
Impact of Climate Change on Insect Vectors and Vector-Borne Plant Viruses and Phytoplasma

23

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Abstract

Plant virus and phytoplasma diseases are emerging as a serious constraint in improving productivity of horticultural crops. Ecological factors, including migration, climate and agricultural practices are considered to play an important role in the emergence of plant virus diseases. Changing climate conditions can contribute to a successful spread of newly introduced viruses or their vectors and establishment of these organisms in areas that were previously unfavorable. A number of plant viruses are transmitted by vectors, many of them are not able to establish at current climate conditions. The most important vectors such as Aphid, whitefly, thrip, and leaf hoppers which are associated with potyviruses, begomoviruses, tospoviruses and phytoplasma, have emerged during the last two decades. Plant virus diseases and vectors are strongly influenced by weather and climate. The temperature and moisture conditions interacting with seasonal phenology, and stress on the host determine infection severity and distribution. Increasing international travel and trade of plant materials enhances the risk of introducing new viruses and their vectors into production systems. However, climate change is expected to have effects on their establishment, spread and reproduction potential as well as on the vector transmission. If climate change increases or decreases environmental conduciveness, the shift in selection pressure on the host populations could result in shifts in the diversity of resistance genes present. Recent observations have shown that resistance to bhendi yellow vein mosaic virus tends to break when okra is grown at higher temperatures. These climatic changes affect the biological and ecological characteristics of insect species, through direct effects on the physiology of organisms and through indirect effects on their habitat. The number of disease epidemics

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has dramatically increased in recent years, as have the threat of emerging new diseases and the reemergence of other diseases. Some of the recent examples are incidence of thrips transmitted tospoviruses and whitefly transmitted begomoviruses in chilli, cucurbits, okra and tomato. Different biotypes of an aphid or whitefly species have been associated to outbreaks and expansions of viral diseases. The other biological changes involved include introduction of new, more efficient virus-vector species and more efficient virus-vector biotypes or variants of existing vector species, and circumvention of host defenses in introduced crops. At the molecular level the genome alterations most likely to occur in different emerging viruses are those caused by recombination, pseudo-recombination, reassortment and modular evolution. Numerous factors have been cited as potential drivers of the emergence of viral outbreaks, including pathogen introduction through global traffic, changes in vector populations, genetic recombination, new farming techniques, changes in weather conditions. As a first and necessary step in obtaining baseline information about climate change impact on different virus diseases and vectors, a survey should be conducted among growers and plant protection officers. The survey will define a list of most important climate-related plant viruses and vectors for specific regions. Awareness of forthcoming significant climate change it is necessary to work out the impact to be able to make predictions.

23.1 Introduction

Global warming is one of the principal challenges facing agriculture, plant pathogens, and insects worldwide. The average global warming trend over the last 50 years is almost twice that of the last 100 years (IPCC 2007). Increases in mean temperature lead to an increased risk of high temperature extremes, such as intense, long-lasting, and more frequent heat waves. Increases in mean precipitation in the tropics, accompanied by greater intensity of precipitation, could lead to flooding, whereas widespread decreases in mean precipitation mid-latitudes bring an increased risk of drought. Likely increases in incidences of wind disturbances are predicted to contribute to a greater number of storms and more intense tropical cyclones (Meehl et al. 2007).

As a consequence of climate change, already challenged global food supply is likely to be further threatened (Beddington 2010; Lobell et al. 2008; Rosenzweig et al. 2001), and crop losses due to pests and diseases are already considerable. One of the consequences of climate

change is the increase in production losses caused by some pests and diseases (Burdon et al. 2006; Garrett et al. 2006, 2010; Easterling et al. 2007; Chakraborty et al. 2008; Jones 2009; West et al. 2012). The causes of these involve complex interactions. Complex relationships between host plant, pest, pathogen, and environment create uncertainty particularly involving vector-borne diseases (Finlay and Luck 2011). Global warming affects individual species and interactions between species by directly affecting their physiology and indirectly their habitat (Hulle et al. 2010). Plant virus and phytoplasma diseases constitute one of the limiting factors to the productivity of agriculture. Changes in host plants and insect vector populations that might result from climate change could affect the spread of plant viruses. At the individual level, alterations in plant physiological processes that are relevant to their molecular interactions with viruses, like changes in metabolism, leaf temperature, and their effects on some processes, like the temperature-sensitive antiviral resistance based in RNA silencing, can also influence the ability of indi-

vidual plants to control viral infections (Canto et al. 2009).

There is already evidence of recent climatic changes affecting a broad range of organisms with diverse geographical distributions (Parmesan and Yohe 2003; Parmesan 2006; IPCC 2007). Nonnative plant and insect species from adjacent areas may shift their distribution ranges and become new elements in communities where they were previously not present. These may include species that might constitute reservoir hosts or vectors for plant viruses, capable of causing epidemics in nearby crops. In addition, global warming may cause alterations in the densities of already present alternative hosts to viruses. Changes in host and vector phenology can also have effects on the probability of contact between viruses and hosts: the sooner a reservoir host is available to vectors for virus transmission, the higher the probability of initial infection foci in crops. Furthermore, there are also important differences in virus–vector relationships that affect the temporal and spatial dynamics of virus epidemics. For example, transient species are often the main vectors of viruses that are transmitted quickly during brief probes, while colonizing species are the main vectors of viruses that require longer feeding times and often direct contact with vascular tissues. Depending on the manner of transmission, a change in environmental conditions will have different consequences on the spread of a virus.

23.2 Insect Vectors of Plant Viruses and Phytoplasma

Sucking insects, such as aphids, thrips, whiteflies, and leaf hoppers, are associated with the transmission of viruses, which can lead to major crop losses. The insect transmission of plant viruses can be classified as persistent, semi-persistent, or nonpersistent. Persistent transmission requires sustained feeding by the insect, while nonpersistent transmission is dependent on a more superficial relationship between the insect and the plant.

Most of the known plant viruses are transmitted by insect vectors and are entirely dependent on the behavior and dispersal capacity of their vectors (Nault 1997; Ng JCK and Falk 2006). Insect vectors of plant viruses belong to several orders like Hemiptera, Coleoptera, Thysanoptera, Orthoptera, Dermaptera, Lepidoptera, and Diptera, but Hemiptera is by far the most important group of vectors of plant viruses. The order is divided into three suborders: Heteroptera (or true bugs), Auchenorrhyncha (hoppers), and Sternorrhyncha (aphids, whiteflies, mealybugs, psyllids). Most of the vectors of plant viruses are included in the latter two suborders and are referred to here as homopterans which include both Auchenorrhyncha and Sternorrhyncha (Richards and Davies 1977). One of the differences between homopterans and heteropterans is in the way they insert their mouth parts into plant tissue.

Homopterans are vectors of about 55% of all known plant viruses (Nault 1997), and the main vectors according to the number of virus species transmitted belong to the families Aphididae (aphids) and Aleyrodidae (whiteflies). Aphids transmit more than 50% of the plant viruses vectored by insects (Nault 1997), while whiteflies transmit 114 virus species within five different virus genera (Jones 2003). Both groups of vectors are very well adapted for virus transmission because their stylets frequently pass between cells to reach the target tissue—the phloem—and can penetrate cells without causing damage. The larger stylet bundles of Heteroptera and Auchenorrhyncha are more likely to take an intracellular path and cause significant damage to plant tissues en route, which reduces the chances of virus infection (Mitchell 2004). Furthermore, the high rates of population increase, the short life cycle, and high dispersal potential make aphids and whiteflies the main group of vectors of plant viruses. Many of these cause severe yield losses and have a great impact on agriculture throughout the world (Feres and Moreno 2009; Pappu et al. 2009; Mandal et al. 2012).

Temperature is the key climate parameter that influences the occurrence and the density of insect vectors (Bale et al. 2002). Mean autumn and minimum winter temperatures have been

identified as key factors for the establishment of field populations of Mediterranean mealybug species (Peacock et al. 2006), while rising summer temperatures are likely to favor the development and population density of endemic potential vectors. The alternative overwintering strategy of some mealybug species, for example, *Heliooccus bohemicus*, that hibernate either as adult females or as second instar larvae might be a measure to adapt to different abiotic conditions and could favor survival of field populations. Species that are able to hibernate in their active stages show increased winter survival in warm winters (Bale et al. 2002). Considerable increases in minimum winter temperatures have been reported for northern and central Europe (Heino et al. 1999).

23.2.1 Impact on Aphids and Aphid-Transmitted Viruses

Insects are the most common vectors, and among these, aphids account for the transmission of 50% of the insect-vector viruses (Nault 1997). Aphids are exquisitely designed for their roles as vector. Piercing–sucking mouth parts facilitate the delivery of virions into plant cells without causing irrevocable damage. With the option of asexual reproduction, aphid populations can increase at extraordinarily high rates, thereby potentiating disease epidemics and furthering the short- and long-distance spread of viruses. Additionally, aphids are globally distributed, and there are more than 200 vector species identified (Nault 1997; Ng and Perry 2004; Braust et al. 2010).

The majority of aphid vectors belong to the subfamily Aphididae (order: Homoptera). Aphid vectors are also found in nine other subfamilies, but they account for only a very small proportion of those that are known to transmit viruses. A number of unique features contribute to the success of aphids as vectors of plant viruses. These include (1) a polyphagous nature for some aphid species (*Myzus persicae*) that allows them to feed on a wide range of plant hosts, a property important for the dissemination of viruses that infect a large number of plant species; (2) the

ability to undergo parthenogenetic reproduction, thus facilitating the rapid production of large quantities of offspring; and (3) the possession of a needlelike stylet capable of piercing plant cell walls and delivering viruses into a host cell. Feeding behavior and host plant selection by an aphid will affect its potential as a vector (Harris and Maramorosch 1977). The extent to which these factors influence virus transmission will depend on the specific virus and its mechanism of transmission. Understanding the spread and control of viral diseases requires an understanding of the vector and its behavior; vector transmission is paramount to epidemiology (Ng and Perry 2004). Aphids show a considerable variation in their life cycle traits and even within species variation can be very high. Some species, termed holocyclic, respond to the oncoming winter with a sexual phase, often placing eggs on woody plants. Anholocyclic aphids, on the other hand, do not go through the sexual phase and continue with parthenogenetic and viviparous reproduction throughout the year. Some species are a mix of holocyclic and anholocyclic clones. Within a species, the proportion of individuals that are holocyclic tends to be greater in colder regions, as the eggs resulting from sexual reproduction are very much more cold hardy than the active, viviparous forms which persist year round in anholocyclic clones.

Among the insects that are commonly associated with virus transmission, aphids are of particular interest in the Nordic region for a number of reasons. Aphids generally have a low developmental temperature threshold and a short generation time, so that when they continuously reproduce in a parthenogenetic manner, they achieve 18 generations a year in British conditions (Harrington 2002; Harrington et al. 2007). Yamamura and Kiritani (1998) suggested that aphids are among the insects best adapted to take advantage of a warming climate and could go through an extra five generations a year following a warming of 2°C. Others have suggested that besides increases in CO₂ concentration, differences in soil nitrogen content and population density also play a part for aphid abundance (Newman et al. 2003), but nevertheless,

they are expected to increase in importance as pests in Sweden (Fågelfors et al. 2009).

Although temperature is a key factor governing insect life in general and that of aphids in particular, aphids are also affected by the environment through the host plants. Increases in concentrations of CO₂ and O₃ are of particular significance. Indeed, increases in CO₂ concentration stimulate plant growth but decrease the nutritional quality of plants for phytophagous insects (Lincoln et al. 1993). By contrast, ozone tends to inhibit plant growth by decreasing carbon fixation through negative effects on the rate of photosynthesis (Chappelka and Chevone 1992). The responses of aphids to high concentrations of CO₂, O₃, or both gases are highly variable. Depending on the aphid species, development and fertility rates may increase (Awmack et al. 1997; Mondor et al. 2005; Sudderth et al. 2005), decrease (Hughes and Bazzaz 2001), or remain unaffected by such atmospheric changes (Percy et al. 2002; Awmack et al. 2004). A single aphid clone may display different responses to high CO₂ content according to the host plant increase (Awmack et al. 1997; Mondor et al. 2005; Sudderth et al. 2005). Consequently, despite the many studies carried out on this subject, it is not possible to establish general rules or to predict whether all aphid populations will be affected by global warming (Newman et al. 2003; Pritchard et al. 2007).

Many of the 275 viruses transmitted by aphids cause diseases of major economic importance. Thus, the indirect damage that aphids cause through virus transmission often far exceeds their direct impact on crops. In vegetables and fruits, viruses are often associated with huge losses in quality with many unmarketable products. In field-grown vegetables, a synthesis by Tomlinson (1987) over 28 countries with temperate climate revealed that the five most economically important viruses are transmitted by aphids (Cucumber mosaic virus (CMV), Turnip mosaic virus (TuMV), Potato virus Y (PVY), Lettuce mosaic virus (LMV), and Papaya ringspot virus (PRSV)). The two most common viruses of potatoes, PVY and Potato leaf roll virus (PLRV), are transmitted by aphids and are of particular concern to seed

potato producers. In India, Banana bunchy top virus (BBTV), Bean yellow mosaic virus (BYMV), Cardamom mosaic virus (CdMV), Chilli veinal mottle virus (ChiVMV), Citrus tristeza virus (CTV), Cucumber mosaic virus (CMV), Dasheen mosaic virus (DsMV), Papaya ringspot virus (PRSV), Potato virus Y (PVY), and Zucchini yellow mosaic virus (ZYMV) are of importance in horticultural crops, which also impacts on crop production under varied climatic conditions (Krishnareddy and Manasa 2012).

23.2.2 Impact on Whitefly and Whitefly-Transmitted Viruses

B. tabaci corresponds to a complex of genetic variants or haplotypes, usually referred to as biotypes (Gill and Brown 2010). Based on mitochondrial cytochrome oxidase subunit (COI) gene consensus sequences, a recent report has suggested that *B. tabaci* is a complex of at least 24 distinct cryptic species (Dinsdale et al. 2010). Although no morphological characteristics can be used to distinguish between *B. tabaci* populations, genetic and behavioral differences have been used for haplotype/biotype characterization. These include isoenzyme profiling, bar coding based on conserved genes like the mitochondrial COI gene, life history traits, host range and/or host preference, virus transmission competency, composition of endosymbionts, dispersal behavior, insecticide resistance, and discontinuous gene flow. Biological differences between *B. tabaci* biotypes can radically affect the emergence of a virus disease by causing differences in transmission efficiency, host range, or mating behavior (Navas-Castillo et al. 2011). Whiteflies can transmit plant viruses in a semi-persistent manner (e.g., criniviruses) or a persistent manner (e.g., begomoviruses). Interestingly, the persistent transmission of some begomoviruses involves a third partner. Thus, persistent transmission of TYLCV by *B. tabaci* depends on chaperonin GroEL homologs produced by endosymbiotic bacteria (Morin et al. 1999).

Over the past 20 years or so, begomoviruses have emerged as serious constraints to the cultivation

of a variety of vegetable crops in various parts of the world but especially in the tropics and subtropics (Moriones and Navas-Castillo 2000; Rojas and Gilbertson 2008; Morales 2010). Some devastating begomoviruses have also moved to temperate regions, where they seriously reduce greenhouse crop production. The emergence of begomoviruses is associated with changes in crop cultivation, increased global movement of plants, and changes in cropping practices, such as the intensive use of insecticides. In particular, the emergence of begomoviruses as important pathogens over the past two decades is closely associated with the increased prevalence of the insect vector, the whitefly *Bemisia tabaci* (Wisler et al. 1998a). The spread of begomoviruses by *B. tabaci* has been facilitated by the introduction in many areas of the polyphagous B biotype of *B. tabaci*, which feeds on a wide range of plants and thus has a high probability of acquiring and transmitting a diversity of begomoviruses into potential new hosts. In the mid-1980s, for example, B biotype was introduced into the New World, where it often displaced the local A biotype, which is less polyphagous than B biotype (Morales 2010). As a result, begomoviruses have supplanted potyviruses as the group of plant viruses with the largest number of recognized species. *B. tabaci* has also been involved in the emergence of new diseases caused by other groups of viruses, such as criniviruses (Wisler et al. 1998a) or ipomoviruses (Adkins et al. 2010). *Trialeurodes vaporariorum*, another whitefly able to transmit some criniviruses, was long restricted to greenhouse crops but in some areas has become increasingly important as a pest in open-field vegetable production over the past 20 years (Wintermantel 2004).

Increased incidence of whitefly-transmitted viruses has been noticed in India in beans, cassava, chilli, cucurbits, okra, potato, and tomato. This may be due to occurrence of B and Q biotypes of whitefly population which rapidly multiply under changed climatic conditions. This also led to the breakdown of resistance to yellow vein mosaic virus of okra and severe incidence of begomoviruses on cucurbits throughout India, which were not known to be

infected with begomoviruses. Recent surveys in vegetable crops have indicated the occurrence of new criniviruses in India such as cucurbits and tomato (Krishnareddy and Manasa 2012).

23.2.3 Impact on Thrips and Thrips-Transmitted Viruses

Thrips are insects belonging to the order Thysanoptera (Mound 2005). Some thrips can affect plants by direct feeding, which may leave visible signs of damage, such as leaf silverying (Palmer et al. 1989). A few of these thrips transmit plant viruses. Thrips-transmitted viruses can cause significant diseases of many crop plants, and their impact worldwide is immense (Mumford et al. 1996; Ullman et al. 1997). Tospoviruses belong to the sole phytovirus genus, *Tospovirus*, in the family *Bunyaviridae*. Tospoviruses are known to be exclusively transmitted by thrips belonging to the family Thripidae and subfamily Thripinae. Of the known 1,710 species of Thripidae, only 14 thrips species are currently reported to transmit tospoviruses. Thrips-transmitted tospoviruses cause severe yield losses to several economically important crops in the United States and worldwide. Global trade and associated movement of plant materials across borders have introduced tospoviruses and their vectors into newer areas (David et al. 2011).

Species in the *Thrips*, *Frankliniella*, *Scirtothrips*, *Microcephalothrips*, *Dictyothrips*, and *Ceratothripoides* genera have been shown to transmit plant viruses. Thrips transmit plant viruses in the Tospovirus, Ilarvirus, Carmovirus, Sobemovirus, and Machlomovirus genera (Jones 2005; Riley et al. 2011). Thrips lay eggs, which hatch to produce two larval instars that feed on plants. Larval instars are followed by two relatively inactive pupal instars that probably do not feed. In warm conditions, the life cycle usually takes about 20 days from egg to adult. Adults are readily dispersed. Thrips can transmit viruses as (1) a mechanical accident of feeding on leaves covered with virus-carrying pollen, (2) by transferring virus-carrying pollen by mechanical accident feeding, and (3) as the result of a more

sophisticated relationship in which the virus is ingested and multiplies within the body of the insect. The third mechanism, which is restricted to viruses in the *Tospovirus* genus, has resulted in the most serious threat to world agriculture.

Thrips development is known to be dependent on temperature. Adult females can survive for 4–5 weeks at 30°C and oviposit 50 eggs (Reitz 2008). *Frankliniella occidentalis* requires a minimum of 194° days (minimum temperature 9.5°C) to complete a generation (Katayama 1997) but has been estimated to be as high as 254° days with a minimum temperature of 6.5°C (Lowry et al. 1992).

The few species of thrips that transmit tospoviruses, which are less than 0.2% of the total, are not closely related to each other (Mound 2001a, 2005). Only six species of *Frankliniella*, three species of *Thrips*, and one species each of *Scirtothrips* and *Ceratothripoides* are known to be vectors. Tospoviruses are transmitted by several species of thrips in a circulative and propagative manner (Mound 1996; Ullman et al. 1997; Whitfield et al. 2005). While there are more than 5,000 thrips species, so far only 10 are known vectors of tospoviruses, suggesting marked coevolution for transmission specificity between tospoviruses and these thrips vector species. Both larval and adult stages of thrips vectors can actively feed on virus-infected host plants, but only early larval instars can acquire the virus, and later instar larvae and adults can transmit the virus after a latent period (Wijkamp et al. 1996a; Ullman et al. 1997; Whitfield et al. 2005; Persley et al. 2006). Adult thrips can acquire tospoviruses, but they do not transmit them. This is presumably because of insufficient multiplication in the midgut, a lack of movement to salivary glands, and a lack of multiplication thereafter. These are prerequisite for *Tospovirus* transmission (Wijkamp et al. 1996b). In addition, tospoviruses are not transmitted transovarially (Wijkamp et al. 1996a). Thus, each new generation of thrips vectors must acquire the virus as larvae. There are distinct associations between thrips species and their ability to transmit specific tospoviruses (Jones 2005).

The transmission of ilarviruses by thrips is a different mechanism. It involves the physical

movement of virus-carrying pollen from one plant to another and its introduction into the plant through feeding wounds. Thrips in the genera *Frankliniella*, *Microcephalothrips*, and *Thrips* have been implicated in the spread of Tobacco streak virus (TSV) (Kaiser et al. 1982; Sdoodee and Teakle 1987; Marchoux et al. 1999) and *Prunus* necrotic ringspot virus (PNRSV) (Greber et al. 1991) ilarviruses though more may be discovered. There has been one report of transmission of a carmovirus by thrips utilizing the same mechanism as for ilarviruses. *F. occidentalis* has been found to transmit *Pelargonium* flower break virus (PFBV) (Krczal et al. 1995), a carmovirus. One sobemovirus can also be transferred with pollen by thrips and plants infected during feeding. This virus can also be carried from one plant to another on the mouthparts of thrips. *T. tabaci* transmit Sowbane mosaic virus (SoMV) (Hardy and Teakle 1992), a sobemovirus and Maize chlorotic mottle virus (MCMV) (Ullman et al. 1992), a machlomovirus. One machlomovirus is also thought to be thrips transmitted, but the actual mechanism is not clear.

23.2.4 Impact on Leafhopper and Psyllids and Vector-Transmitted Phytoplasma

Phytoplasmas are phloem-limited plant pathogens that are spread by sap-sucking insect vectors belonging to the families Cicadellidae (leafhoppers) and Fulgoridae (plant hoppers) (Brack 1979; Tsai 1979; Bantari and Zeyen 1979; Nielson 1979). Insects feed on phloem tissues, where they acquire phytoplasmas and transmit them from plant to plant. During their transmission cycle, phytoplasmas cross the insect midgut lining, circulate and reproduce in the hemolymph, and invade and multiply in insect tissues including salivary glands, where phytoplasmas are integrated into saliva and injected into the plant phloem during feeding (Lherminier et al. 1990; Lefol et al. 1994; Nakashima and Hayashi 1995; Bertamini et al. 2002). Phytoplasmas may overwinter in infected vectors, as well as in perennial plants that serve as reservoirs for phytoplasmas.

Additionally, phytoplasmas can be spread by vegetative propagation through cuttings, storage tubers, rhizomes, or bulbs (Lee and Davis 1992). Phytoplasmas that cause many ornamental and fruit tree diseases are spread by vegetative propagation and grafting.

Weintraub and Beanland (2006) have reviewed the vectors of phytoplasmas. The single most successful order of insect phytoplasma vectors is the Hemiptera, which includes the Sternorrhyncha and Auchenorrhyncha. They point out that this group collectively possesses several characteristics that make its members efficient vectors of phytoplasmas: (a) they are hemimetabolous; thus, nymphs and adults feed similarly and are in the same physical location, and often both young ones and adults can transmit phytoplasmas; (b) feed specifically and selectively on certain plant tissues, which makes them efficient vectors of pathogens residing in those tissues; (c) have a propagative and persistent relationship with phytoplasmas; and (d) have obligate symbiotic prokaryotes that are passed to the offspring by transovarial transmission, the same mechanisms that allow the transovarial transmission of phytoplasmas. Climate change is predicted to have a progressively negative effect on the yield of food crops. Climatic variability can affect not only the pathogen but also plant host and insect vector, as well as the interactions between or among these organisms (Luck et al. 2011). Vector–host plant interactions play an important role in limiting or expanding phytoplasma spreading. Broadly polyphagous vectors have the potential to inoculate a wider range of plant species, depending on the susceptibility of each host plant. Several studies have shown that insects that normally do not feed on certain plant species can acquire and transmit phytoplasma to those plants under laboratory conditions. Hence, in many cases, the plant host range of a vector, rather than lack of phytoplasma-specific cell membrane receptors, will limit the spread of phytoplasma by that species (Weintraub 2007; Nault and Ammar 1989).

Bois noir in grapevine and potato stolbur are caused by phytoplasmas of the stolbur (16Sr-XII-A) group and transmitted by the plant hopper *Hyalesthes obsoletus*, a southern European,

xerothermic species. The fact that stolbur phytoplasma and its vector were present for a long time at viticultural sites but occurred just recently in potatoes appears contradictory. However, potatoes are grown in areas where ambient temperatures were not sufficient for the vector to complete its life cycle. Changing climatic conditions could have allowed *H. obsoletus* not only to spread to new viticultural sites but also to potato-growing areas with a rather mild climate. Since early maturing varieties are grown there, stolbur symptoms might become visible only in years when high spring temperatures lead to an exceptionally early flight of *H. obsoletus* and an inoculation of the potato plants ahead of the normal time in July (Lindner et al. 2007).

23.2.5 Changes in Vector Population Dynamics

The population dynamics is the aspect of population ecology dealing with factors affecting changes in population densities. The seasonal effects of weather and ongoing changes in climatic conditions will directly lead to modifications in dispersal and development of insect vector species. The changes in surrounding temperature regimes certainly involve alterations in development rates, voltinism, and survival of insect vectors and subsequently act upon size, density, and genetic composition of populations, as well as on the extent of host plant exploitation (Bale et al. 2002). The change in the environment affects the pest population dynamics in two ways either directly or indirectly by altering the host physiology. Host availability and the probability of vector outbreaks are further determined by the incidence and character of abiotic disturbances. The developmental success of insect herbivores also indirectly depends on climate, as environmental parameters impact on plant physiology. Insects and plants are exposed to complex interactions among changes in temperature, precipitation conditions, and increased levels of CO₂ and variations in nutrient availability (Karuppaiah and Sujayanad 2012).

Changes in vector populations are frequently the result of human activities such as the introduction of exotic insects into new areas or the intensive use of insecticides. Vector insect populations may also be altered by climate change (Canto et al. 2009; Jones 2009). There are numerous examples of human-mediated introduction of different biotypes of *B. tabaci*. Human activity, for example, was responsible for the spread of the B biotype from its presumed origin in the Mediterranean–Asia Minor region to rest of the world. As noted earlier, the introduction of the B biotype has often led to the displacement of indigenous *B. tabaci* populations (Brown et al. 1995).

The importance of changes in biotype composition of *B. tabaci* populations lies in the biological differences between biotypes that are relevant to the emergence of virus diseases. These biological differences include differences in virus transmission efficiency, plant host range, mating behavior, and rate of population increase. It has been well documented that the B biotype of *B. tabaci* has larger populations and a broader host range than the A biotype. This probably explains why, in many regions of the New World, the exotic B biotype has displaced the native A biotype (Morales 2010). Mating behavior also differs among *B. tabaci* biotypes. Caged experiments and behavioral observations have shown that the males of the invading B biotype copulate more frequently than native males in China and Australia. This behavior of B biotype males interferes with mating by native males and increases the production of female progeny of the B biotype. Such asymmetric mating interactions may help explain the capacity of the B biotype to invade and displace indigenous populations (Liu et al. 2007).

Aphids show a considerable variation in their life cycle traits and even within species variation can be very high. Some species, termed holocyclic, respond to the oncoming winter with a sexual phase, often placing eggs on woody plants. Anholocyclic aphids, on the other hand, do not go through the sexual phase and continue with parthenogenetic and viviparous reproduction throughout the year. Some species are a mix of holocyclic and anholocyclic

clones. Within a species, the proportion of individuals that are holocyclic tends to be greater in colder regions, as the eggs resulting from sexual reproduction are very much more cold hardy than the active, viviparous forms which persist year round in anholocyclic clones. Research from Poland suggests that there has been a radical reduction in the proportion of holocyclic clones of some aphid species in recent years (Ruszkowska et al. 2010; Dedryver et al. 2010). If this trend is reflected in Sweden, then aphids may soon be reproducing asexually all year round. This biological change may take place simultaneously with human-mediated changes in the availability of host plants. Autumn sowing, for example, will become more common, and autumn sown cereals have doubled in acreage in Sweden from 1981 to 2009 (Svensson 2010). This leads to the risk of a so-called green bridge, when winter crops may emerge sufficiently early to receive insects migrating from maturing crops, which can be especially important for vectors such as aphids and the transmission of virus. Warmer autumns and winters will increase the risk for insect transmission of viruses into winter crops, such as winter wheat, winter barley, and winter oilseed rape. They are now sown when the number of active insect vectors has decreased significantly.

Wheat dwarf virus (WDV) is transmitted in a persistent manner by the leafhopper *Psammotettix alienus*. At the beginning of the last century, a disease presumed to be caused by WDV severely affected wheat in central Sweden (Lindsten and Lindsten 1999). It has since then periodically damaged winter wheat in the central parts of Sweden. The periodic reappearance of the disease has been associated with changes in agricultural practices (Lindsten and Lindsten 1999; Lindblad and Waern 2002). The host range of WDV includes many common grasses, and a recent study has shown that grasses growing in vicinity to WDV-affected wheat fields are infected (Ramsell et al. 2008). These grasses may act as a long-term reservoir for the virus. The leafhoppers acquire WDV from infected volunteer plants or grasses and then transmit the virus into winter wheat at the beginning of the autumn.

They overwinter as eggs, and in spring, wingless nymphs transmit WDV from the infected wheat plants in the field (Lindblad and Sigvald 2004). A study in Sweden showed that the catches in autumn of adult *P. alienus* in fields of winter wheat increased with higher temperatures. During weeks with an average maximum temperature below 10°C, only few leafhoppers were caught in yellow water traps, but during weeks above 10°C, the numbers increased with temperature, with high insect numbers noted above 15°C (Lindblad and Arenö 2002). When the crop is not infected in the autumn, the damage from WDV will be very limited. Mature wheat plant shows resistance against WDV with at growth stage DC31, when the first node is detectable (Lindblad and Sigvald 2004). Therefore, when the winged adult form of *P. alienus* is ready to transmit WDV between wheat fields, the wheat has already reached the resistant stage. In continental and southern Europe, winter barley is affected by the barley strain of WDV. This strain is distinct from the wheat strain infecting wheat in Sweden and other parts of Europe and Asia (Ramsell et al. 2009). There is now a risk that the barley strain of WDV may also appear in Sweden. Similar problems with autumn infection of winter crops are expected with Barley yellow dwarf virus-PAV (BYDV-PAV) and BYDV-MAV, which are persistently transmitted by different aphid species. With increased temperatures in temperate regions, disease epidemics caused by aphid-borne viruses are likely to be more severe (Jones 2009). In Germany, a clear relation was recently found between the number of infection days in autumn and BYDV attack in winter barley fields (Habekuß et al. 2009).

23.3 Climate Change and Plant Virus Diseases

The dynamics of plant virus epidemics and the losses they cause are likely to be influenced greatly by (1) the direct consequences of climate change such as altered rainfall patterns, increased temperature, and greater wind speeds and (2)

indirectly by factors such as regional alterations in the areas cropped and the ranges of crops grown, and changes in the distribution, abundance, and activity of vectors. Such influences are likely to alter the geographic ranges and relative abundance of viruses, their rates of spread, the effectiveness of host resistances to virus infection, the physiology of host–virus interactions, the rate of virus evolution and host adaptation, and the effectiveness of control measures. However, the magnitude of such effects on the frequency and duration of virus epidemics will vary depending on the pathosystem and geographical region concerned making it difficult to generalize (Norse and Gommers 2003; Garrett et al. 2006; Krishnareddy et al. 2010).

23.3.1 Geographical Distribution of Host, Vector, and Virus

New virus disease complexes may arise, and some diseases may cease to be economically important if warming causes a poleward shift of agroclimatic zones and host plants migrate into new regions. Viruses and vectors would follow the migrating hosts and may infect remnant vegetation of natural plant communities not previously exposed to the often more aggressive strains from agricultural crops (Coakley et al. 1999). The mechanism of pathogen dispersal, suitability of the environment for dispersal, survival between seasons, and any change in host physiology and ecology in the new environment will largely determine how quickly pathogens become established in a new region. In India, Tobacco streak virus occurred after severe drought during 1997 on sunflower crop in Karnataka. Soon this virus shifted to groundnut in Andhra Pradesh, causing severe yield loss during 2002. Later this virus started appearing epidemic on vegetable crops causing epidemic in gherkin and okra in Karnataka (Krishnareddy et al. 2003a, b).

If the frost line moves north in the Northern Hemisphere, higher winter temperatures could be accompanied by increased survival of insects. For virus–vector aphids, this could lead to higher incidence of virus diseases, especially in those

regions where the timing of virus arrival is linked to winter survival and spring flight of aphids. Barley yellow dwarf potyvirus (BYDV) is an example of a virus that causes more severe disease following mild winters. Since BYDV is exclusively transmitted by aphids, increased survival of pathogen reservoirs could greatly increase the economic losses caused by infection. Similar increases in viruses of potato and sugar beet have also been observed following warmer winters (Carter and Harrington 1991). Polák (2009) monitored climate change impacts on plant pathogen distribution such as *Zucchini yellow mosaic virus* (ZYMV), quarantine *Plum pox virus* (PPV), and phytoplasma European stone fruit yellows (ESFY). ZYMV has spread from Northern Italy across Austria up to Central Moravia and Bohemia. PPV has been continuously spreading from the lowlands of Central Bohemia and Moravia up to plains. Later, from the 1960s and 1970s of the last century, due to climate warming and human activities, the virus quickly spread to uplands, foothills, and mountains of the Czech Republic. Phytoplasma ESFY was spreading in a manner similar to ZYMV in the 1980s of the twentieth century from Northern Italy and currently is affecting mainly apricot and peach trees in Southern Moravia. The range of plant species that can be infected by a given phytoplasma in nature is determined by the number of insect vector species capable of transmitting the phytoplasma and by the feeding behaviors of these vectors. Mixed phytoplasma infections in a single plant are found in nature and can be experimentally generated (Lee et al. 1995; Alma et al. 1996; Bianco et al. 1993; Marcone et al. 1995). Co-infection also provides opportunities for the exchange of genetic information which may also contribute to the evolution of new strains.

23.3.2 Impact on Emergence of Viruses and Increase in Virus Epidemics

Small changes in average temperatures can suffice to bring about substantial shifts in the distribution and abundance of arthropod vectors of

plant viruses (Anderson et al. 2004). Aphid vectors, in particular, are expected to react strongly to climatic changes because of their short generation time and low developmental threshold temperatures (Harrington et al. 2007). Increases in their numbers will lead inevitably to a higher risk of damaging epidemics of aphid-borne viruses. The spread of Papaya ringspot virus (PRSV) throughout the country recently, which was earlier restricted to the few places in northern India, is the best example. *A. gossypii* is one of the predominant vectors, followed by *A. craccivora* and *M. persicae* (Kalleshwaraswamy and Krishnakumar 2008). Peak aphid population of *A. gossypii* during March and April was a primary factor for a high incidence of new PRSV infections during April to May. The seasonal dynamics of *A. gossypii* was linked to the large-scale cultivation of cucurbitaceous vegetables from November to late March in south India (Kalleshwaraswamy et al. 2007).

With aphid vectors, ability to overwinter in temperate climates is enhanced by shorter cold spells and fewer days with frosts, allowing them to increase the duration of their activity annually and expand their geographical ranges (Norse and Gommers 2003). Harrington et al. (1995) suggested that, particularly for *Myzus persicae*, an increase of 1°C in the mean winter (January–February) temperature will advance the timing of spring aphid migration by 2 weeks. Such an advance taking place comes from the UK (Harrington 2002). In general, the date of first recording of aphid species in Europe is expected to advance by an average of 8 days over the next 50 years, the actual rate of advance varying with location and aphid species (Harrington et al. 2007). In temperate zones, a warming of 2°C is anticipated to give rise to an extra five generations of aphids/year (Yamamura and Kiritani 1998). In such zones, epidemics of diseases caused by aphid-borne viruses are likely to be more severe in the future as a result of increased aphid activity. These diseases include “yellow dwarf” in cereals, “virus yellows” in sugar beet, and “leaf roll” in potatoes (Harrington 2003; Qi et al. 2005). The opposite scenario applies in regions with Mediterranean-type climates and

rain-fed, winter cropping, as the ability of aphid vectors to overwinter is likely to be decreased by the hotter, dryer summer conditions, for example, with the cereal aphid vectors of BYDV in parts of Southwest Australia (Hawkes and Jones 2005; Thackray et al. 2009). Although temperature and rainfall are the principal factors that influence aphid numbers, others connected with climate change such as elevated carbon dioxide also have the potential to do so. Taking these into account, model predictions for the effect of climate change on abundance and distribution of cereal aphids in the UK and Canada gave conflicting results, with populations declining in summer in some regions but increasing in others (Newman 2004, 2005, 2006). Watermelon mosaic virus (WMV, genus Potyvirus, family Potyviridae) was reported for the first time in France in 1974, and it is now the most prevalent virus in cucurbit crops. In 2000, new strains referred as ‘emerging’ (EM) strains were detected in South-eastern France. EM strains are generally more severe and phylogenetically distinct from those previously reported in this country and referred as ‘classic’ (CL) strains. Since 2000, EM strains have been progressively replacing CL strains in several areas where they co-exist (Desbiez et al. 2009). In order to explain this rapid shift in virus populations, the biological properties of a set of 17 CL and EM WMV isolates were compared. No major differences were observed when comparing a limited host range including 48 different plant species or cultivars. Only two species were differential; *Chenopodium quinoa* was systemically infected by CL and not by EM isolates whereas *Ranunculus sardous* was systemically infected by EM and not by CL isolates. A considerable variability was observed in aphid transmission efficiencies but this could not be correlated to the CL or EM types. Two subsets of five isolates of each group were used to compare aphid transmission efficiencies from single and double (CL–EM) infections using six different cucurbit and non-cucurbit hosts. EM isolates were generally better transmitted from mixed CL–EM infections than CL isolates and CL transmission rates were significantly lower from double than from single infections (Lecoq et al. 2011).

Temperature and rainfall are two of the principal factors affecting the important vector whitefly species, *B. tabaci*, with its population being diminished drastically by low temperatures and heavy and persistent rainfall. To flourish, it requires a dry season with duration of 4 months of rainfall less than 80 mm a month and a mean monthly temperature of at least 21°C in the hottest month of the year (Morales and Jones 2004). Such conditions are likely to occur over increasingly wide areas in middle latitude regions as global warming progresses. As more regions of Asia, Australia, Latin America, and Africa develop longer dry seasons, the likelihood of damaging epidemics of viruses transmitted by *B. tabaci*, such as begomoviruses on many important crops, will occur more frequently (Morales and Jones 2004).

The high incidence of new *Tospovirus* spp. in tropical Asian regions suggests a “hot spot” of viral genetic diversity in reservoir host variants from where they are transmitted to commercial crops through increasing vector populations (Rojas and Gilbertson 2008; Gent et al. 2006). The tospoviruses have been known in India since 1968 (Reddy et al. 1968) and have become a major problem for several field and horticultural crops. Because of varied climatic conditions, crop diversity, and both intensive and extensive cultivation of agri-horticultural crops, India has a variety of tospovirus isolates. There have been at least more than five tospoviruses reported on different crops from India (Prasada Rao et al. 1980; Reddy et al. 1992; Singh and Krishnareddy 1996; Jain et al. 1998; Krishnareddy et al. 2008; Kunkalikar et al. 2010, 2011). The results also revealed an expanded host range of GBNV and WBNV that may facilitate their natural mixed infections in tomatoes and watermelons (Kunkalikar et al. 2011).

23.3.3 Impact on Incidence and Spread of Viruses

Although most of the information available on the influence of whitefly populations on virus emergence comes from studies with *B. tabaci* and

begomoviruses, emerging diseases caused by criniviruses may also be affected by shifts in whitefly populations (Wintermantel 2010). Unlike begomoviruses, criniviruses can be transmitted by species of both *Bemisia* and *Trialeurodes*. *Tomato chlorosis virus* (ToCV), for example, is transmitted by *T. vaporariorum*, *T. abutiloneus*, and by the A, B, and Q biotypes and perhaps other biotypes of *B. tabaci* (Wisler et al. 1998b; Navas-Castillo et al. 2000). Most criniviruses, however, are transmitted by only one whitefly species. Therefore, the prevalence of different whitefly species can greatly affect the incidence of crinivirus outbreaks. A clear example has been reported from southeastern Spain, where melons (*Cucumis melo*) and cucumbers (*Cucumis sativus*) have been seriously affected since the late 1970s by yellowing diseases transmitted by whiteflies. Two criniviruses have been associated with these diseases: *Beet pseudo-yellow virus* (BPYV), which is transmitted by *T. vaporariorum*, and *Cucurbit yellow stunting disorder virus* (CYSDV), which is transmitted by *B. tabaci*. CYSDV-associated yellowing emerged in Spain in the early 1990s, coinciding with the displacement of *T. vaporariorum* by *B. tabaci* as the prevalent whitefly species in the greenhouses of this area. As a consequence of this, CYSDV displaced BPYV, present in the area since the late 1970s.

Climate change models predict an increase in global average temperature that could affect both host plants and insect vector populations. In particular, changes in a vector's overwintering biology, geographical distribution, density, migration potential, or phenology could affect virus survival, movement, and distribution and therefore could affect virus epidemics and the emergence of virus diseases in new areas or new crops (Garrett et al. 2006; Canto et al. 2009; Hanssen et al. 2010). The distribution of *B. tabaci* and other whitefly species depends largely on climatic conditions, in that high temperatures and low rainfall and humidity favor its reproduction (Morales and Jones 2004). Such conditions are likely to occur over increasing areas in middle latitudes if global warming continues. Thus, emergence of viruses transmitted by this insect can be expected in new

areas following its expansion. Direct effects on plant health of climate warming, increased pollutants and CO₂ concentrations (Kliejunas et al. 2008; McElrone et al. 2010; Davies et al. 2011; Eastburn et al. 2011) will be accompanied by the easier introduction of exotic invasive species (Chakraborty et al. 2000; Lonsdale and Gibbs 2002; Ganley et al. 2011; Chytrý et al. 2012). Introductions of novel plant pathogens have already occurred in many regions (Brown and Hovmøller 2002; Dehnen-Schmutz et al. 2010; Stenlid et al. 2011), but climate changes are likely to often facilitate their further establishment and spread (Anderson et al. 2004; Shaw 2009; Hannukkala 2011). There is a consensus that prediction and management of climate change effects on plant health are complicated by interactions between globalization, shifts in climate, pollution and increasing numbers of invasive plants, pests and pathogens (Mistretta 2002; Desprez Loustau et al. 2007; Danon et al. 2011).

23.3.4 Impact on Phytoplasma Distribution and Multiplication

The increasing threat of phytoplasma diseases worldwide comes both from emerging diseases in Africa, Latin America, and the Caribbean mainly in sugarcane, corn, coconuts, papaya, and vegetables and from devastating epidemics in the rest of the world in grapevines, citrus, forest trees, oil-seed crops, alfalfa, stone, and pome fruits. In both cases, diseases have the potential to spread to other crop species throughout the world and/or impact on global trade. There are concerns that climate changes resulting from global warming may facilitate the spread of these phytoplasma diseases to new areas and to additional crops, particularly if the vectors become more widespread and able to survive during warmer winters. Phytoplasmas usually do not kill the host plant in short time; however, unusually cold conditions kill infected plants, while under tropical conditions, asymptomatic plant presence is frequent with severe epidemiological consequences (McCoy et al. 1989).

The geographical distribution and impact of phytoplasma diseases depend on the host range of the phytoplasma as well as the feeding behavior of the insect vector. Some have a broad range of plant hosts and polyphagous vectors and therefore have a wide distribution. This is the case for "*Candidatus (Ca.) Phytoplasma asteris*," which has been reported in many crops worldwide. But many phytoplasmas have restricted host ranges and oligophagous or monophagous insect vectors, which restrict their geographical distribution. To date, no studies have linked changes of phytoplasma disease impact or geographical distribution to changes in climatic conditions. Many biological parameters influencing phytoplasma epidemiology can theoretically be affected by climate change. As a result of global warming, local increase in mean temperature can act at the level of insect vector population dynamics, biology, and fitness, but also at the level of the interaction between the phytoplasma and its two hosts: the plant and the insect vector. Events such as a storm or change in wind conditions can affect insect vector dispersal (Lee et al. 2000).

The predicted increase of mean temperature over the planet will increase the phytoplasma multiplication rate early in the season, when temperature is suboptimal. For example, in a temperate climate, it may be surmised that an increase in mean temperature during spring will result in a higher multiplication of phytoplasmas in plants and insects. On the infected plant side, it will result in an earlier development of symptoms, which might also be more severe, as a higher number of phytoplasmas in the plant may result in an increased disease severity. This reduction of the incubation period in the plant should also reduce the acquisition access period: the time necessary for acquisition of the pathogen by the insect vector feeding on the infected plant. Phytoplasmas will also multiply faster in the insect vector, thus decreasing the latency period necessary for the insect colonization by the phytoplasma (Foissac and Wilson 2010). Galetto et al. (2011) studied multiplication patterns of two phytoplasmas, "chrysanthemum yellows" and "flavescence dorée," in insect vectors and plant hosts under different climatic

conditions. Phytoplasma multiplication was faster under cooler conditions in insects (P1, 18–22°C; CO₂ 400 ppm) and under warmer conditions in plants (P2, 22–26°C; CO₂ 800 ppm). An influence of temperature and CO₂ concentrations was observed for chrysanthemum yellows latency in the vector only. Results suggest that T and CO₂ influence on phytoplasma multiplication is host dependent.

Conversely, the detrimental influence of phytoplasma infection on insect fitness can reduce the opportunities of phytoplasma disease propagation. It is known that the maize bushy stunt phytoplasma (group 16SrI) and the flavescence doree phytoplasma (group 16SrV) reduce the lifespan of their respective insect vectors, *Dalbulus longulus* DeLong and *S. titanus* (Nault et al. 1984; Bressan et al. 2005). Interestingly, the pathogenicity of the Western-X phytoplasma (group 16SrIII) to its vector *Paraphlepsius irroratus* (Say) is temperature dependent (Garcia-Salazar et al. 1991). Phytoplasmas have a broad host plant range, which depends on the plant feeding range of their insect vectors. With more than 100 isolates, the aster yellows phytoplasma (AYP) subclade *Candidatus (Ca.) Phytoplasma asteris* previously known as 16srI clade phytoplasmas comprises the largest among the *Ca.* phytoplasma subclades (Marcone et al. 2000; Seemuller et al. 1998). Aster yellows phytoplasma are vectored by at least 30, often polyphagous, insect species and, as a consequence, are capable of infecting more than 80 plant species (Firrao et al. 2007), including many weeds that surround crop fields (Marcone et al. 2000). For example, aster yellows phytoplasma strain Witches' Broom (AY-WB) can be transmitted by the polyphagous *Macrostelus quadrilineatus* (Forbes) to China aster and lettuce (Zhang et al. 2004). The broad plant and insect host ranges make phytoplasma outbreaks unpredictable. Further, because of the long incubation periods of phytoplasmas in plants and insects, outbreaks are often detected too late, that is, close to harvesting of the crops and after dispersion of the phytoplasmas by the insect vectors.

23.3.5 Impact on Host Resistance

In addition to the impacts on vectors, climate change alters the frequency and duration of virus epidemics when increased temperature changes the rates of virus multiplication, modifies host resistance, and changes the physiology of host–virus interactions. Viruses have different temperature optima for multiplication. Some are adapted to warmer regions and others to temperate regions. The distributions of the former are likely to increase as the world warms, and the ranges of crops currently restricted from being grown in cooler regions by temperature expand. Temperature-sensitive resistance genes which are currently effective (Fraser 1986, 1990) may become ineffective when virus epidemics occur in formerly resistant cultivars of crops grown under warmer conditions than previously. In semiarid and arid mid-latitude regions, increased drought stress may enhance crop vulnerability to virus infection by changing the physiology of host–virus interactions, thereby increasing the occurrence of damaging virus epidemics, for example, of begomoviruses. Moreover, drought stress and disease stress may have additive effects resulting in greater damage, as with *Beet yellows virus* and *Maize dwarf mosaic virus* (Olson et al. 1990; Clover et al. 1999).

Elevated carbon dioxide and ozone also have the potential to influence the effectiveness of host resistance and suppress pathogen-induced resistance (Garrett et al. 2006) and so alter the occurrence of virus epidemics. Warmer growing conditions will alter selection pressures on viruses and modify virus evolution rates, thereby influencing the magnitude of virus epidemics. Changes in the ranges and geographical distributions of crops and geographic expansion of virus and vector distribution resulting from increasing temperatures and altered rainfall patterns will inevitably increase the occurrence of “new encounters” between viral pathogens, their vectors, and host plants. This process of bringing more viruses into contact with more potential hosts will provide new opportunities for virus evolution and host species “jumps,” and further increases the rate of invasion of indigenous flora by introduced viruses and

of introduced plants by indigenous viruses emerging from native plants to infect them (Anderson et al. 2004; Garrett et al. 2006). Conversely, in some situations, climate change may diminish the encounter rate between virus and host by changing the ranges of both so that they coincide less, for example, in middle latitude arid and semiarid regions by decreasing the overall amount of land in use for cropping or diminishing the fragmentation of remnant native vegetation.

Elevated ozone altered gene expression in soybean and induced a nonspecific defense response. Although the host defense response was not induced specifically to stop SMV infection but to cope with the environmental changes, it retarded the replication and spread of the host-dependent pathogen temporarily. The induced nonspecific defense has multiple components. Transcriptional increases of PR genes and ethylene, salicylic acid, and jasmonic acid signaling genes contributed to the defense response to a certain degree. The increase in flavonoid biosynthesis genes and the increase in several flavonoids indicated that flavonoid biosynthesis was one of the major players in the nonspecific defense response (Bilgin et al. 2008).

23.3.6 Impact on Host–Pathogen Interaction

Plant virus diseases severely constrain agricultural production worldwide (Van Den Bosch, et al. 2006), but the roles played by pathogens in determining an ecosystem response to elevated CO₂ have rarely been examined (Malmstrom and Field 1997; Malmstrom et al. 2011; Lake and Wade 2009). Elevated CO₂ levels directly impact plant physiology and result in an increase in the photosynthetic rate, which alters the growth and aboveground biomass (Agrell et al. 2000; Hartley et al. 2000). On the other hand, Malmstrom and Field (1997) found that the biomass of BYDV-infected barley decreases by 50–60% compared with healthy barley under atmosphere CO₂ levels, while the biomass of infected barley decreases by 39–40% compared with healthy plants under elevated CO₂. Generally speaking, few studies on

pot-grown plants have discovered an insignificant growth response to elevated CO₂ (Sindelarova et al. 2005).

Ye et al. (2010) reported that elevated CO₂ increased plant aboveground biomass but did not significantly influence TNCs or nitrogen content, while PVYN infection had adverse effects on biomass, markedly affected the later two indices, but no interactive effects between elevated CO₂ and PVYN infection on these three indices were detected. As single factor, elevated CO₂ or PVYN infection reduced chlorophyll content, while elevated CO₂ increased the soluble protein content; interaction between two factors was observed on free amino acid and nicotine content. Variations in peroxides activity revealed that CO₂ influenced infected plant primary production by reducing virus resistance cost. Results suggested that plants grown under elevated CO₂ have alleviated damage of the virus infection or delayed the viral spread to some extent (Roos et al. 2011).

The transmission efficiency of many vector-borne plant viruses has been shown to be affected by temperature (Lowles et al. 1996; Sylvester 1980; Smyrnioudis et al. 2001). Temperature has also been demonstrated to have an impact on Banana bunchy top virus (BBTV) symptom development (Anhalt and Almeida 2008; Wu and Su 1990), spread (Allen 1978), transmission efficiency (Wu and Su 1990), and on vector biology (Anhalt and Almeida 2008; Smith et al. 1998). Wu and Su (1990) compared BBTV acquisition efficiency at 16°C, 20°C, and 27°C using groups of aphids for transmission experiments, demonstrating that temperature affected efficiency, with no transmission at 16°C and maximum efficiency at 27°C.

2 3.4 Conclusions

The world is undergoing a period of accelerated climate change accompanied by rapid expansion in human activity. Both of these factors are impacting plants, vectors, phytoplasma, and viruses, causing increased instability within virus–plant pathosystems. This has major implications on effective control of viral epidem-

ics that diminish food production, especially those associated with virus emergence. It also makes this an exciting opportunity to study the changing dynamics of viral epidemiology, ecology and evolution in different regions, and their implications. This is especially so when new encounter scenarios render once reliable control measures less effective, or even entirely ineffective, in the future. A crucial component of such studies involves understanding viruses within wild plant populations and cultivated plants at natural and manmade ecosystem interface. This can provide critical information not only on the potential threats posed to cultivated species and biodiversity but also on virus evolution in response to rapidly changing conditions (Jones 2009).

Invasive viruses, vectors, and vector biotypes are increasing the frequency of new encounters. The other biological changes involved introduction of new, more efficient virus–vector species and more efficient virus–vector biotypes or variants of existing vector species, and circumvention of host defenses in introduced crops. At the molecular level, the genome alterations most likely to occur in different emerging viruses are those caused by recombination, pseudo-recombination, reassortment, and modular evolution. Alterations will also arise by selection from existing variants within virus populations, new mutations, synergism, genetic drift, population bottlenecks and “founder effects,” presence of satellite viruses and nucleic acids, or genome integration (Anderson et al. 2004; Fargette et al. 2006; Jeger et al. 2004, 2006, 2011; Morales 2006; Seal et al. 2006a, b; Gibbs et al. 2008; Sacristan and Garcia-Arenal 2008).

The current rapid expansion in human activity includes adopting more intensive, extensive, and diverse agricultural practices; more widespread cultivation in monocultures; greater loss of genetic diversity; increased fragmentation and disturbance of indigenous vegetation; and misuse and overuse of chemical control measures, irrigation, and protected cropping. All of these provide conditions that favor emergence of viruses and development of damaging epidemics at the interface. It also includes the effects of continually expanding

volume and greater rapidity of international trade in plants and plant products, combined with expanding travel by modern transport systems for tourism and business purposes, in moving plants away from their centers of diversity and dispersing previously localized weeds, viruses, and vectors widely. The spatial and temporal shifts in climate that will occur because of changes in temperature, rainfall, and wind patterns will cause regional alterations in the ranges of introduced crops grown and areas cropped, occurrence of introduced weed species, and the distribution, abundance, and activity of vectors. New encounter rates will increase as crops and weeds newly introduced to a region intermingle with the local native vegetation for the first time. The geographical ranges of vectors within continents will change, bringing them into first contact with indigenous viruses, and newly introduced weeds or crop plants that boost virus inoculum levels or vector populations will alter epidemic dynamics (Anderson et al. 2004; Morales and Jones 2004; Garrett et al. 2006; Harrington et al. 2007).

A less predictable climate will cause uncertainty in decision making over the timing of control measures (Garrett et al. 2006). Control measures likely to be less reliable to suppress future virus epidemics include manipulation of sowing date; timing of sprays with oils, repellents, or pesticides; adjusting harvesting times; and planting upwind. Crops grown where the climate is too warm or under drought stress may tend to be physiologically weak to withstand infection. Including nonselective control methods will be particularly important when attempting to tackle emergence of unknown or little understood viruses. In such instances, “interim” IDM tactics that use all available “generic” information on related pathosystems and situations need to be deployed.

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