Global Dimensions of Plant Virus Diseases: Current Status and Future Perspectives

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Keywords

virus diseases, new technologies, food security, climate change, integrated disease management, subsistence agriculture

Abstract

Viral diseases provide a major challenge to twenty-first century agriculture worldwide. Climate change and human population pressures are driving rapid alterations in agricultural practices and cropping systems that favor destructive viral disease outbreaks. Such outbreaks are strikingly apparent in subsistence agriculture in food-insecure regions. Agricultural globalization and international trade are spreading viruses and their vectors to new geographical regions with unexpected consequences for food production and natural ecosystems. Due to the varying epidemiological characteristics of diverent viral pathosystems, there is no one-size-fits-all approach toward mitigating negative viral disease impacts on diverse agroecological production systems. Advances in scientific understanding of virus pathosystems, rapid technological innovation, innovative communication strategies, and global scientific networks provide opportunities to build epidemiologic intelligence of virus threats to crop production and global food security. A paradigm shift toward deploying integrated, smart, and eco-friendly strategies is required to advance virus disease management in diverse agricultural cropping systems.

1. INTRODUCTION

The world is currently facing a plethora of societal challenges, including climate change, rapid human population growth, food insecurity, and environmental degradation, all with negative consequences for farming systems, human and livestock health, and fragile ecosystems worldwide. Simultaneously, the world is transitioning into an exciting era of unprecedented scientific and technological breakthroughs that offer great promise toward overcoming these challenges (1–3).

Because of rapidly accelerating population growth, expected to reach 10 billion by 2050, achieving global food security constitutes a major challenge for the twenty-first century (4, 5). Minimizing risks from crop diseases is crucial if humanity is to reach the 60% increase in food production needed by 2050 and meet its future nutritional requirements. This requires not only effective management of plant diseases in diverse cropping systems worldwide but also achieving this objective without impairing natural ecosystems (6–10). Viruses constitute a major cause of plant disease and have an estimated economic impact of >$30 billion annually (11). They constitute almost 50% of pathogens responsible for emerging and reemerging plant diseases worldwide, and they damage natural vegetation as well as cultivated plants (12–17).

Virus diseases threaten cultivated plants not only by impairing their growth and vigor, thereby diminishing gross yields, but also by spoiling produce quality and thus decreasing marketable yields. Such crop losses occur globally, causing damage varying from small scale to total failure (13–15, 18–23). Their economic and societal consequences are often greatest in the world's tropical and subtropical regions, where most people's livelihoods depend on agriculture. This is particularly apparent in subsistence agriculture in developing countries (13, 17, 20, 24–30). In temperate regions, damaging virus disease losses tend to occur more frequently in organic and protected cropping systems (25, 26, 31, 32). They arise in all types of cultivated plants, including crops grown to feed humans or livestock and for fiber, medicinal, or ornamental purposes. These cultivated plants include critically important ones for food security in developing countries, such as the staple food crops that provide 60% of the world's food energy intake requirements and grain legumes, oilseeds, vegetables, and fruits (19, 24, 26, 27, 33, 34). Virus diseases threaten natural ecosystems by altering the species composition of plant communities and causing genetic erosion, potentially leading to species extinction (12, 16, 17, 35–38). Increasing global warming–induced climate instability is making viral disease epidemics more difficult to control (17, 20–22, 39). However, new innovations in science and technology hold immense promise for improving their management (40, 41).

Given the ubiquity of plant viruses and lack of direct curative measures, increased prevalence of viral diseases is exposing farming systems to greater risks. Therefore, a systems biology approach is required to provide a holistic understanding of factors triggering their epidemics. Such understanding is crucial for the design of sustainable integrated disease management (IDM) approaches suited to different agroecological conditions and geographic regions. In this review, we provide an overview of the current state of knowledge concerning virus diseases and the approaches likely to help alleviate future virus-induced crop losses resulting from the rapid pace of agricultural transformation occurring worldwide. We focus particularly on the situation in food-insecure developing countries, where plant viral diseases have the greatest impact.

2. CURRENT SITUATION

Members of the begomoviruses, tospoviruses, and potyviruses—transmitted by whiteflies, thrips, and aphids, respectively—belong to three large plant virus groups that endanger food security by causing devastating diseases in tropical and subtropical food crops (17, 28–31, 42–49) (**Figure 1**). Examples include groups of begomoviruses that cause cassava mosaic disease in cassava

in sub-Saharan Africa (SSA) and the Indian subcontinent or tomato yellow leaf curl disease in most continents (48–52); the tospoviruses *Tomato spotted wilt virus* in peanut (groundnut), pepper, and tomato globally and *Peanut bud necrosis virus* in tomato and peanut in south and Southeast Asia (31, 47); and the potyviruses *Zucchini yellow mosaic virus* (ZYMV) and *Papaya ringspot virus* (PRSV) in cucurbits worldwide (53, 54). In addition, when present in mixed virus infections, potyviruses often elicit synergistic interactions that accentuate disease symptoms, resulting in devastating diseases that endanger food security—for example, sweet potato virus disease caused by mixed infection with *Sweet potato chlorotic stunt virus* and potyviruses, such as *Sweet potato feathery mottle virus* (55), and maize lethal necrosis disease caused by mixed infection between *Maize chlorotic mottle virus* and potyviruses, such as *Maize dwarf mosaic virus* (56, 57).

Examples of viruses belonging to other groups that induce diseases that threaten food security include *Rice tungro spherical virus*, either alone or in mixed infection with *Rice tungo bacilliform*
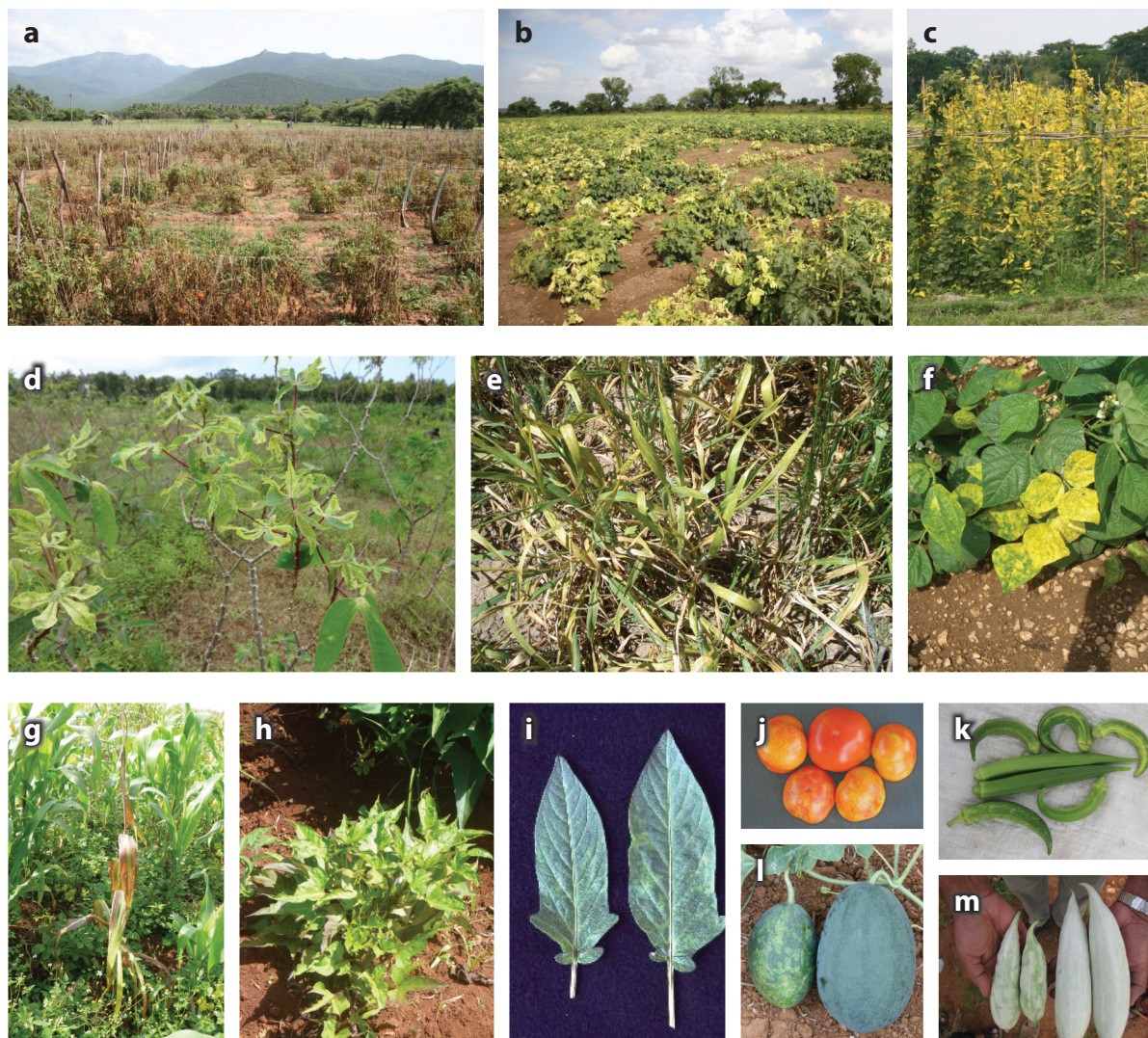
(Caption appears on following page)

Figure 1 (*Figure appears on preceding page*)

Examples of the damage caused globally by virus diseases of staple food crops, fruit crops, and vegetables. (*a*) A diseased tomato crop growing in India was devastated by infection with *Peanut bud necrosis virus* (PBNV), causing premature plant death. (*b*) A diseased okra crop growing in India showed stunted plants with leaf yellowing and deformation symptoms caused by infection with *Bhendi yellow mosaic virus*. (*c*) A diseased yard long bean crop growing in Bangladesh was devastated by leaf yellowing and deformation symptoms caused by infection with *Mung bean yellow mosaic virus*. (*d*) A diseased plant from a devastated cassava crop growing in Zanzibar showed leaf mosaic, deformation, and defoliation symptoms caused by infection with *Cassava mosaic virus*. (*e*) A wheat plant growing in Australia among a crop devastated by a 100% infection incidence of *Wheat streak mosaic virus*–affected plants all showed severe stunting with leaf yellow mosaic and streaking symptoms and lower leaf death. (*f*) A common bean plant infected with *Bean golden mosaic virus* growing in Florida showed leaf symptoms of yellowing and deformation. (*g*) A maize plant growing in Kenya showed lethal necrotic symptoms caused by infection with maize lethal necrosis disease syndrome; the surrounding plants were healthy. (*h*) A sweet potato plant growing in Kenya showed severe stunting and leaf symptoms of chlorosis and deformation caused by infection with the sweet potato virus disease syndrome. (*i*) Leaves from a pepino plant growing in Peru showed yellow mosaic symptoms caused by infection with *Pepino mosaic virus*. (*j*) Tomato fruits produced by PBNV-infected tomato plants growing in India showed symptoms of chlorotic mottled skin and distortion; the middle fruit in the upper row was from a healthy plant. (*k*) Fruits produced by okra plants infected with *Tobacco streak virus* growing in India showed symptoms of reduced size, curling, and chlorotic mottled skin; the five curled fruits and two larger normal fruits came from infected plants or healthy plants, respectively. (*l*) Watermelon fruits produced by *Watermelon bud necrosis virus*–infected watermelon plants growing in India showed symptoms of chlorotic skin mottle and reduced size (*left*, infected; *right*, healthy). (*m*) Snake gourds produced by *Zucchini yellow mosaic virus*–infected plants growing in Bangladesh showed symptoms of reduced size and yellow mottled skin (*left*, infected; *right*, healthy).

virus, causing rice tungro disease in south and Southeast Asia (58); *Faba bean necrotic yellows virus* (FBNYV) causing severe disease in grain legumes in west and central Asia and North Africa (34, 59); *Banana bunchy top virus* severely damaging banana and plantain in SSA and both south and Southeast Asia (60); *Rice yellow mottle virus* causing a severe rice disease in SSA (61, 62); and *Groundnut rosette virus* with its satellite RNAs causing groundnut rosette disease in SSA (63).

The need to produce enough food for the rapidly increasing human population is driving a swift increase in human activity, including agricultural practices involving extensification, intensification, and diversification. This, in turn, means that new encounters between viruses and plant species occur increasingly (13, 17, 20, 27, 35, 62). By facilitating viral host species jumps, new encounters result in invasion of introduced crops by indigenous viruses from native plants and native plants by viruses from introduced crops and weeds (17, 18, 27, 62, 64–66). The subtropics and tropics provide many examples of new encounter situations where viruses emerge from native vegetation at its interface with managed vegetation, causing devastating diseases in introduced crop plants far from their original domestication centers (15–18, 24, 27). Examples of new encounters causing virus epidemics threatening food security in SSA include whitefly-transmitted *Cassava mosaic virus* and *Cassava brown streak virus* spread to cassava, leafhopper-transmitted *Maize streak virus* (MSV) spread to maize, and aphid-transmitted groundnut rosette disease agents spread to peanut, all after these crops were introduced from South America (SA); and beetle-transmitted *Rice yellow mottle virus* spread to rice following its introduction from Asia. Similarly, when cacao was introduced from SA to west Africa, it encountered mealybug-transmitted *Cacao swollen shoot virus* (CSSV) spreading from native trees. By the early 1940s, CSSV had destroyed cacao production over large areas (17, 18, 24, 27). Also, when tomato was introduced from SA to the eastern Mediterranean region, it encountered *Tomato yellow leaf curl virus*, which caused a devastating tomato disease in the Middle East and Mediterranean regions before spreading worldwide (17, 42, 43, 45, 50).

When virus-infected, newly introduced crops grow next to native vegetation, new encounters between viruses and vulnerable native plants may have serious consequences. Factors such as grazing, flower collection, woodcutting, and fragmentation into remnant vegetation can magnify virus epidemics in native plant communities (12, 16, 17, 20, 35–37). This contrasts with undisturbed native plant communities infected by indigenous viruses that coevolved with them

New encounter:
first-time exposure of a newly introduced plant species to an indigenous virus spreading from native plant species or vice versa

where natural control measures limit virus epidemics, often resulting in mild or latent infections (16, 17, 26, 64, 66). However, such infections can still participate in shaping plant species mixtures by diminishing infected plant fitness and competitive ability in the presence of nonhost species or acting as virus sources for spread to more sensitive plant species (16, 36–38). Wild ancestors of cultivated plants constitute rich virus resistance gene sources for use in resistance breeding, providing evidence of past struggles between viruses and their natural hosts (16, 17, 67).

Introduction of a more efficient virus vector can also have serious virus emergence consequences (68, 69)—for example, the early 1990s arrival of *Bemisia tabaci* B biotype in Brazil resulted in the emergence of indigenous whitefly-transmitted viruses that caused unprecedented crop losses in many agricultural crops (42, 43). Moreover, epidemics of indigenous viruses can first appear, or be magnified, by introduction of genetically vulnerable cultivars of introduced crops (18, 27, 70). For example, after cotton was introduced from Central America to south Asia in the late 1960s, a cotton disease caused by the indigenous begomovirus *Cotton leaf curl virus* appeared but became serious only after 1988 when highly susceptible cultivar S12 became widely grown, causing a devastating pandemic (24, 27, 70).

3. TRANSMISSION PATHWAYS

Because viral pathogens are obligate, intracellular parasites, their long-term survival depends on their transmission to new hosts, which is therefore one of the most important processes in plant virus ecology and epidemiology (16, 17, 20, 27, 64, 71–73). Viruses use various transmission pathways to infect plant hosts (**Figure 2**). These pathways influence their disease cycles and patterns of spread. Vertical transmission involves transmission between parents and their progeny, whereas horizontal transmission involves transmission to new plants. Vertical transmission occurs through vegetative propagation from virus-infected planting material, sowing seeds with infected embryos, or parental pollen fertilizing its own progeny plants. Horizontal transmission commonly involves vector transmission by winged insects or wind-blown mite vectors, zoosporic fungus-like organisms (protists) or ectoparasitic nematodes that invade roots, or contact transmission where mechanical damage occurs (23, 74). Contact transmission occurs when virus-infected and healthy leaves rub each other; healthy leaves rub against virus-contaminated surfaces; humans prune or handle infected plants before healthy ones; or animals brush past, trample, or graze plants. It was formerly considered to occur solely when virus particles reach very high concentrations in infected plants, remaining stable outside the infected cell and infectious on contaminated surfaces (23, 74). However, recent studies revealed it occurs among viruses that neither reach such high concentrations nor produce highly stable particles (e.g., ilarviruses and potyviruses) (74). In addition, other virus transmission pathways exist whose contribution to virus spread is often underestimated, including pollen, wind-mediated contact, contaminated soil and water, parasitic plants, natural root-to-root grafts, and nonspecific chewing insect transmission (23, 74).

Plant viruses often move between countries that share land borders. This is especially so where national borders lack any interruption by major obstacles, such as mountain ranges or deserts. Their movement across seas is assisted by trade in infected plants and plant products (13, 15, 17, 20–22, 27) but can also occur when viruliferous vectors are blown by winds, migrating birds carry seed-borne viruses in their intestines, or fishermen from one country camp on the shore of another, leaving infected food debris (17, 75–78). Long-distance virus dispersal between continents is accelerated by trade globalization, international agreements over free trade and tariff reductions, increasing agricultural diversification, and climate change. The dominant role of multinational companies, increased speed of air and sea transport, and weak quarantine and regulatory systems in many developing countries also contribute to this (13, 15, 17, 20–22, 79). The most important

Genetically vulnerable cultivars: refers to cultivars with high susceptibility to infection with viral pathogens they may not have coevolved with

Pandemic: virus epidemic causing grave damage to crop(s) and occurring over a very wide area, often crossing international boundaries

Disease cycle: a distinct sequence of events that occurs in development of virus disease

Globalization: the integration of global economies through trade, investment, capital flow, labor migration, and technology
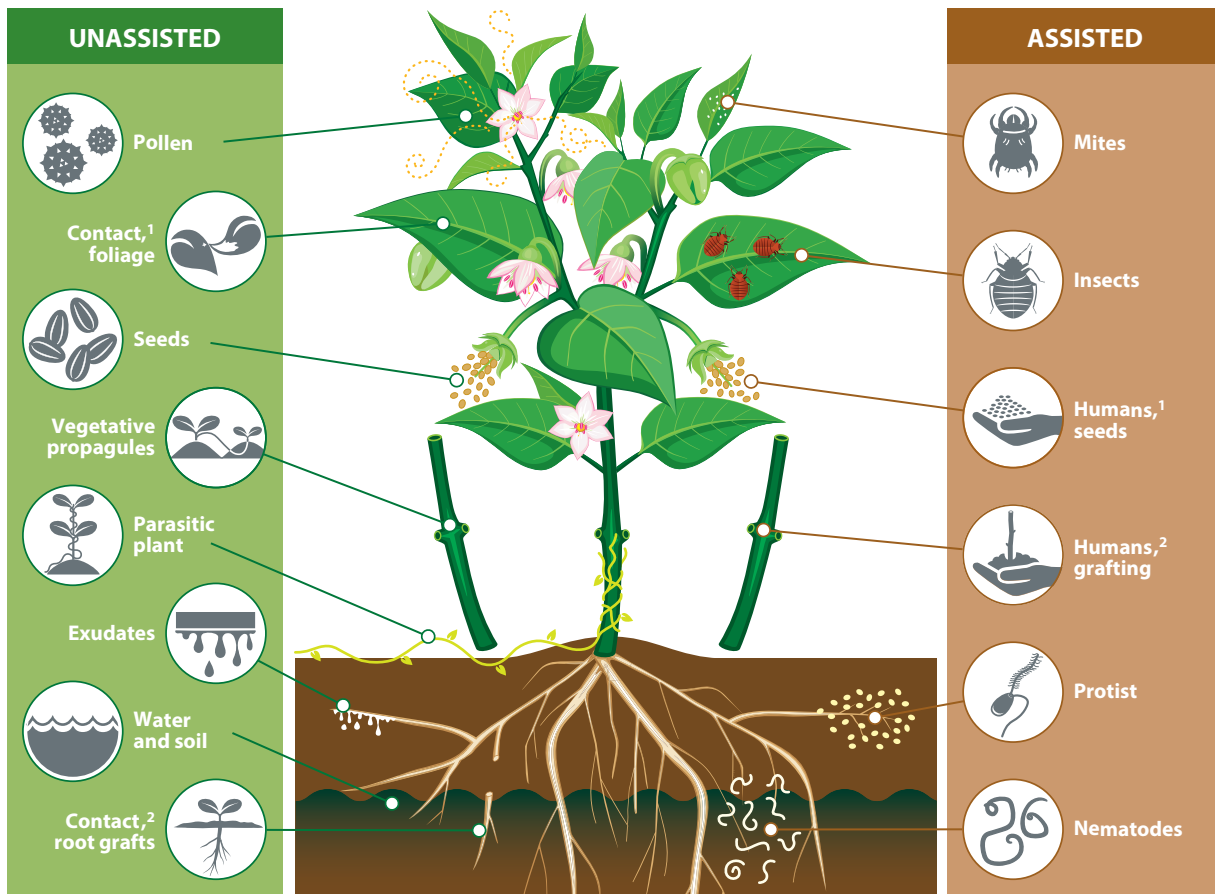
Figure 2

The diversity of virus transmission pathways, both assisted and unassisted, by which plant viruses can spread from infected to healthy plants, leading to local, regional, and global virus spread. Superscripts 1 and 2 in the assisted and unassisted categories indicate different virus transmission pathways that rely on the same virus transmission mechanism.

Genetic connectivity: a term used when genetically similar nucleotide sequences are found among virus populations derived from different countries

dissemination pathways include transcontinental trade involving the seed supply chain; vegetatively propagated material; and plant products that are virus infected or contaminated with soil containing virus particles, viruliferous nematode vectors, or virus-carrying vector resting spores (11, 15, 17, 24, 27). For example, **Supplemental Figures 1 and 2** illustrate rapid global distribution of ZYMV and *Pepino mosaic virus* (PepMV) (80) mainly (ZYMV) or entirely (PepMV) by the international seed trade. The **Supplemental Text** describes transport of viruliferous arthropod vectors over great distances by wind currents infecting plants when they land, including a staple food crop example (81, 82), and how genetic connectivity between arthropod vectored virus populations in countries separated by seas can provide evidence of this (68, 76, 77). Additional dissemination pathways include international movement of plant virus-contaminated pollinator beehives (83).
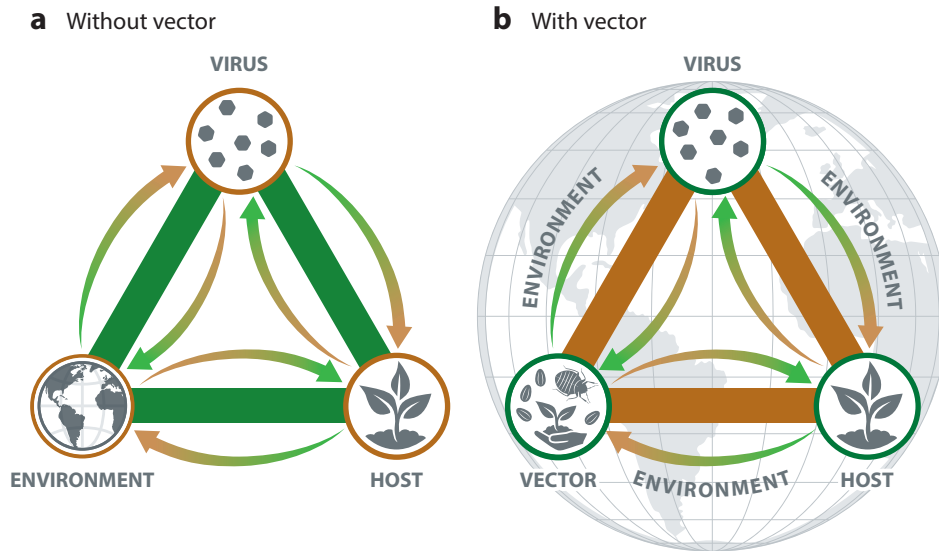
4. FACTORS INFLUENCING VIRUS DISEASE OUTBREAKS

To manage plant virus diseases effectively, one must have knowledge of their epidemiology. Obtaining this knowledge necessitates studying each virus pathosystem in different agroecological

a Without vector

VIRUS

ENVIRONMENT   HOST

b With vector

VIRUS

ENVIRONMENT

VECTOR   ENVIRONMENT   HOST

Figure 3

Disease triangles for plant virus pathosystems without (*a*) and with (*b*) the involvement of virus vectors. Arrows indicate two-way interactions between virus, host, and environment (*a*) and virus, host, and vector with their shared environment shown influencing all three pathosystem components (*b*). Panel *a* shows that when no vector is present, the virus disease triangle resembles that of other nonvectored plant pathogens. The world map image that represents the environment is placed at the corner of the disease triangle in panel *a* but is enlarged in panel *b* so that it covers the entire background of the figure.

situations. With vector-borne viruses, many intrinsic and extrinsic factors influence the trilateral interactions between host plants, viruses, and vectors (22–27, 64) (**Figure 3**). The diverse scenarios arising from these complex interactions dictate the spatiotemporal dynamics of virus spread (17, 20, 24, 27, 64, 71, 72, 84, 85). Where no vector is involved, this simplifies the situation so that the disease triangle is less complex (20, 22, 23, 27).

Virus epidemics need to develop afresh ever year in annual plant populations but continue to progress year by year in perennial plant populations. They develop in diverse growing conditions that influence how they spread, from crop monocultures to species mixtures, intercropping, irrigated to rainfed systems, open field to protected environments, extensive low input to intensive high input, large-scale cropping, plantations and managed pastures to small-scale subsistence smallholdings, market gardens, nurseries and hydroponic systems, and disturbed to undisturbed natural vegetation. Unless occurring in protected environments, plant virus epidemics are shaped by the climatic region involved, ranging from cool temperate to hot tropical, and by factors that influence climate locally, such as landscape features, altitude, and proximity to large water expanses (15, 17, 18, 21–23, 27, 84–86).

The disposition, magnitude, and nature of the primary virus infection source, how the virus spreads from plant to plant and over distance to new locations, and how it survives outside the main growing period all constitute critical factors influencing epidemic development (25, 26, 62, 71, 86–90). Epidemic magnitude often varies widely with locality and year due to local weather conditions, especially temperature and rainfall, on vector populations. Moreover, which type of vector is involved and, with arthropod-borne viruses, whether virus transmission is persistent, semipersistent, or nonpersistent all influence epidemic development (22, 23, 72, 81, 85–87). Additional factors determining the shape and magnitude of epidemic scenarios include

Spatiotemporal:
a description of virus spread over time and space

Persistent virus transmission: refers to transmission when viruses are acquired and inoculated during long feeding periods and require latent periods in their vectors

Semipersistent virus transmission: refers to transmission when viruses are retained for longer periods than with nonpersistent virus transmission but are lost during molting

Nonpersistent virus transmission: refers to transmission when viruses are acquired and inoculated during very brief periods, without any latent periods in their vectors

whether primary virus sources are internal or external, temporal spread patterns are polycyclic or monocyclic, spatial patterns are clumped or random, and vectors are single or multispecies. They also include whether any nonvector-specific transmission by vegetative means, seed, pollen, contact, or other forms of transmission is involved (23, 27, 86) (**Figure 2**). In addition, to enhance transmission to new plants insect-borne viruses manipulate host plant phenotypes and insect vector behavior (91) (**Figure 3**). See **Supplemental Text** for details and a staple food crop example.

Altering agricultural practices and cropping patterns to increase agricultural productivity is favoring development of more frequent and widespread virus disease outbreaks. New encounters are increasing due to the greater frequency of spatial and temporal shifts in distributions of introduced cultivated plants and weeds. This process speeds up development of epidemics caused by viruses and vectors that emerge from native plants to threaten newly introduced crop plants and introduced viruses and vectors that arrive with newly introduced plants and invade native vegetation. These processes are inextricably linked to climate and threaten both food security in developing countries and species diversity in wild plant populations (13, 17, 18, 21, 22, 27).

Climate change is shaping future virus epidemics by altering the environment on scales varying from global to local and microclimatic. It influences them directly by increasing temperature, greenhouse gas concentrations, and the frequency of extreme weather events, as well as altering rainfall patterns and wind velocities and directions. Climate change influences them indirectly by causing alterations in cultivation systems, types of crops grown, areas cropped, and the abundance and distribution of cultivated and weed virus reservoir hosts and virus vectors. It alters virus and vector geographical distributions and rates of spread and host-virus-vector interactions, drives transboundary spread of vector-borne viruses, triggers disease outbreaks due to altered intrinsic characteristics of ecosystems, increases rates of virus evolution and host adaptation, and diminishes virus control measure efficacy. Moreover, shifting climate variables are modulating interactions between different plant virus pathosystem components (**Figure 3**) with serious consequences for agriculture (17, 21–23, 92–95). Depending on the pathosystem, global warming will mostly enhance virus epidemics and consequent virus disease-induced crop losses and natural ecosystem damage. However, in drying mid-latitude regions where irrigation is lacking, the opposite overall outcome whereby epidemics diminish is likely (17, 21, 22).
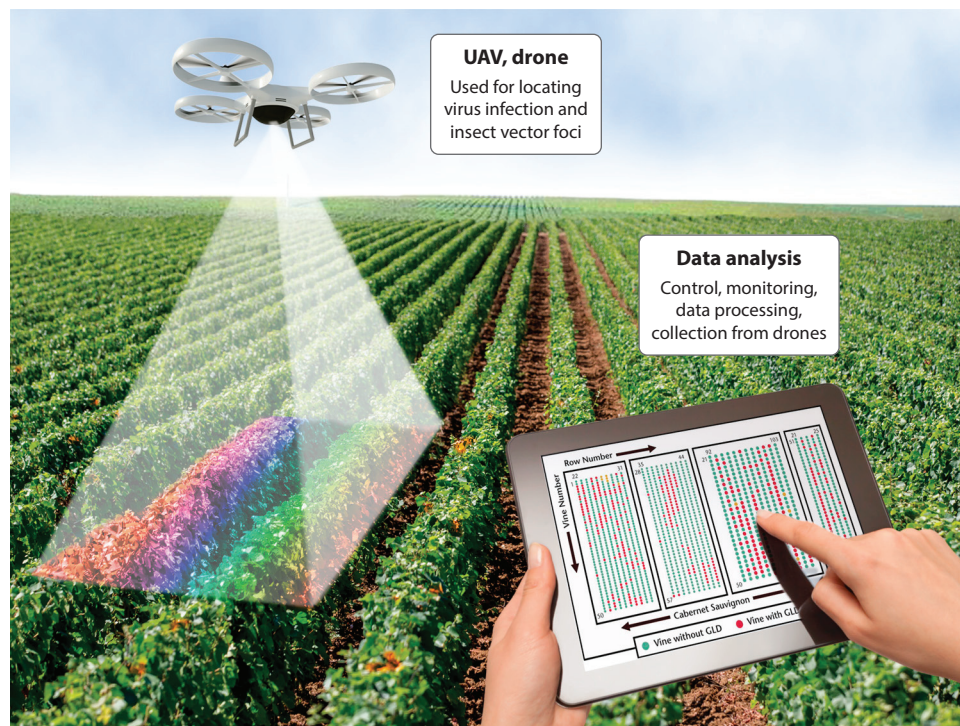
5. NEW AND EMERGING TECHNOLOGIES

New technological innovation holds great promise through the many opportunities it provides to enhance understanding of plant virus epidemics threatening food security, global crop production, and vulnerable natural ecosystems. It can help by predicting new virus disease threats, improving virus disease management approaches and outcomes, and alleviating climate change's influence on virus epidemics. Moreover, it can help achieve these objectives on global or continental to very small scales (40). However, optimizing the advantages new technological innovation provides can be achieved only by building upon the firm foundations of knowledge and concepts about plant virus epidemiology and management developed using traditional data collection procedures (12, 15, 17, 18, 24–27, 64, 70–72, 81, 84, 85, 87, 96, 97).

5.1. Remote Sensing, Artificial Intelligence, Unmanned Aerial Vehicles, and Precision Agriculture

Recent progress in remote sensor and information technologies combined with amplification of Geographic Information Systems (GISs) or Global Positioning Systems (GPSs) is providing exciting possibilities for improving virus disease management and virus resistance breeding

Plant virus pathosystem: unique combination of a virus pathogen, plant host, and virus vector occurring in a shared environment

Supplemental Material >

UAV, drone
Used for locating virus infection and insect vector foci

Data analysis
Control, monitoring, data processing, collection from drones

Figure 4

Example of new technology likely to revolutionize virus disease management in the future. Remote sensing delivered from lightweight UAVs will give detailed information about the progress of virus disease epidemics and vector infestations occurring within fields over time and space. Through the use of precision agriculture approaches, targeted spraying of pesticides or herbicides can be harnessed to remove localized arthropod vector infestations or virus infection foci from affected crops and alternative hosts, respectively, without any need for entire crop applications. The background image is a grapevine cv. Cabernet Sauvignon field in Washington state. Abbreviations: GLD, grapevine leaf roll disease; UAV, unmanned aerial vehicle.

(40, 98–103). Indeed, application of machine learning to big sensor data sets has the potential to provide real-time artificial intelligence–enabled programs that greatly improve recommendations for decision support (104), including for virus disease management. Hyperspectral, multispectral, thermal, and other types of optical sensors are becoming increasingly effective at distinguishing virus-diseased from healthy plants (105–108), establishing virus incidence, and predicting yield losses caused by virus disease (101, 109). They can also identify crop foci colonized by insect vectors (110, 111). Remote sensing that is ground based or delivered from lightweight unmanned aerial vehicles (UAVs) can give detailed information about the progress of virus disease epidemics and insect vector infestations within single fields (**Figure 4**), whereas remote sensing from satellites provides information on single farm, entire district, regional, or continental scales. Manned aircraft provide information on intermediate scales (40, 98, 112–114). Only lightweight UAV-based remote sensing is suitable for deployment with small-scale, high-value monocultures (40). Combining UAVs with suitable remote sensors even allows identification of disease foci at early stages in crop development and end-of-cropping-cycle quantification of losses (98, 103). Precision farming equipment that is GPS or GIS based can selectively target chemical sprays at remote sensing–identified areas within crops (115–117).

Large-scale future deployment of remote sensing using suitable platforms has the potential to advance knowledge of spatiotemporal dynamics of virus epidemics, deliver advance warning of epidemics, monitor epidemic progress, and distinguish virus-resistant from susceptible lines during plant breeding. Suitable software will make possible the targeted spraying of pesticides or herbicides using precision agriculture capable of removing localized arthropod vector infestations or virus infection foci from affected crops (40). Also, once suitable software programs are available, smartphone-based proximal sensing technologies will provide rapid virus and vector diagnoses and early detection warnings (118, 119). Examples of remote sensing already being deployed to tackle virus diseases in staple food crops include establishing MSV incidence in maize crops in southern Africa (109) and *Wheat steak mosaic virus* in wheat in North America (112, 113). However, in small-scale cropping where diverse crop species occur in close proximity—for example, in subsistence smallholder agriculture, market or home gardens, or protected cropping—only remote sensing that is ground based is currently suitable for virus epidemic monitoring (40). The same applies to mixed herbaceous species populations growing in managed pastures or natural ecosystems where virus epidemics threaten endangered plant species (120). In the future, in such cases remote sensing with nano or micro UAV versions (121) would enable virus epidemic and vector infestation monitoring (40).

5.2. Internet and Predictive Models

The internet's rapidly growing sophistication, complexity, and speed of operation combined with rapid advances in capacity, availability, and speed of computers and the increasing availability and sophistication of computer programs are providing enormous benefits in terms of understanding and effectively managing plant virus epidemics (40, 122) (see **Supplemental Text**). The same improvements in computers and computer programming, combined with advances in statistical and computational techniques, are making it much easier to model virus epidemics on both regional and local scales and use forecasting models that provide timely intervention and decision support recommendations concerning virus and vector control measures (40, 86, 123). Incorporating aerial surveillance and automated weather station data recovery into models allows supply of remotely collected data directly to computers, enabling continuous updating for online delivery (40, 86). Incorporation of other biotic variables, such as vector life history parameters and influences of their predators and parasitoids, is underway (123–125). Additional factors also warrant inclusion, such as virus ability to manipulate vector behavior (20, 40, 91, 123), currently neglected virus transmission pathways (see Section 3) (74), and landscape features (123). The **Supplemental Text** lists additional benefits from applying recent innovations to predictive models.

5.3. Virus Detection

Testing samples for virus presence requires access to reliable, cost-effective, and user-friendly diagnostic procedures. In inadequately equipped laboratories, the simplest and least expensive assays should always be employed. If reliable antisera are available, the best approach without compromising results is using immunostrip assays, tissue-blot immunoassay, or enzyme-linked immunosorbent assay. In addition, fast technology for analysis cards with sample extract applied to them can be sent to well-equipped laboratories for molecular diagnostic assays, such as reverse transcription polymerase chain reaction, polymerase chain reaction, and high throughput sequencing. New innovations in virus detection techniques are continually being evaluated to establish their suitability for plant virus detection (126, 127). The **Supplemental Text** provides a detailed account, describes the many insights and applications provided, and gives examples of their application.

5.4. Genetically Modified Plants

In protein-mediated genetically engineered (GE) resistance, viral proteins, including coat proteins, replicases, and defective movement proteins, have been employed to engineer plant virus resistance. More recently, RNA-mediated resistance and RNA interference are being used (128–130). Likely practical benefits from planting crops with GE virus resistance were revealed 20 years ago when PRSV-resistant papaya rescued the Hawaiian crop (131). However, although GE resistance has been developed to many viruses infecting diverse crops including food staples, because GE crops became associated with largely unsubstantiated concerns over insertion of so-called foreign genes, only seven have been approved for release (131). Recently, genome editing using CRISPR/Cas technologies has provided novel avenues for introducing resistance against DNA and RNA viruses in plants (132, 133). In the future, genome-edited crops seem likely to not only provide exciting opportunities for viral disease control but also be more widely accepted as they avoid foreign DNA insertion. With increased awareness of the benefits of these technologies and improved regulatory frameworks for their commercial adoption, genome-edited crops would become an integral component of future virus IDM strategies (see **Supplemental Text**).

6. MANAGEMENT

One-size-fits-all or so-called silver bullet approaches are rarely effective at managing plant virus epidemics. Instead, the approach adopted needs to be intelligent and adaptable, and those adopting the approach need to make shrewd and locally appropriate choices and take any local ecosystem impairment into account (25). Host resistance is often promoted as the single most effective means of obtaining sustainable and durable plant virus disease management (134–136). However, with a few notable exceptions [e.g., in tomato (31) and peanut (63)], farmers rarely plant cultivars bred specifically for virus or virus vector resistance, including in food-insecure regions. This is because where such cultivars are available, unless a virus disease is devastating their crops, farmers value other cultivar traits such as greater yield, produce quality, and adaptation to local environments more highly. Also, plant breeders rarely succeed in producing new virus-resistant cultivars with these critical traits over a reasonable time frame (24, 25, 137). Therefore, even when the economic threshold value above which virus infection's likely detrimental impact is sufficient to justify using virus-resistant cultivars, farmers normally prefer to rely on other virus control methods (25). Moreover, although there are notable instances where natural single gene virus resistances have continued to hold in the field, resistance-breaking strains generally overcome them (138, 139), and, when challenged in the field, genetically modified virus resistance is likely to suffer from similar resistance breakdown (140). Fortunately, an increasingly sophisticated and diverse array of alternative virus control measures, belonging to phytosanitary, cultural, chemical, and biological categories, is available (24–26, 31, 34, 59, 141).

Individual control measures diminish final virus crop incidence and yield or quality losses by minimizing infection sources (x_o) or diminishing rate of spread (r) (24–26, 84). Depending upon the control measure, they may have only minor effects on virus incidence when used on their own. However, the likelihood of major losses is minimized if an appropriate combination of complementary phytosanitary, cultural, chemical, host resistance, and/or biological control measures is deployed. This is because the different categories of control measures act in different ways, often synergistically, to diminish x_o and/or r (24–26). Such combinations are termed IDM, which can supply robust, economically feasible, environmentally sustainable, and socially acceptable solutions to virus outbreaks yet still protect farmers from losses leading to economic hardship. However, a sound understanding of virus epidemiology (see Section 4) and the mode of action and effectiveness of each individual control measure is required to devise effective IDM strategies

appropriate for each individual circumstance. This understanding is necessary so that diverse IDM solutions can be devised that address the unique characteristics of each individual scenario being considered (24–26, 141, 142). Devising such IDM strategies also requires knowledge of local circumstances regarding how crops are grown, likely weather conditions during the growing period, and the feasibility of deploying each potential control measure. In addition, they must avoid disrupting normal farming operations and preexisting measures operating against other pathogens and pests and consider the costs of deploying each control measure, additional labor demands, probability of adoption, and environmental and social concerns (24–26, 141, 142).

Simple, inexpensive IDM approaches against virus diseases may be all that is feasible in low-input, large-scale agricultural systems, such as cereal cropping in North American and Australian grainbelts, but more costly and comprehensive approaches become practical propositions in high-value systems, such as intensive horticulture and protected cropping. There are many examples of effective plant virus IDM strategies for food-insecure regions (24)—for example, using chemical, phytosanitary, and cultural measures to minimize FBNYV virus spread in small-scale Egyptian faba bean cropping (34, 59). Deploying an IDM mix consisting solely of phytosanitary control methods may be all that is achievable in resource-poor subsistence farming where labor is abundant but financial resources and technical knowledge are lacking (25, 26). In undisturbed natural plant communities, phytosanitary approaches and biological measures involving released predators or pathogens of specific vectors seem most suited to managing epidemics caused by insect-transmitted viruses. Soil disturbance and applying chemicals are too destructive to finely balanced ecosystems, while knowledge of host virus resistances is unavailable, except for wild native species used as parental lines in plant breeding (see Section 2).

For each virus pathosystem, acquiring sound data on the reliability of each control measure deployed alone or with others requires replicated field experimentation, undertaken under conditions that mimic those used commercially. Ideally, such field experiments are repeated over different sites and years to optimize data collection (25, 26, 141, 142). However, this scale of operation is expensive, so that may not be feasible, and advice on controlling serious virus epidemics is often required immediately. In such cases, an interim IDM strategy can be deployed. Devising this type of strategy requires using all existing knowledge of a pathosystem's epidemiology and generic information on the effectiveness of control measures already deployed with comparable pathosystems (25, 26). Wherever possible, these interim strategies need subsequent validation by field experimentation or, if impossible, by case history studies comparing virus incidence in commercial plantings where the interim IDM is in place or absent (26). Alternatively, where sufficient epidemiological data are available for a virus pathosystem, predictive models can estimate whether a control measure is likely to become a reliable component of an IDM strategy (40, 86, 123).

Accumulated past knowledge about the spatiotemporal dynamics of virus spread (20, 27, 84, 85, 88–90, 143, 144) was used to dissect the ways different kinds of control measures act against viruses infecting annual crops (26). The approach adopted followed an earlier one dissecting how control measures act against field crop pests (145). Knowing the mode of action of an individual virus control measure depends on knowledge of its selectivity (general versus specific) and activity against x_o (external versus internal source) and r (early versus late spread) (26). **Table 1** shows how a wider range of virus control measures than those considered previously (26) operate against each component of x_o and r. Some measures have low selectivity and act generally, influencing a wide range of viruses or their vectors, but others are highly selective, being effective against only a specific virus, virus strain, or vector species. Cultural control measures have low selectivity, whereas host resistance always has high selectivity. Phytosanitary measures mostly have low selectivity but can have high selectivity if a single virus is targeted. Chemical measures have high selectivity if a pesticide with narrow-spectrum activity against vectors is employed but low

Method	Measure(s)	Selectivity		Primary source (x_o)		Rate of spread (r)		Reference
		Low	High	External	Internal	Early	Late	
Phytosanitary, against virus	Hygiene	+	−	+	+	+	−	26
	Roguing	+	+	−	+	+	−	26
	Healthy propagules and seedlings	+	+	−	+	+	−	26
Phytosanitary, against virus and/or vector	Soil solarization, compost sterilization, fallowing	+	−	−	+	+	−	TR
	UV nutrient solution irradiation, filtered irrigation water (PCO)	+	−	+	−	+	−	TR
	Disinfectants and surfactants, sterilized tools	+	−	+	−	+	−	TR
Cultural	Isolation, safe planting distances	+	−	+	−	+	−	26
	Planting upwind, nonhost barrier, large field size, windbreaks	+	−	+	−	+	−	26
	Protective row covers, fine nets, UV-absorbing plastic	+	−	−	−	+	−	TR
	Mixture with nonhost, nonhost cover crops	+	−	+	+	+	+	26
	Manipulate sowing date to avoid peak insect vector numbers	+	−	−	−	+	−	26
	Minimum tillage, ground cover, mulches, reflective surfaces	+	−	−	−	+	−	26
	Early canopy cover, high plant density, narrow row spacing	+	−	+	+	−	+	26
	Early harvest, early maturing cultivar, early foliage destruction	+	−	−	−	−	+	26
	Crop- and weed-free periods, single and phased rotations	+	−	+	+	+	−	26
	Manipulate soil pH, irrigation to minimize vector activity in soil	+	−	−	+	+	(+)	TR
	Manipulate grazing or mowing, remove stock, cut for feed (PAO)	+	−	−	+	−	+	26

(Continued)

Table 1 *(Continued)*

Method	Measure(s)	Selectivity		Primary source (x_o)		Rate of spread (r)		Reference
		Low	High	External	Internal	Early	Late	
Chemical, against vector	Specific, regular foliar applications (PTO)	−	+	−	−	+	+	26
	General, regular foliar applications (PTO)	+	−	−	−	+	+	26
	Specific, seed dressing (PTO)	−	+	−	−	+	−	TR
	General, seed dressing (PTO)	+	−	−	−	+	−	TR
	Specific, in furrow or soil before or directly after planting (PTO)	−	+	−	−	+	−	26
	General, in furrow or soil before or directly after planting (PTO)	+	−	−	−	+	−	26
	General, soil fumigation	+	−	−	+	+	−	TR
	Oils and repellents, regular foliar application	+	−	−	−	+	(+)	26
Natural host resistance, against virus	Partial, polygenic	−	+	−	−	+	(+)	TR
	Strain-specific, single gene, resistance-breaking strain absent	−	+	−	−	+	+	TR
	Extreme resistance, single gene	−	+	−	−	+	+	26
Natural host resistance, against vector	Partial, polygenic	−	+	−	−	+	(+)	TR
	Specific, single gene, resistance-breaking vector race absent	−	+	−	−	+	(+)	TR
Genetically modified host resistance, against virus	Partial	−	+	−	−	+	(+)	TR
	Extreme resistance	−	+	−	−	+	+	TR
Biological	Cross protection	−	+	−	−	+	(+)	26
	Predator, parasite, or pathogen—specific (PCO)	−	+	−	−	−	+	26
	Predator, parasite, or pathogen—general (PCO)	+	−	−	−	−	+	26
	Biopesticide	+	+	−	−	−	+	26

Symbols: + = active; − = inactive; (+) = partially active. Abbreviations: PAO, pasture only; PCO, protected cropping only; PTO, persistent insect transmission only with arthropod vectors (ineffective with nonpersistent transmission); TR, this review; UV, ultraviolet. Table modified and considerably expanded from Reference 26.

selectivity if broad-spectrum pesticides, oils, or repellents are used. Different biological measures have either or both selectivity types. Phytosanitary measures can tackle internal or external virus sources or both together but are effective only against early spread. Different cultural control measures demonstrate all possible scenarios in addressing the virus source and can diminish early spread, late spread, or both. Host resistance diminishes early and late spread either fully or partially, whereas biological control measures address late or both types of spread. Neither have any activity against primary virus sources. Chemical measures address early or both types of spread but, with the sole exception of soil fumigation, have no activity against the primary virus source. Highly selective measures suffer from drawbacks, such as single gene resistance being overcome by virus or vector variants that break resistance (see Section 6). Also, during vegetative propagation, the phytosanitary measure roguing can select mild virus strains by failing to remove plants with subtle symptoms (24, 26, 146). In addition, although effective against vectors of persistently insect-transmitted viruses, application of general insecticides is often problematic because it can kill beneficial insects, select insecticide-resistant insect vector variants, and leave toxic residues (24–26). Moreover, knowledge of mode of virus transmission is important—for example, insecticides are ineffective against nonpersistently transmitted viruses (26, 68). Thus, success of IDM is optimized by combining measures with low and high selectivity such that both virus source types and virus spread phases are addressed and the measures included act in as many different ways as possible (26).

Successfully managing epidemics in perennial crops is more challenging because of the greater period that virus spread continues. When compared with annual crops, control measures that diminish r become of greater importance compared with those addressing x_o. Thresh (24) emphasized the importance of including measures that decrease x_o and r in perennial tropical crop IDM strategies, such as for CSSV in west African cocoa plantations. However, dissecting how diverse types of virus control measures operate regarding their selectivity and activity against both components of x_o and r has not been attempted with perennial crops.

Under a climate becoming increasingly unpredictable due to global warming, the ideal way to achieve reliable virus disease control involves deploying a combination of IDM, predictive modeling, and newer technologies, such as remote sensing and precision agriculture (21, 40). Predictive models help with deciding when control measures are required, which measure combinations are likely to be reliable, and whether damaging new viruses are likely to emerge (17, 21, 22, 86, 123). Continued planting in regions where temperature becomes too high for a crop species to grow well means it becomes physiologically less capable of withstanding virus infection. Control methods with low selectivity will become especially important in managing the spread of little-known or unknown virus diseases appearing due to climate change. Moreover, as peak vector flights and optimum sowing dates become increasingly less predictable, cultural control measures addressing them will become less reliable. Also, optimum timing for pesticide, repellent or mineral oil applications, and biological control agent releases will become increasingly difficult to forecast. In addition, temperature-sensitive host resistance genes will become less effective (17, 21, 22). Therefore, the importance of phytosanitary control measures within IDM approaches that address virus epidemics will increase.

7. GLOBAL NETWORKS

Currently, due to the increased likelihood of their dissemination by a broad range of transmission pathways, global agriculture is faced with a wide range of challenges from known and emerging viral pathogens. Moreover, virus diseases pose an increasing challenge for producers,

scientists, and policy makers endeavoring to keep abreast of their epidemics and the need to devise reliable and appropriate technologies suitable for managing them under a wide spectrum of environments and agricultural practices and in changing climates and cropping systems worldwide. With changing modern farming strategies, increasing complexity of viral pathosystems, and inherent disparities in institutional maturity in dealing with viral diseases, there is a critical need for multidisciplinary, trans-institutional partnerships with sufficient breadth and durability of scientific and institutional capacity to be capable of solving viral disease challenges. Although fundamental knowledge on plant viruses is increasing dramatically, colearning between researchers and farmers and integration of scientific discoveries with farmers' knowledge would advance translating the principles of IDM into practical solutions adopted in local contexts. In this regard, expansion of international collaborative networks between researchers in different countries is of utmost importance, as they play critical roles in solving virus disease problems (147). Such networks need to be multidisciplinary, including not only plant virologists but also specialists in other areas, such as plant breeding, agronomy, statistics, ecology, entomology, nematology, mycology, modeling, socioeconomics, and molecular biology (18, 20, 29, 35, 62, 72, 73, 84). Moreover, effective collaborative networks between researchers in developed and developing countries are crucial when research projects address major food-insecurity issues caused by virus diseases. Recent examples of such collaborative networks include tackling virus diseases of cassava (148), maize (56), rice (149), sweet potato (150), common bean (151), cool season pulses (34), and vegetables (152).

Since 1980, the International Society for Plant Pathology's International Committee on Plant Virus Epidemiology (**http://www.isppweb.org/icpve**) has fostered global collaborative networking successfully by highlighting virus diseases threatening global food security through its regular symposia, special journal editions, and books. Its achievements owe much to the inspiration contributed by its foundation chairman, the late Michael Thresh (20, 22, 153), and the many reviews he wrote on the subject, several of which are cited here. Examples of other collaborative international networks playing important roles in helping solve food insecurity caused by virus diseases include the US Agency for International Development's (USAID) Feed the Future Innovation Laboratory for Integrated Pest Management (**https://ipmil.cired.vt.edu/**), Gates Foundation's Agricultural Development Strategy (**https://www.gatesfoundation.org/**), Consultative Group on International Agricultural Research's International Agricultural Research Centers (**https://www.cgiar.org/**), and the CONNECTED: Community Network for African Vector-Borne Plant Viruses (**https://www.connectedvirus.net/**). Lessons learned and experiences gained from such collaborative avenues benefit agricultural systems well beyond national boundaries of participating scientists and institutions.

8. FUTURE NEEDS

1. Devise many more IDM approaches tailored to specific virus pathosystems, agronomic practices, and geographical regions that provide robust, economically feasible, environmentally sustainable, and socially acceptable solutions to plant virus disease outbreaks.
2. Promote new technological innovation that enhances understanding of plant virus epidemics; improves virus disease identification, forecasting, and prediction capabilities; and optimizes virus IDM approaches and outcomes.
3. Increase research into providing better understanding of the interactions between climate change and different components of viral pathosystems and use this knowledge to help build the comprehensive epidemiologic intelligence required for future sustainable crop management.

4. Increase use of traditional field experimentation designed to acquire comprehensive and sound information on plant virus pathosystems and evaluate the effectiveness of virus control measures.

5. Ensure that molecular, biochemical, and ecophysiological approaches toward researching viral diseases always integrate with, and build upon, firm foundations of knowledge and concepts about plant virus biology, epidemiology, and management developed using traditional data collection approaches.

6. Strengthen international supply chain systems that provide healthy seeds and other propagules via global trade routes through enhanced pathogen testing capacities and improved containment strategies that minimize geographic expansion of plant viruses and virus diseases.

7. Encourage global networks of researchers to use a participatory model of agricultural research and development when devising and deploying sustainable virus management strategies and practical solutions that cross national borders, especially for improved food security in developing countries.

8. Implement participatory approaches to increase farmers' awareness and knowledge of plant virus diseases, their identification and epidemiology, and IDM strategies, and prepare a next generation of agricultural and extension professionals with a global perspective toward addressing agricultural and food security challenges arising from plant viral diseases.

Additional items are in **Supplemental Text**: Summary points, related resources, and detailed term explanations.

Supplemental Material >

DISCLOSURE STATEMENT

The authors are unaware of any affiliations, memberships, funding or financial holdings affecting this review's objectivity.

ACKNOWLEDGMENTS

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