aerial nematodes migrate aerially to the stem and leaves and feed on the bulbs, foliage and the stem [314, 579]. Sedentary root nematodes are known to cause devastating infection compared to the migratory nematodes and this is mainly enabled by the specific exploitation of the host immune responses altering the host defence mechanism [53, 278, 314].

Insect as pests and vectors

Insects are the six-legged small invertebrates of the *Arthropoda* phyla that mostly feed on plants and crops for their nutrition. For example, bees feed on nectar and pollen from plants, larvae of many insects like beetles, moths, and flies live on plants and crops feeding on leaves and plant parts, and bugs thrive on plants saps as their major source of nutrients. Almost all the four stages of metamorphosis of insects are known to involve plants as their habitat. Among which, caterpillars are the most important stage of the insect's life cycle which causes significant damage to the crops and plants. Similarly, they act as vectors transmitting various fungal, bacterial, and majorly virus pathogens that could cause severe infections to crop impeding the crop yield.

General plant injuries caused by the plant feeding insects include (i) consumption of the infested parts (leaves, stems, roots, and flowers) of the plants by chewing, (ii) pit feeding of leaves by caterpillars, beetles, and flea beetles, (iii) edge notch of leaves caused by weevils, grasshoppers, large caterpillars, and katydids, (iv) semi-circular cut causes by cutter bees, (v) leaf mining by beetles, flies, sawflies, and moths, (vi) stem boring by long-horned beetles, and (vii) metallic wood boring beetles, engraver beetles, clearwing moth, American plum borer, and moths. Similarly, root chewing insects like weevils and root maggots, and sap feeding insects like aphids, leafhoppers, thrips and scales also cause major damage to plants. Oviposition damage is also a serious problem caused by insects when the insects lay their eggs in deep tissues of plants especially in the stems [105, 449].

Transmission of vector-borne pathogens like bacteria and viruses are enabled by the colonization of the pathogens through insects in the plants. Plants vascular systems help in the transportation and colonization of the pathogens to various parts of the plants. Further, phloem favours the transportation and nutrient supply required for the pathogens with the help of the nutrient rich sap and the sieve elements available in them [60, 343, 346, 606]. Despite the low nutrient contents available in the xylem some pathogens have also been observed to colonize the xylem [28, 454, 473]. Along with the pathogens many insect pests like whiteflies, aphids, psyllids, and leafhoppers were also reported to acquire their nutrients from the xylem and phloem of the plants [454]. Purcell [472] has stated that the specialized mouth parts of these insects enable their penetration to the epidermis to reach the preferred locations like the mesophyll and vascular system involving phloem and xylem. This activity favours the transportation of the pathogens present in the phloem and xylem of the infected plants through their body parts making them a potential vector for transmitting diseases to healthy plants [411, 433].

Major crop diseases and their global implications

Generally, crop/plant diseases are majorly caused by biotic factors supported by the abiotic factors. The factors influencing the crop diseases are classified into three major categories as the abiotic, biotic, and the meso-biotic factors [588].

Disease caused by abiotic factors

Abiotic factors are the reason for the general deficiencies of the crops and the associated diseases. They are caused by malnutrition including minerals and ions, impaired soil conditions like type and fertility, relative humidity, temperature, reduced or excess light source, reduced and excess water availability, wind or aeration conditions, concentration of the CO_2 available, effect of impurities carried by the aerosols, and by the presence of toxic compounds in the soil and air [136, 246, 305, 588]. The major diseases caused by abiotic factors include chlorosis, stunted growth, interveinal chlorosis, purplish-red colouring, necrosis, black tip of mango due to SO_2 toxicity, whiptail of cauliflower crops caused due to molybdenum deficiency, khaira disease of rice caused by zinc deficiency, hollow and black heart of potato caused by excessive usage of CO_2 during postharvest storage, and apple bitter pit caused due to calcium deficiency [459].

Disease caused by biotic factors

Crop diseases caused by biotic factors are the diseases caused by various crop pathogenic species belonging to the kingdom *Fungi*, *Chromista*, *Monera, Animalia,* etc. Bioaerosols are considered as the key factor in the spread and dissemination of the disease-causing pathogens to the crops worldwide [124, 183]. Along with bioaerosols, various environmental factors are also involved in influencing the sedimentation, survival, and penetration or ingress of the pathogens into the crop tissues [484, 550, 588]. Moreover, these factors influence the onset of disease symptoms and progression of disease in the crops. Table 1 describes the details of the specific/optimum temperature, relative humidity, water activity, light intensity, and nutritional requirement of various pathogens causing major crop diseases. Temperature being an important meteorological parameter which plays a pivotal role in deciding the weather conditions especially the four different seasons, directly influences the susceptibility of the crops to infections, influences the pathogen survival, transport, germination on the host as well as source, and also alters the visual disease symptoms in the crops [201, 248, 459].Similarly, relative humidity observed and the water activity of the soil like the dry and wet conditions alters and triggers the disease onset, progression, severity, and dissemination [101]. It is reported that dry soil and a high relative humidity (almost > 85%) substantially enhances the disease onset, severity, and spread compared to the wet soil and low relative humidity levels [108]. Also, pathogen invasion, survival, and onset of disease symptoms were reported to be dependent on the CO_2 concentration in the atmospheric air and the light availability. It is also estimated by the researchers worldwide that the elevated CO_2 concentration and increased light availability including the long day-length period helps in promoting as well as controlling the infections [145, 296, 341, 524, 587]. Further, soil conditions like the pH of the soil and the nutrients available (nitrogen, calcium, potassium, phosphorus, zinc, manganese, molybdenum, and microelements) influences the pathogen entry into the plants through the roots [7, 465]. Table 2 elaborates the symptoms, details of the susceptible crops, and the pathogen responsible for the various crop diseases reported worldwide.

It is well evident from numerous studies worldwide that leaves are the main organs of interest for the crop pathogens as it provides the required space for its settlement and entry into the plant's inner tissues [371]. Powdery mildew,

Table 1 Details of the specific and optimum range of abiotic factors required for the crop pathogenic infections

Disease caused	Pathogen	Optimum temperature, ºC	Optimum relative humidity, %	Water activity	Light intensity	CO_2 concentration	Reference
Onion smut disease	*Urocystis cepule*	10 -12	-	Dry soil	-	-	[17]
Yellow dwarf virus disease of barley	Yellow dwarf virus	16	-	-	-	Low CO_2 concentration	[238]
Cyst nematode of potato	*Globodera pallida*	15	-	-	-	-	[377]
Bunchy top of bananas disease	Banana bunchy top virus (BBTV)	25	-	-	-	-	[111, 327]
Seedling death of cereals disease	*Fusarium nivale*	-	-	Dry soil	-	-	[101]
Downey mildew of rose plants	*Peronospora sparsa*	15-20	85-100	Low moisture in soil	-	-	[491]
Early blight of potato	*Alternaria solani*	28-30	-	-	-	-	[597]
Late blight of potato	*Phytophthora infestans*	12-20 and above	-	Low moisture in soil	High light intensity	-	[7]
Bacterial leaf blight of rice	*Xanthomonas oryzae*	27	-	-	-	-	[204]
False smut of rice	*Ustilaginoidea virens*	20	-	-	-	-	[162]
Papaya ring spot	Papaya Ring Spot Virus (PRSV)	26-31	-	-	-	-	[575]
Black rust of wheat	*Puccinia graminis*	25-30	>85	High leaf wetness	Darkness	Elevated CO_2 concentration	[248]
Stripped rust of wheat	*Puccinia striformis*	18-30	>85	High leaf wetness	Low light intensity	Low CO_2 concentration	[248]
Loose smut of wheat	*Ustilago nuda var, tritici*	16-22	-	-	-	-	[613]
Brown spot of rice	*Helminthosporium oryzae*	28-30	-	-	-	-	[31]
Sheath blight of rice	*Rhizoctonia solani*	28-32	-	-	-	-	[519]
Damping off	*Pythium* sp., *Phytophthora* sp., *Rhizoctonia* sp., *Fusarium* sp., *Sclerotia* sp.	< 24	-	Low moisture in soil	-	-	[7]
Club root of cabbage	*Plasmodiophora brassicae*	18-25	-	Wet acidic soil with 70-80% moisture	-	-	[50]
Leaf spot of cole crops	*Alternaria brassicicola*	28	-	High leaf wetness	-	-	[248]
Downy mildew of cole crops	*Peronospora parasitica*	12-27	-	Low moisture in soil	-	-	[7]
Downy mildew/ crazy top of maize	*Peronosclerospora sorghiis*	21-33	-	Low moisture in soil	-	-	[7]
Anthracnose of citrus	*Colletotrichum acutatum*	High temperatures	-	-	-	-	[290]

Table 1 (continued)

Disease caused	Pathogen	Optimum temperature, ℃	Optimum relative humidity, %	Water activity	Light intensity	CO_2 concentration	Reference
Bunt of wheat	*Tilletia controversa*	High temperatures	-	-	-	-	[55]
Root knot of coffee	*Meloidogyne incognita*	High temperatures	-	-	-	-	[200]
Wilt of tomato	*Ralstonia solanacearum*	-	>75	High moisture in soil	-	-	[262, 306]
Rice blight	*Pyricularia oryzae*	-	>85	-	-	-	[24]
Wheat blotch	*Septoria tritici*	-	-	-	High light intensity of 8000 lux	-	[572]
Bean rust	*Uromyces phaseoli*	17-22	>95	-	Both high and low intensity	-	[392]
Downy mildew of grapes	*Plasmopora viticola*	12-30	>85	Low moisture in soil	Long day light	-	[321]
Turnip mosaic infection	Turnip mosaic virus	High temperatures	Less humidity	Less moisture	-	-	[465]
Bunch rot of grapes	*Botrytis cineria*	20-25	100	-	-	-	[98]
Crown rot of wheat	*Fusarium pseudograminearum*	-	-	-	-	Elevated CO_2 concentration	[382]
Smut of barley	*Ustilago hordei*	-	-	-	-	Elevated CO_2 concentration	[359]
Downey mildew of barley	*Blumeria graminis*	-	-	-	-	Low CO_2 concentration	[237]
Leaf spots caused by foliar nematodes	*Aphelenchoides ritzemabosi*	22	High humidity	High moisture	-	-	[84]
Early blight of tomatoes and potatoes	*Alternaria solani*	28-30	Humid environment is required	Alternate dry and moist conditions	Day light is essential for development	-	[86]
Smut disease of sugarcane	*Sporisorium scitamineum*	25-30	65-70	-	-	-	[475]
Wart disease of potato	*Synchytrium endobioticum*	10-27	-	Moist soil with rainfall exceeding 70 cm	-	-	[426]

downy mildew, and leaf spots are the prominent leaf diseases of the crops, and the causative agents include fungi, bacteria, and nematodes causing characteristic symptomatic disease which on progression leads to altered crop growth and reduced yield. Powdery mildew is the fungal pathogenic infection of crops caused by various fungal species affecting a wide range of crops like fruits, vegetables, cereals, and other common and ornamental plants (Table 2). These fungi invade the epidermis layer of the leaves immediately after the sedimentation of the spores on the leaf surface by supressing the host immune response [211]. This causes the green island effect on the infected leaves i.e., the leaf area of the fungal colonization remains green whilst the surrounding area has chlorosis leading to the systematic cell death and formation of nutrient sinks promoting monosaccharide transport at the site of infection [174]. Which enables the utilization of the monosaccharide by the fungi favouring the fungal colonization with the formation of the characteristic symptomatic white powdery growth on the leaves surface that leads to about 30% loss in the crop yield [249, 548]. Downy mildew is caused by *Oomycetes* [104] that hampers the crop quality and yield worldwide and have caused severe losses during 1970s of about 7.5 billion USD in USA as stated by USDA [580, 582]. They have a broader host range compared to the powdery mildew, almost infecting all the crops with the characteristic yellow lesions on the leaves (Table 2) [491]. Xu and Pettitt [620] has reported that the symptomatic lesions formed on the leaves, stem, peduncles, calyxes, and petals by downy mildew are very difficult

Table 2 Major crop diseases caused by biotic and meso-biotic factors like fungi, bacteria, virus, viroid, parasitic nematodes, and insects casing severe economic loss globally

Crop disease	Symptoms	Crops affected	Pathogen involved	Reference
Blight disease	Blight is caused by bacterial or fungal infestation with characteristic symptoms like sudden and severe yellowing, browning, spotting, withering, and drying of leaves, flowers, fruits, twigs, sheath, stem, and the whole plant	Potato, corn, chestnut, citrus, fruit, rice, wheat, tomato, grass, oak, grains, pulses, cereals, vegetables, etc.	Fungi: *Phytophthora infestans, Cochliobolus heterostrophus, Bipolaris maydis, Cryphonectria parasitica, Alternaria sp., Alternaria triticina, Tubakia iowensis, Colletotrichum capsici, Phytophthora parasitica, Cochliobolus heterostrophus* Bacteria: *Erwinia amylovora, Xanthomonas oryzae, Burkholderia plantarii, Xanthomonas axonopodis*	[133, 234, 358, 422, 451, 452, 480, 500]
Rot disease	Rot disease is caused by bacteria, fungi, and Oomycetes. This affects the roots, basal or bulb rots, heart rot, grey rot, seed rot, soft rot, red rot, tuber rot, and wood rot. It is characterized by plant decomposition and putrefaction with a hard, dry, spongy, watery, mushy, or slimy tissue decay	Flowers, fruits, vegetables, wood, celery, barley, bean, carrot, faba bean, lettuce, oat, oilseed, pea, rye, soybean, sugar beet, tomato, triticale, wheat, alfalfa etc.	Fungi: *Fusarium avenaceum, Fusarium culmorum, Fusarium graminearum, Fusarium pseudograminearum, Fusarium solani, Fusarium verticillioides, Phoma betae, Phoma terrestris, Phoma sclerotioides, Thielaviopsis basicola* Oomycetes: *Aphanomyces cochlioides, Aphanomyces euteiches, Phytophthora citrophthora, Phytophthora nicotianae, Phytophthora cactorum, Phytophthora cinnamomic, Phytophthora fragariae, Phytophthora sojae, Phytophthora capsica, Phytophthora medicaginis, Pythium ultimum* Bacteria: *Pectobacterium carotovorum, Erwinia* sp., *Pseudomonas* sp.	[36, 43, 91, 115, 155, 156, 223, 241, 330, 573, 607, 621]
Wilt disease	Wilt is caused by bacterial, fungal and nematode pathogen. Affects the vascular system, alters the xylem activities by hindering the transport of water to different parts of plants. Leads to rapid death of plants and trees	Cucurbits, elm trees, mimosa, oak, persimmon, pine, Stewart's wilt of corn, chillies, potatoes, tomatoes, aubergine, banana, geranium, ginger, tobacco, sweet peppers, olives, cotton	Fungi: *Ophiostoma ulmi, Fusarium oxysporum, Bretziella fagacearum, Acromonium diospyri, Verticillium* sp. Bacteria: *Erwinia tracheiphila, Ralstonia solanacearum, Pantoea stewartia* Nematode: *Bursaphelenchus xylophilus*	[114, 131, 153, 177, 369, 513, 518]
Rust disease	Fungal disease that affects the economically important crops. Appears as yellow, orange, red, brown, and black powdery pustules on the leaves, stems, young shoots, and fruits causing leaf rust, stem rust, stripe rust, crown rust, blister rust, apple rust, coffee rust, bean rust, leek rust, etc.	Wheat, rye, coffee, gooseberry, cereals, cedar- apple, grasses, crabapple, white pine, asparagus, pine, bean, chrysanthemum, hollyhock, snapdragon, sugarcane, ornamental plants	Fungi: *Puccinia graminis, Puccinia striiformis, Puccinia recondita, Puccinia sorghi, Phakopsora pachyrhizi, Melampsora epitea, Melampsora lini, Cronartium ribicola, Gymnosporangium juniperi-virginianae, Hemileia vastatrix, Phakopsora meibomiae, Puccinia coronata, Puccinia hemerocallidis, Puccinia triticina, Uromyces appendiculatus, Puccinia melanocephala, Puccinia kuehnii, Puccinia porri, Puccinia xanthii*	[151, 256]

Table 2 (continued)

Crop disease	Symptoms	Crops affected	Pathogen involved	Reference
Smut disease	A fungal disease identified with their dirt like sori which is dark coloured, thick-walled structures containing dust like teliospores. Sori generally appears in the leaves, flowers, stems, bulbs, and seeds. Commonly known as covered smut, loose smut, false smut	Rice, sugarcane, maize, barley wheat oats, forage grass, potato	Fungi: *Ustilago esculenta, Sporisorium scitamineum, Ustilago maydis, Ustilago nuda, Ustilago tritici, Thecaphora solani, Ustilago virens*	[18, 51, 269, 530]
Canker disease	Cankers are caused by both fungal and bacterial pathogen. Generally, occurs on woody trunks with the characteristic lesions with irregularly sunken, swollen, flattened, cracked, discoloured, and dead areas on the stem, twigs, and trunk	Sweet and sour cherries, tomatoes, strawberries, kiwi fruit, hazelnuts, olives, apple, stone fruit, almond, blueberry, chestnut, apricot, citrus fruits, butternut, rapeseed, rose, oak, mulberry	Fungi: *Valsa mali, Neonectria galligena, Sirococcus clavigignenti-juglandacearum, Seiridium cardinale, Geosmithia putterillii, Discula destructiva, Eutypa lata, Thyronectria austro-americana, Lachnellula willkommii, Gibberella baccata, Diplodia quercina, Fusarium circinatum, Apiognomonia veneta, Leptosphaeria maculans, Leptosphaeria coniothyrium, Cryptosporella umbrina, Gremmeniella abietina* Bacteria: *Pseudomonas syringae, Clavibacter michiganensis, Xanthomonas campestris, Xanthomonas citri, Xanthomonas axonopodis, Pseudomonas savastanoi, Xanthomonas populi*	[64, 74, 165, 168, 178, 179, 212, 316, 481, 505, 506, 599, 609]
Blast disease	Fungal and bacterial disease that affects grains, leaves, leaf collars, nodes, panicles, and seedlings. It forms, elliptical leaf spots with grey, white centre and red to brown margins	Rice, wheat, millets, citrus, rye, barley, cereals, apple	Fungi: *Magnaporthe oryzae, Helminthosporium sativum, Magnaporthe grisea* Bacteria: *Pseudomonas syringae*	[196, 232, 263, 626]
Leaf spot disease	Caused by bacteria, fungi, viruses, nematodes, and insects which can lead to cankers and blights. It is a light-coloured circular spot with brown coloured edge	Olives, legumes, vegetables, cereals, pulses, fruits, almost all crops are affected	Fungi: *Phoma sp., Sclerotinia sp., Alternaria brassicae, Cercosporidium personatum, Cercospora dolichi, Pseudocercospora griseola, Phyllosticta sp., Colletotrichum gloeosporioides* Bacteria: *Xanthomonas campestris, Pseudomonas savastanoi, Curtobacterium flaccumfaciens, Xanthomonas begoniae* Virus: *Trichovirus,* Cocadviroid Nematodes: *Aphelenchoides ritzemabosi* Insects: Aphids, leafhoppers, lace bugs, plant bugs, mites,	[23, 84, 233, 297, 318, 332, 435]

Table 2 (continued)

Crop disease	Symptoms	Crops affected	Pathogen involved	Reference
Downy mildew disease	Majorly caused by Oomycetes. Symptoms include the appearance of yellow to white patches on the leaf surface especially due to the growth of white to greyish cotton like fungi. With time the infected leaves turn crisp, brown, brittle, and fall off	Cucumber, cantaloupe, pumpkin, squash, watermelon, basil, grapes, hops, ornamental plants, soyabeans, spinach, sunflower, rose plants, blackberries, caneberries, and almost all crops are susceptible	Fungi: *Peronospora belbahrii, Pseudoperonospora cubensis, Plasmopara viticola, Pseudoperonospora humuli, Peronospora manshurica, Peronospora effuse, Plasmopara halstedii, Peronospora sparsa*	[321, 471, 491, 631]
Powdery mildew disease	A fungal disease with characteristic spots or patches with white to greyish powdery appearance on the leaves	Affects all plants including fruits, vegetables, cereals, grasses, weeds, shrubs, roses, creepers. Mainly infects wheat, barley, grapes, legumes, onions, strawberries, apple, pears, melons, gourds, pumpkins	Fungi: *Blumeria graminis, Microsphaera diffusa, Erysiphe necator, Leveillula taurica, Podosphaera leucotricha, Podosphaera xanthii, Erysiphe cichoracearum, Leveillula taurica, Microsphaera syringae, Podosphaera aphanis, Sawadaea tulasnei, Erysiphe berberidis, Golovinomyces orontii*	[2, 387, 474, 494]
Anthracnose disease	A common fungal disease of leaves with the characteristic symptomatic spots, cupping, and curling of leaves leading to blight and cankers. Also affects stems, fruits, and flowers	Tomatoes, melons, chillies, oak, maple, ash, avocado, cashew, mango, banana, vegetables, cucumber, bean, pumpkin, spinach, almost all plants grown in shade	Fungi: *Colletotrichum sp., Gloeosporium sp.*	[116, 565]
Gall disease	Formation of round and wart-like growth on the lower stems and branches mostly near the soil line	Woody plants, shrubs, grapes, raspberries, blackberries, roses	Bacteria: *Agrobacterium tumefaciens, Agrobacterium rubi, Agrobacterium vitis*	[33, 205]
Wart disease	Otherwise known as black wart, black scab, potato tumour, potato cancer or canker, cauliflower disease, warty disease with symptoms like formation of green parenchymatous tissues on stems base, stolon buds, and tuber eyes which may turn black on maturation	Potatoes	Fungi: *Synchytrium endobioticum*	[426]
Scab disease	Twisted and puckered leaves, black circular scabby spot on the underside of the leaves, spot looks velvety, sooty, olive-green appearance on the upper side, finally the leaves turn yellow and drop down	Apple, potato	Fungi: *Venturia inaequalis* Bacteria: *Streptomyces scabies, Streptomyces bottropensis, Streptomyces stelliscabiei, Streptomyces aureofaciens*	[203, 495]
Damping off disease	It is soilborne disease. Rotting of stem and root tissues, leaf spotting, decay of seeds and seedlings	Affects all agricultural and forestry crops	Fungi: *Rhizoctonia solani, Aphanomyces cochlioides, Pythium sp., Phytophthora sp., Botrytis sp., Fusarium sp., Cylindrocladium sp., Diplodia sp., Phoma sp., Alternaria sp.*	[315]

Table 2 (continued)

Crop disease	Symptoms	Crops affected	Pathogen involved	Reference
Mosaic disease	Discoloration of leaves, mottled leaves, yellow spots and stripes on the leaves, twisting of young leaves, stunted growth, poor leaf and fruits formation, reduced photosynthesis, and reduced grain production	Tobacco, pepper, potato, tomato, eggplant, cucumber, petunia, melons, squash, spinach, celery, beet, cereals, wheat, sugarcane, lettuce, maize, and other plants	Virus: Tobacco mosaic virus, cauliflower mosaic virus, sugarcane mosaic virus, lettuce mosaic virus, maize mosaic virus Transmitting insect vectors: insect, aphids, leafhoppers	[87, 338, 344, 446, 601]
Leaf roll disease	Severely affected crops appear stunted and erect with leaves rolling upwards and appear leathery, chlorotic, and die eventually. Necrotic lesions are observed in the tuber tissues of potatoes	Grapes, potato	Virus: Grapevine leafroll associated virus, potato leafroll virus Transmitting insect vectors: Aphids	[307, 363]
Leaf curl disease	Upward and downward curling of leaves with thickening of leaves	Cotton, Papaya, Okra, Chilly, Capsicum, Tomato, Tobacco	Virus: Leaf curl virus Transmitting insect vectors: White flies	[362]
Stunt disease	Discoloration and distortion of leaves with stunted growth. Vulnerable to secondary infections	Peanuts	Virus: Peanut stunt virus Transmitting insect vectors: Aphids and sap insects	[408, 443]
Root knot disease	Formation of root-knot galls that results in stunted growth, poor quality and yield of crops, discoloration and nutrient deficiency, and reduces resistance to draught conditions and secondary infections by other pathogens	All horticultural and field crops	Nematode: *Meloidogyne javanica, Meloidogyne arenaria, Meloidogyne incognita, Meloidogyne hapla*	[268]
Cyst disease	Stunted growth, yellow discoloration, and death	Soyabean, peas, sugar beet, potato	Nematode: *Heterodera schachtii, Heterodera goettingiana, Heterodera glycines, Globodera pallida*	[245, 377]
Lesion disease	Plant root stress with necrotic lesions. Lesions turn from reddish-brown to black. Initially appear as spotty lesions and coalesce to form larger lesions with time	Over 400 crops species including potato, peanut, monocots, fruits, cereals	Nematodes: *Pratylenchus pratensis, Pratylenchus brachyurus, Pratylenchus coffeae, Pratylenchus penetrans, Pratylenchus scribneri, Pratylenchus vulnus, Pratylenchus zeae, Pratylenchus crenatus, Pratylenchus thornei*	[394]
Sting disease	Ceases the growth of the root tips leading to reduced strength, slow growth, stunted growth, and eventual death of crops. Foliage appears nutrient deficient with yellow to red discoloration which leads to chronic wilting	All agricultural crops, vegetables, grains, and trees	Nematode: *Belonolaimus longicaudatus*	[310]

Table 2 (continued)

Crop disease	Symptoms	Crops affected	Pathogen involved	Reference
Chloric dwarf disease	Depending on crop variety and environmental conditions it causes stunted growth, reduced internode length, foliar irregularities, chlorosis, necrosis, purpling of leaflets, downward curling of leaves	Tomato	Viroid: Tomato chloric dwarf viroid - *Pospiviroid*	[591, 592]
Fruit crinkle disease	Russet ring symptom, leaf pucker symptom, and appearance of green crinkles	Apple	Viroid: Apple fruit crinkle viroid - *Apscaviroid*	[329]
Citrus exocortis disease	Affects trees and plants with the characteristic symptoms like scaling of bark, severe chlorosis, and stunted growth	Citrus, tomato	Viroid: Citrus exocortis viroid - *Pospiviroid*	[600]
Columnea latent disease	Stunted growth, distorted and vein necrosis. Necrosis observed in stem, branch, and leaves	Tomato, cucumber, potato, eggplant, capsicum, petunia, ornamental plants	Viroid: Columnea latent viroid - *Pospiviroid*	[560]
Tomato apical stunt disease	Stunting, apical proliferation, apical leaf narrowing and yellowing, leaf crinkling, tissue brittleness, necrosis	Tomato	Viroid: Tomato apical stunt viroid - *Pospiviroid*	[21]
Tomato planta macho disease	Stunted growth, exhibit strong epinasty in leaves, and produce fewer fruits	Tomato	Viroid: Tomato planta macho viroid - *Pospiviroid*	[372]
Potato spindle tuber disease	Stunted growth, chlorosis, reddening or purpling of leaves, brittle leaves, waviness or distorted leaf margins, significant reduction in the quality of fruits and tubers	Potato, tomato, ornamental plants	Viroid: Potato spindle tuber viroid - *Pospiviroid*	[520]

to differentiate from the lesions formed due to nutritional deficiencies, spray injury, and black spots [85]. Further, researchers have stated that the yellowing and abscise formation on the leaves are the severe symptoms observed on the leaves surface followed by enlargement of abscise, appearance of black spots, lesions on the petals, leaf fall in about one month period of infection, arrest of root formation, and collapsing of buds [6, 85, 186, 620]. Similarly, leaf spots affecting almost all the crops and plants are caused by various species of fungi, bacteria, and nematodes as describe in Table 2. Fungal leaf spot disease occurs when the fungal spore settles on a wet leaf surface on a warm weather which enables the immediate sporulation and formation of characteristic irregularly edged spots measuring about 0.5–1.5 cm demarcated with black edges, brown to reddish spot, and yellow halo. Brown leaf spot disease caused by the fungal pathogens such as *Cercospora henningsii, Cercospora manihotis*, and *Cercospora vicosae* were reported to cause a yield loss of about 20–30% in a wide range of crops [555]. While the white spot causing fungal species like *Cercospora caribaea,* that are found mostly in lower temperatures are known to cause considerable defoliation in casava plants [614]. Consequently, bacterial leaf spots appear as water-soaked lesions of 0.6 cm in diameter with characteristic black colour. They develop only during cool and wet conditions especially during rainy seasons or as sprinkler effect in the fields using sprinkler irrigation methods. *Xanthomonas* sp. and *Pseudomonas* sp. are the predominant pathogens found to cause bacterial leaf spots in many economically important crops hampering their quality and yield [518]. Unlike the common root nematodes, the foliar nematodes like *Aphelenchoides ritzemabosi*, *Aphelenchoides besseyi*, and *Aphelenchoides fragariae* have distinguishing properties of feeding on the leaves. Infection generally occurs when the nematode crawls up to the leaves from the soil or carried by wind and water film to the leaf surface, where they enter the leaf surfaces through stomata and cause progressive diseases as they feed on the parenchymal cells. The major symptoms include the formation of 0.25–1 cm necrotic lesions on the leaf surface near the vein especially occurrence of stripe necrotic lesions on the leaves with parallel veins and angular necrotic lesions on the leaves with netted veins. With time the stripe lesions spread to most of the leaves causing leaf blotches and the angular lesions progress to fan shaped pattern with the characteristic yellow–brown-grey colour. Severe diseases cause chlorosis of the crops with stunted growth [84, 350].

However, blight, anthracnose, wilt, blast, rust, and smut are also some of the major crop/plant diseases caused by the pathogens that target the leaves as their mode of colonization and entry into the plant's inner tissues. Blight and anthracnose disease of crops are caused by both bacterial and fungal pathogens (Table 2) which leads to the sudden spotting, drying, and withering of leaves, flowers, twigs, sheath, stem, and the whole plant affecting the yield with progressive crop loss [628]. There are many pathogens that belong to a widespread genera like *Phytophthora, Alternaria, Cochliobolus, Bipolaris, Cryphonectria, Tubakia, Colletotrichum, Gloeosporium* etc. (Table 2). Of which, *Phytophthora* genus was reported to have 120 crop/plant pathogenic species and the most prominent species being the *Phytophthora infestans* causing devastating disease i.e., late blight of potato and tomato [281]. The other prominently known fungal blight disease is the sheath blight caused by *Rhizoctonia solani* on paddy crops causing around 50% loss in the crop yield worldwide during favourable conditions [46, 220]. It is a soilborne *Basidiomycete* containing 100 different crop pathogenic species affecting various crops with sheath blight, banded leaf, aerial blight, and brown patch [9, 635]. Similarly, the bacterial pathogen *Xanthomonas oryzae* are the causative agent of bacterial blight and leaf streak disease in paddy crops which leads to about 16–50% yield loss worldwide depending on the paddy variety grown [267, 427]. Ou in 1985 [436] have stated that bacterial blight especially the kresek syndrome under favourable conditions could cause even 75% loss in the crop yield worldwide. Analogously, [340] have observed that bacterial leaf streak under favourable conditions could cause severe to very severe damage in the paddy crops leading to about 8–32% loss in yield. The major symptoms of the bacterial blight include the appearance of water-soaked lesions on the tips and the margins of leaves which may progress to chlorosis and necrosis [325] and the symptoms of bacterial leaf streaks are the formation of water-soaked lesions anywhere on the leaf surface resulting in translucent and yellowish streaks which on time turns greyish-white, die, and wither [267, 420].

The causative agents of the wilt disease in crops are the fungi, bacteria, and nematodes and are generally caused due to the moisture stress created by the pathogens while attacking the vascular system of the crops [308, 554]. The common symptoms include the water loss in the leaves and stem leading to dryness and death of the plant. Fungal pathogens like *Ophiostoma ulmi, Fusarium oxysporum, Bretziella fagacearum, Acromonium diospyri, Verticillium* sp. etc. are well known for their ability to cause wilt disease in various economically important crops like vegetables, flowers, and fruits (Table 2) [369]. Affected leaves turn to dull green with water-soaked appearance which curl upward and cling to the stem, and the margins are often observed to turn yellow to bronze in colour [270, 271, 342]. *Verticillium* sp. are the prominent species among the wilt causing fungal pathogens that affects a variety of crops and plants like trees, shrubs, vines, flowers, ornamental plants, vegetables, fruits, and economically important crops [49, 177, 450, 528]. There are about ten reported species of *Verticillium* namely *Verticillium* *dahliae, Verticillium albo-atrum, Verticillium alfalfae, Verticillium longisporum, Verticillium nonalfalfae, Verticillium tricorpus, Verticillium zaregamsianum, Verticillium isaacii, Verticillium nubilum,* and *Verticillium klebahnii,* among which *Verticillium dahliae* is the potential pathogen with economically importance [146, 258, 288, 295, 450, 528]. The specific symptoms include the early drop of green leaves from the twigs and branches leading to complete defoliation, necrosis, and death [288]. Bacterial wilt caused by the genera *Corynebacterium*, *Erwinia, Pseudomonas, Ralstonia, Pantoea,* and *Xanthomonas* species (Table 2) induces the formation of the discoloured water-soaked lesions resulting in stunting, wilting, and withering of leaves which on progression to stems lead to the formation of the lesions in the stem with characteristic bacterial ooze from the infected stems [153]. Nematode, *Bursaphelenchus xylophilus* a causative agent of pinewood wilt disease leads to a severe economic loss in various countries causing dramatic irreparable changes to the pine wood available in their native forest [8, 518].

Apparently, blast is a crop disease caused by the fungal and bacterial pathogens that majorly infects the cereals including the economically important varieties affecting the grains, leaves, leaf collars, nodes, panicles, and seedlings with the characteristic symptoms like elliptical leaf spots with grey, white centre and red to brown margins (Table 2) [292]. Fungal pathogens like *Magnaporthe oryzae, Helminthosporium sativum, Cochliobolus miyabeanus,* and *Magnaporthe grisea* are known for their pathogenic effects on crops among which *Magnaporthe oryzae* and *Magnaporthe grisea* are the potential pathogen affecting the paddy crops at various growth stages leading to severe losses to about 10–30% worldwide [523]. The necrotrophic fungi *Cochliobolus miyabeanus* causing rice brown spots and the hemibiotrophic bacteria *Xanthomonas oryzae* causing rice blight are generally found in association with the blast fungal species in the paddy crops leading to the improved crop and yield loss [279]. The bacterial blast also known as the citrus blast is caused by *Pseudomonas syringae* especially during the winter seasons with the formation of black lesions which leads to the curling and withering of leaves [263]. Also, it is well known for its blossom blast disease on apple with the characteristic disease symptoms including the necrosis of the lateral flower buds which on disease progression gets wilted and drooped [196]. Furthermore, rust and smut diseases are the significant fungal diseases that affect a wide range of crops and plants hampering their growth, yield, and quality substantially. About 7000 species of *Basidiomycetes* are known to cause yellow, black powdery, brown, orange, and red rust to various crops and plant worldwide [42, 66, 117]. Among these the most important genera includes the *Puccinia, Phakopsora, Melampsora, Cronartium, Gymnosporangium, Hemileia,* and *Uromyces* sp. (Table 2). These fungi are the biotrophic organisms that depend on their host for the nutrients, growth, and reproduction [11, 106, 144]. Wheat being the mostly affected crops by the rust fungi are susceptible to the infection caused by three potential species namely *Puccinia striiformis* causing yellow stripe rust [339], *Puccinia triticina* causing leaf brown rust [56, 208], and *Puccinia graminis* f. sp. *tritici* causing brown rust of stem [45, 326, 521] which leads to about 15–20% annual yield loss [166]. Yellow stripe rust is a devastating disease that causes an annual loss of about 5.5 million tons of wheat worldwide [42]. More than 88% of the wheat varieties worldwide are known to be vulnerable to the yellow stripe rust resulting in almost 100% yield loss with the characteristic stunted growth of the crops and immature kernels [42, 88, 166, 602]. Prank et al. [464] have estimated that the *Puccinia graminis* f. sp. *tritici* causing brown stem rust of wheat crops could cause as close to 100% loss in the yield of the crops with the formation of characteristic symptomatic brick red to brown lesions containing urediniospores on the leaves, sheath, stem, awns, and glumes. Around 90% of the wheat crop varieties worldwide are susceptible to the brown rust associated with reduced grain size and lodging of the crops [326, 521]. Wheat leaf rust is a common and widely distributed disease [56, 250], and the yield losses are attributed by the reduction in the kernel size and the number of grains in the head [250, 299]. Similarly, crown rust of cereals and the coffee rust are the other two imperative rust disease leading to severe economic loss caused by the pathogens *Puccinia coronata* and *Hemileia vastatrix* respectively. Former affects the crops with the formation of light orangish pustules on the leaf sheath, peduncles, and awn leading to stunted growth and reduced yield [166, 412]. Whereas the later forms yellow-orange powdery lesions with pale yellow chlorotic spots leading to leaf fall with a reduction in the quality and quantity of the flowers and fruits produced [571]. Smut is the other disease caused by *Basidiomycete* fungal pathogens which leads to great economic losses and are characterized by the formation of a dirt like structures or soot-like spores called as “sori” on the leaves, grains, and the ears of the affected crops. It mostly affects cereals, spices, vegetables like potato, and some cash crops like sugarcane by the fungal species belonging to the genera *Ustilago, Sporisorium, and Thecaphora* (Table 2). *Sporisorium scitamineum* is the causative agent of whip smut disease of sugarcane crops in about 120 countries worldwide [475]. It is generally characterized by the emergence of the smut whip in sugarcane crops which usually causes stunted growth, thin and slender canes with broad spaced nodes, appearance of whip like sorus at the top of the stalk or at either side of the canes with narrow leaves, profuse tillers, and spindlier shoot with an average yield loss of up to 12–75% [100, 424, 475, 489]. The common smut (boil or blister smut) of cereals especially maize is caused *Ustilago maydis* with the formation of thick and fleshy galls filled with spores impeding the yield of the crops [477]. Similarly, *Ustilago nuda, Ustilago nigra, Ustilago hordei, Ustilago avenae, Ustilago kolleri,* and *Ustilago tritici* are the other potential species that causes smut of other cereals like wheat, oats, barley, etc. [386]. *Thecaphora solani* is responsible for the destructive disease caused to potato crops with high yield loss of about > 90% worldwide [18].

Canker is the disease affecting various parts of the crops like leaves, stem, woody trunk, fruits etc. with characteristic symptoms like lesions with irregular sunken appearance, swollen, flattened, cracked, discoloured, and dead areas caused by both bacteria and fungi. *Valsa mali, Neonectria galligena, Sirococcus clavigignenti-juglandacearum, Seiridium cardinale, Geosmithia putterillii, Discula destructiva, Eutypa lata, Thyronectria austro-americana, Lachnellula willkommii, Gibberella baccata, Diplodia quercina, Fusarium circinatum, Apiognomonia veneta, Leptosphaeria maculans, Leptosphaeria coniothyrium, Cryptosporella umbrina,* and *Gremmeniella abietina* are some of the fungal species and the species like *Pseudomonas syringae, Clavibacter michiganensis, Xanthomonas campestris, Xanthomonas citri, Xanthomonas axonopodis, Pseudomonas savastanoi,* and *Xanthomonas populi* are some of the bacterial species causing cankers to various crops [64, 74, 165, 168, 178, 179, 212, 316, 331, 481, 505, 506, 599, 609]. Symptoms of fungal stem or branch cankers are associated with dieback syndrome and are caused by almost 150 different species of fungi infecting about 130 species of woody hosts [3, 10, 162, 294, 537]. Besides, bacterial cankers of citrus fruits are characterized by the lesions on the twigs, leaves, and fruits which leads to defoliation and fruit drop causing severe economic loss [267, 503].

Neoplastic plant disease like crown galls (tumours) of the herbaceous plants are caused by bacterial species such as *Agrobacterium tumefaciens, Agrobacterium rubi,* and *Agrobacterium vitis* on the stems, branches, leaves, roots, canes, and veins with a characteristic wound appearing like cauliflower head leading to severe damage with weakened appearance, stunted growth, and death of the plants [33, 205]. However, potato warts caused by the fungi *Synchytrium endobioticum* are said to result in substantial economic losses worldwide as it is a social disease observed in almost all the countries with severe damage to the tubers [426]. Nevertheless, scab disease of potatoes caused by the bacterial pathogens *Streptomyces scabies, Streptomyces bottropensis, Streptomyces stelliscabiei,* and *Streptomyces aureofaciens* are known to cause severe loss of the tubers with the formation of crustaceous lesions on the leaves, stem, fruits, and tubers [495]. Furthermore, apple scabs caused by the *Ascomycetous* fungi *Venturia inaequalis* leads to considerable yield loss worldwide affecting the quality and quantity of the fruits produced [203]. Likewise, damping-off is a soilborne infection caused by fungal pathogens like *Rhizoctonia solani, Aphanomyces cochlioides, Pythium sp., Phytophthora sp., Botrytis sp., Fusarium sp., Cylindrocladium sp., Diplodia sp., Phoma sp.,* and *Alternaria sp.* affecting almost all agricultural and forestry crops causing severe damage to the yield and leads to death of crops worldwide [315].

Parasites like nematodes are also known to cause various diseases to crop globally, namely the root-knot disease, cyst disease, leaf spots, sting, wilt, and lesion disease. Root-knot disease is caused by the nematodes of the genus *Meloidogyne* with the formation of the root-knot galls containing the nematodes in roots of the crops [576, 615]. The major species of the root-knot nematodes include *Meloidogyne javanica, Meloidogyne arenaria, Meloidogyne incognita,* and *Meloidogyne hapla* [173]. It is estimated by researchers like [268, 496, 632], and [429] that these nematodes cause severe damage to economically important crops especially the varieties like tomato, watermelon, pepper, eggplant, potato, carrot, and cucumber leading to a yield loss of about 15–25% and sometimes as high as 75% with an estimated loss of about 100 billion USD per year worldwide. Nematode cyst disease is caused by the nematodes like *Heterodera schachtii*, *Heterodera goettingiana, Heterodera glycines, and Globodera pallida* affecting various crops like soya beans, peas, sugar beet, and potatoes causing a yield loss of about 10–30% and estimated loss of about 1 billion USD [245, 377]. Lesion nematode disease is also a devastating disease of root tissues that are majorly soilborne and are caused by *Pratylenchus pratensis, Pratylenchus brachyurus, Pratylenchus coffeae, Pratylenchus penetrans, Pratylenchus scribneri, Pratylenchus vulnus, Pratylenchus zeae, Pratylenchus crenatus,* and *Pratylenchus thornei* affecting various crops including cereals, peanuts, potatoes, fruits, and all monocots leading to a yield loss of about 50–85% and estimated loss of about 216 billion USD worldwide [394, 418, 423]. Similarly, *Pratylenchus penetrans* causes about 30–50% yield loss of potatoes with the characteristic early dying disease associated with premature vein senescence [317, 486, 487]. Sting nematode *Belonolaimus longicaudatus* is a soilborne ectoparasitic nematode that generally affects all agricultural crops especially the peanuts with the characteristic chronic wilting leading to great economic losses [310].

Disease caused by meso-biotic factors

Disease caused by the meso-biotic factors are the disease caused by parasites like viruses and viroids that are capable of existing in dormant stage for a relatively longer periods, gets activated once after entering a favourable host cell, and requires a host for their survival [302, 379]. Virus pathogens are transmitted to healthy plants through sap contamination, vectors, nematodes, soilborne, seedborne, and pollen borne transmissions [508]. Of which, insects (vectors) play a vital role with the existence of 200 known species of aphids that transmit the mosaic viruses, > 100 species of leafhoppers known to transmit viruses causing yellow discoloration in crops, and other insects like whiteflies, thrips, mealybug, planthoppers, grasshoppers, scales, and some beetle which help in transmitting a wide range of viruses affecting agricultural crops [189]. Nematodes feeding on roots are also responsible for the virus transmission in the host plants from the soil for e.g., grape fanleaf virus, tobacco and tomato ringspot virus, and many strawberry viruses are known to be transmitted by nematodes [19, 185]. Similarly, many studies worldwide report that viruses like big vein of lettuce, soilborne wheat mosaic, and tobacco necrosis viruses are transmitted by the swimming spores of the soil inhabiting fungal pathogens [129, 589].

Viruses cause various damages to the host crops like the mosaic damage, yellowish discoloration, chlorosis, stunted growth, and necrosis which significantly hampers the growth and yield of the crops to about 40–100% [357, 508]. Mosaic viruses affects the foliage of the crops with the formation of yellowish to dark green patches, mottled appearance, curled leaves, and appearance of light-coloured veins [87]. Many mosaic viruses are known till date to affect a vast range of crops. Wherefrom, the most potential viruses are the tobacco mosaic virus, rice stripe mosaic virus, cauliflower mosaic virus, sugarcane mosaic virus, lettuce mosaic virus, and maize mosaic virus infecting tobacco, paddy, pepper, potato, tomato, eggplant, cucumber, petunia, melons, squash, spinach, celery, beet, cereals, wheat, sugarcane, lettuce, maize, and other economically important agricultural crops [633]. Among these, the rice stripe mosaic viruses affecting paddy crops, transmitted by flies were reported to have a field incidence of about 70% with severe loss in the grain production [87, 601]. Tobacco mosaic virus is of profound economic significance as it causes mottled browning of tobacco leaves and stunted growth hampering the quality and market value of the leaves [338]. The virus has also been reported to infect various solanaceous crops affecting their yield and quality [446]. Sugarcane mosaic virus being the next potential pathogen belonging to the genera *Potyvirus* and family *Potyviridae* are transmitted by aphids [344] and causes severe damage to the economically significant sugar and energy producing crops sugarcane by reducing their yield to about 10–50% and sometime as high as about 60–80% worldwide [595, 612].

Similarly, the leaf roll viruses affecting the fruits (grapes) and vegetable (potato) crops are transmitted by aphids with the characteristic symptoms like stunted growth with erected appearance and leaves roll upwards with leathery and chlorotic texture and appearance [363]. Grapevine leafroll disease caused by grapevine leafroll virus have been known since 1936 for their symptomatic downward leaf rolling, chlorosis, and delayed ripening of fruits reducing the fruit quality and yield to about 40% [13, 367]. It is also estimated by [25] that the virus results in a loss of about 25,000–40,000 USD per hectare of vineyard. Potato leafroll virus being the most devastating virus of the leafroll viruses which belongs to the genus *Polerovirus* and family *Luteoviridae* leads to a global yield loss of 20 million tons i.e., 90% loss worldwide [303]. [307] has observed the latent infection caused by the virus in the planting tubers directly affects the rate of tuber germination, crop strength, and the yield of potatoes. Likewise, the leaf curl viruses belonging to the *Geminiviridae* family are generally transmitted through whiteflies and are known to affect a variety of crops with stunted growth, chlorosis, curling of leaves, and considerable reduction in the fruit yield globally [107, 198, 399, 442, 586]. Among the know leaf curl viruses, tomato yellow leaf curl virus is a potential pathogen causing devastating disease of many crops and tomatoes with severe effects on the fruits especially the depletion in the fruit taste, reduced size, un-uniform ripening of fruits, and severe yield losses worldwide [362, 438, 538]. Further, peanut stunt virus of the family *Bromoviridae* are known for their stunt disease of peanut crops and soyabean with severe dwarfing or stunting of peanut crops with an annual yield loss of about 10–50% [408, 443].

Likewise, the viroid, which are also called as mini-viruses lacking capsid are the low molecular weight single stranded RNA (usually the size ranges between 246–399 nucleotides), covalently closed, circular, highly structured non-coding RNAs that replicate autonomously affecting a vast range of economically important crops [302]. Further, they can cause non-symptomatic latent infections in their host which on transmission to susceptible hosts causes devastating infections. Table 3 lists the available information of various viroids known to affect the crops and their lineage. Viroid belongs to the two major families namely *Pospiviroidae* and *Avsunviroidae* with the common genera *Pospiviroid, Hostuviroid, Cocadviroid, Apscaviroid,* and *Coleviroid* of *Pospiviroidae* family and *Avsunviroid, Pelamoviroid,* and *Elaviroid* of *Avsunviroidae* family (Table 3) [128, 437]. *Pospiviroids* are majorly known to affect tomato crops with the characteristic diseases like chloric dwarf disease, citrus exocortis disease, columnea latent disease, tomato apical stunt disease, and tomato planta macho disease (Table 2) leading to chlorosis, bronzing, leaf distortion, and growth reduction with an estimated yield loss of about 39–82% worldwide [591, 592]. Similarly, potato spindle tuber disease caused by *Pospiviroid* are known to affect tomatoes and potatoes with a field infection rate of about 25–50% affecting the tuber and fruit quality resulting in a yield loss of about 80% [520]. Nonetheless, the economically important hop stunt disease caused by hop stunt viroid of *Hostuviroid* has shown a field infection rate of about 10–20% [365] to multiple crops like mulberry, almond, apple, apricot, cherry, peach, pear, plum, pistachio, citrus fruits, and the flower *Hibiscus rosa-sinensis* with severe loss in quality and yield [15, 347, 349, 619]. Further, fruit crinkle disease caused by the fruit crinkle viroid of the genus *Apscaviroid* is known to have a narrow host range affecting apple fruits with a significant loss in yield and quality of the fruits [329]. Similarly, *Avsunviroid, Pelamoviroid,* and *Elaviroid* of *Avsunviroidae* family are known to cause severe yield loss of fruits and vegetable especially the crops like avocado, chrysanthemum, peach, and eggplant hampering the fruit quality and yield worldwide [77, 93, 158, 510].

Devastating crop diseases of Southeast Asian nations

The ten member states association forming the Southeast Asian nations include the countries like the Brunei Darussalam, Cambodia, Indonesia, Laos, Malaysia, Myanmar, Philippines, Singapore, Thailand, and Vietnam [244]. A wide variety of crops are cultivated in these countries namely cotton, millets, peanuts, paddy, sunflower, maize, palm, soybean, and sugarcane that are affected by major crop diseases impeding the crop yield and causing severe to heavy economic losses. Paddy crops with profound significance in the Southeast Asian nations are majorly affected by the devastating and destructive biotrophic fungal pathogen *Rhizoctonai solani* with a yield loss of about 6 million tons of rice grains annually [635]. Similarly, Naqvi [409] has reported the prevalence of bacterial blight of paddy caused by *Xanthomonas oryzae* in the countries like Philippines and Indonesia leading to severe loss in the grain yield. Oña et al. [431] has reported the epidemic developed by the bacterial leaf streak disease of paddy causing severe loss in the yield of the crops especially in the variety IR1695 compared to IR24. Another study on the devastating pathogen, *Fusarium oxysporum* (soilborne fungi) causing the *Fusarium* wilt of banana was reported by [398] in Philippines outlines the severity of infection and loss caused by the TR4 strain. Further, [57] has documented the major pathogenic disease affecting the vegetables in Philippines and has reported that the bacterial wilt caused by *Ralstonia solanacearum* has led to severe damage and yield loss of the crops like tomato, pepper, eggplant, bitter gourd, and lettuce. Further, the study has also stated the prevalence of the devastating diseases like downy mildew affecting bitter gourd and Chinese cabbage, *Cercospora* disease affecting pepper, eggplant, bitter gourd, and tomato, *Phytophthora* disease of tomato, eggplant, pepper, and Chinese cabbage, *Fusarium* wilt of tomato and pepper, disease of tomato crops caused by *Phytoplasma* sp. and *Corynespora* cassiicola, and various other diseases caused to tomato which includes bacterial canker, bacterial speck, target spot, *Septoria* leaf spot, and pith necrosis. Similarly, it is reported that the popular fruit trees Durian is highly vulnerable to the stem canker or patch canker disease caused by *Phytophthora palmivora* impeding the fruit yield and fruit quality in Sungai Liang, Brunei Darussalam [522]. Furthermore, Pearce et al. [447] and Bigirimana et al. [52] has reviewed the destructive rice sheath disease caused by *Sarocladium oryzae* causing considerable reduction in the crop yield in the countries like Brunei Darussalam, Indonesia, Philippines, Vietnam, and Thailand. *Pyricularia oryzae* causing destructive rice blast, leaf blast, and neck blast of paddy crops in Cambodia [95] is reported to cause elliptical lesions on the leaves during the vegetative and the reproductive phases of the crops, grain sterility, reduced grain size, loss in yield, and reduced grain quality [35, 289]. Also, [311] has reported an annual yield loss of about 55 million UDS in Southeast Asian countries due to the devastating infection of paddy cause by *Pyricularia oryzae*. According to the study reported by [102], bacterial sheath brown rot of rice caused by *Pseudomonas fuscovaginae* was found to be prevalent in Cambodia leading to sever loss in the grain yield with the appearance of the characteristic brown lesions on the sheath. It was also reported that the coinfection caused by several bacterial pathogens like *Acidovorax avenae, Burkholderia gladioli, Burkholderia cepacian*, and *Pantoea ananatis* resulted in the severing of the disease along with the formation of sheath lesions and grain discoloration [27, 534].

Casava being the most importantly cultivated food crops of the Southeast Asian countries has been majorly affected by a variety of disease-causing pathogens [569]. The most prevalent disease of casava is the casava mosaic disease caused by the cassava mosaic begomoviruses of the genus *Begomovirus* and *Geminiviridae* family resulting in the poor leaf development with reduced photosynthesis leading to the poor tuber quality with improved yield loss [581]. Shallots are one among the crops with high economic value worldwide and are largely cultivated in the South Kalimantan of Indonesia are reported to be infected by the Moler disease by *Fusarium oxysporum* and anthracnose by *Colletotrichum* sp. causing a severe damage to crop with a resulting yield loss ranging from 24 to 100%. Likewise, Adiyoga et al. [5], Bambang and Khusnul [30], and[188] have reported that *Fusarium* wilt disease, anthracnose, and porch blotch of onions could lead to a sever yield loss of about 27–27%, 21–100%, and 30% respectively in Southeast Asian countries and Indonesia. Further, bacterial stalk rot of corn a devastating disease caused by the bacterial species *Dickeya zeae* is reported to cause severe yield loss of corn in Indonesia [547]. Similarly, [546] has reported the vulnerability of the corn crops to various insects like grasshopper, katydid, sweet potato bug, derbid plant hopper, cotton stainer, largid bug, corn leaf hopper, corn rootworms, green chafer beetle, tussock moth, Asian lady beetles, transverse lady beetle, and assassin bug along with two fungal pathogenic

Table 3 Details of various viroid known to affect crops and their yield (classification as given in [170])

Disease	Viroid	Size of the viroid RNA, nucleotides	Family	Genera	Host plant	Variants known	New host infected	Reference
Chloric dwarf disease	Chloric dwarf viroid	360	*Pospiviroidae*	*Pospiviroid*	Tomato	2	-	[591, 592]
Citrus exocortis disease	Citrus exocortis viroid	366-475			Tomato, citrus	86	-	[600]
Columnea latent disease	Columnea latent viroid	359-456			*Columnea consanguinea*, *Nematanthus* sp., *Brunfelsia pauciflora*	17	Tomato	[560]
Tomato apical stunt disease	Tomato apical stunt viroid	360-363			Tomato	5	-	[21]
Tomato planta macho disease	Tomato planta macho viroid	360			Tomato	2	-	[372]
Potato spindle tuber disease	Potato spindle tuber viroid	341-364			Potato	109	Tomato, avocado	[520]
Chrysanthemum stunt disease	Chrysanthemum stunt viroid	348-356			Chrysanthemum	19	-	[406]
Iresine disease	Iresine viroid	370			*Iresine herbstii*	3	-	[590]
Mexican papita disease	Mexican papita viroid	359-360			*Solanum cardiophyllum*	6	-	[370]
Hop stunt disease	Hop stunt viroid	294-303		*Hostuviroid*	Citrus, grapevine, *Prunus* sp.	144	Hop, cucumber	[282]
Coconut cadang-cadang disease	Coconut cadang-cadang viroid	246-301		*Cocadviroid*	Coconut palm	8	Monocots and African oil palm	[231, 476]
Coconut tinangaja disease	Coconut tinangaja viroid	254			Coconut palm	2	-	[240]
Citrus bark cracking disease	Citrus bark cracking viroid	284-286			Citrus	6	-	[507]
Hop latent disease	Hop latent viroid	255-256			Hop	10	-	[445]
Apple scar skin disease	Apple scar skin viroid	329-333		*Apscaviroid*	Apple, pear	8	-	[515]
Apple dimple fruit disease	Apple dimple fruit viroid	306			Apple	2	-	[485]
Apple fruit crinkle disease	Apple fruit crinkle viroid	368-372			Apple	29	-	[329]
Australian grapevine disease	Australian grapevine viroid	369			Grapes	1	-	[150]
Citrus bent leaf disease	Citrus bent leaf viroid	315-329			Citrus	24	-	[76]
Citrus dwarfing disease	Citrus dwarfing viroid	291-297			Citrus	53	-	[109]
Grapevine yellow speckle 1 disease	Grapevine yellow speckle 1 viroid	365-368			Grapes	49	-	[617]
Grapevine yellow speckle 2 disease	Grapevine yellow speckle 2 viroid	363			Grapes	1	-	[561]
Pear blister canker disease	Pear blister canker viroid	314-316			Pear, quince	18	-	[169]
Coleus blumei -1 disease	*Coleus blumei* -1 viroid	248-251		*Coleviroid*	*Coleus blumei*, *Mentha* sp.	9	-	[578]
Coleus blumei -2 disease	*Coleus blumei* -2 viroid	295-301			*Coleus blumei*	1	-	[184]
Coleus blumei -3 disease	*Coleus blumei* -3 viroid	361-364			*Ocimum basilicum, Melissa officinalis*	3	-	[536]
Coleus blumei -5 disease	*Coleus blumei* -5 disease	NA			*Plectranthus scutellarioides*	NA	Aurora black cherry	[577]

Table 3 (continued)

Disease	Viroid	Size of the viroid RNA, nucleotides	Family	Genera	Host plant	Variants known	New host infected	Reference
Avocado sun blotch disease	Avocado sun blotch viroid	239-251	*Avsunviroidae*	*Avsunviroid*	Avocado	83	-	[77]
Chrysanthemum chlorotic mottle disease	Chrysanthemum chlorotic mottle viroid	397-401		*Pelamoviroid*	Chrysanthemum	21	-	[93]
Peach latent mosaic disease	Peach latent mosaic viroid	335-351			Peach, nectarine	168	-	[510]
Eggplant latent disease	Eggplant latent viroid	332-335		*Elaviroid*	Eggplant	9	-	[158]

NA, Not available

infections caused by *Fusarium* sp. and *Puccinia* sp. affecting the crop yield in Malaysia. Myanmar being the second largest producer of sesame seeds globally experiences an annual yield loss of about 5–50% by phyllody, 10–75% by charcoal rot caused by *Macrophomina phaseolina*, 5–50% by *Cercospora* leaf spot, and 5% by bacterial leaf spot caused by *Xanthomonas campestris* [389].

Furthermore, [54] have reported the prevalence of various pathogens infecting a variety of crops like paddy disease of sheath and bakanae caused by *Gibberella fujikurol*, paddy sheath blight by *Rhizoctonia* sp., sheath rot by *Sarocladium attenuatum*, rice blast by *Pyricularia oryzae*, paddy false smut by *Ustilaginoidea virens*, downy mildew of soya bean by *Peronospora manshurica*, anthracnose of soya bean by *Colletotrichum lindemuthianum*, late blight of vegetables by *Phytophthora infestans*, fruit leaf anthracnose by *Glomerella cingulate*, and coffee leaf rust by *Hemileia vastatrix* impeding the crop yield. Similarly, *Phytoplasma* sp., a destructive pathogen infecting sugar cane in Vietnam are reported to reduces the sucrose content of the crops to about 60–80% [239].

Measures to control crop diseases- overview of the resistant varieties

Globally, around 16–30% of the crops grown are estimated to be lost to the devastating infections caused by pathogens [427, 428, 498]. To control the crop and yield losses, several practices have been followed by the farmers worldwide like the usage of healthy seeds for sowing, seed and soil treatment, crop rotation, usage of biological and chemical pesticides, etc., but development of host resistance have attracted researchers worldwide as it is considered as a comparatively reliable method ever [415, 583]. Generally, plant's innate immune system provides protection against the ingression of pathogens, but the species specificity expressed by the immune system makes it difficult to manage the infections caused by multiple pathogens [261]. Hence, deployment of the gene conferred resistant varieties of crops are considered as a potential measure to control crop diseases in an effective, eco-friendly, robust, and economic means [267]. Ji et al. [266] have reported the identification of about 40 different resistant *R* genes of paddy crops which could confer resistance against the major paddy crop infections especially the bacterial blight caused by *Xanthomonas oryzae*. Among which, the most frequently used *R* genes as rice breeders are *xa5, Xa7, xa13, Xa21,* and *Xa23* due to their wider resistance spectrum compared to the other known genes. Xu et al. [618] have reported the multiple pathogenic resistance conferred by the transformation of the specific *R* genes namely *Xa7* and *Xa21* to Yihui 1577 rice variety. Similarly, Pathi et al. [444] have stated that the generated loss-of-function mutations in the *Lox3* gene of maize crops using the Cas endonuclease technology improved the durability in the resistant properties of the crops to various pathogens. The *Pto* gene of the tomato crops were found to confer resistance against the pathogen *Pseudomonas syringae* which are well known for their devastating vegetable and fruit crop diseases [293, 368, 456, 504, 559]. Further, identification of the *NLR* gene [352, 493] in various *Arabidopsis* crops led to a significant progress in the genetic resistance to crop diseases as these genes conferred resistance to wide range of pathogens which include fungi [132, 277], bacteria [44, 210, 390], oomycetes [58], and viruses [298, 603]. Furthermore, discovery of *R* gene stacking or pyramiding helped in the deployment of multiple *NLR* gene into a single potato cultivar improving the resistance of the crops to multiple diseases [273, 291]. Identification of the quantitative trait locus (*QTLs*) of various pathogens (cucumber mosaic virus, zucchini yellow mosaic virus, whitefly-transmitted begomoviruses, melon chlorotic mosaic virus, tomato leaf curl virus, watermelon chlorotic stunt virus, *Fusarium* wilt, downy mildew, and powdery mildew) and insects (aphids and whitefly) that are co-localized in the *Vat* gene were found to confer resistance in fruit trees and crops improving the fruit yield and quality [483, 492, 532, 594, 629].

Likewise, several researchers worldwide are actively working in identifying and improving the resistance gene that could confer resistance to a vast range of pathogens that could be used to protect a wide range of crops from the pathogenic infections.

Conclusion

Bioaerosols act as potential source of crop pathogens and enable their dissemination across geographical barriers. Their dispersal in the atmospheric air is largely dependent upon several intrinsic and extrinsic factors like the availability of source, meteorological factors, aerosolization behaviour, properties of the microorganisms, etc. Once dispersed, they can cause severe to very severe diseases in crops. Crop pathogenic bioaerosols are generated due to various natural and anthropogenic activities such as rain, splashing of water, usage of sprayers in crop field, mechanical activities observed in the canopy, especially the movement of leaves, ooze of infected crops, infected plant sap etc. Leaves and external tissues of crops play a pivotal role in the ingress of pathogens from the surface to the inner parenchymal tissues of the crops. Also, it is reported that about 30% of the global crop production is lost to the devastating diseases caused by the crop pathogens known till date. Hence, it is imperative to have a better understanding of the crop pathogen dissemination through bioaerosols, sedimentation, invasion, and the onset of symptomatic disease of the region-specific crop cultivated. To achieve this, a detailed study on the season-specific regional diversity and community composition of bioaerosols and their implications on the crops must be conducted globally. Global modelling of the data obtained would give us a better insight on the dispersion and spread of crop pathogens on a global scale. Based on the knowledge and information obtained on the season-specific regional diversity, bioaerosol composition, and global modelling, proper measures required to control various crop diseases like crop rotation practises, usage of resistant varieties, fumigation of soil, seed selection, etc. must be developed and implemented. Moreover, advanced research on the resistant varieties have shown promising results in controlling multiple crop pathogens. Though many studies have explained the identification and existence of various *R* genes responsible for gene conferred resistance in crops, good understanding on the mechanism of the gene conferred plant response and resistance could give a better insight in the development of an appropriate and potential gene for the crop resistance. Further, forthcoming studies on the identification and development of a crop specific gene mediated resistance to multiple pathogens would enable the development of potential resistant varieties of crops in the future era.

Future need and measures to be adopted

Crop diseases and pests are critical problems in farming since earlier days. Although there have been many advancements in the understanding and eradication of various crop diseases worldwide, further measures need to be taken to improve the crop yield and crop resistance to diseases to overcome the yield loss caused by pathogens. Following are the future needs that need to be adopted and implemented by the farmers and officials to control the pathogenic crop diseases.

- Proper insight on the regional climatic conditions and the bioaerosols seasonal community composition
- Implementation of various farm practises like seed selection, season-specific crop growth, crop rotation, soil fumigation, soil treatment, seed treatment, etc.
- Breeding and adaptation of the resistant crop varieties
- Elimination of the source of bioaerosols
- Early prediction of spread of crop pathogenic bioaerosols and onset of disease
- Thorough knowledge of the disease cycle followed by each pathogen would help in improving the disease management strategies
- Proper understanding of the regional bioaerosols composition and implementation of appropriate methods e.g., growing appropriate resistant crop varieties
- Dissemination of knowledge to officials and farmers regarding the region-specific disease management strategies

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Declarations

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