

Review

The Impact of Climate Factors on the Epidemiology and Management of *Potato virus Y*

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Abstract: Plant viruses give rise to potential loss to global crop production and have the potential to cause widespread damage. *Potato virus Y* (PVY) is a plant virus that belongs to the genus Potyvirus and the family Potyviridae and it is considered a major concern, particularly for solanaceous crops such as potatoes. PVY represents the largest cluster of plant viruses, encompassing over 111 recognized and 86 tentative species across 30 plant families. Its broad geographic distribution extends over the globe, with a notable prevalence in temperate and subtropical climates where potato cultivation is extensive. As a monopartite virus with a single strand of positive-sense RNA, PVY manifests diverse strains that induce varied symptoms in potato plants, presenting challenges in strain categorization. PVY transmission occurs through both vertical and horizontal pathways, with aphids being the most efficient vectors. Mechanical transmission and agricultural practices can also contribute to the spread of the virus, impacting the growth and physiological functions of plants. Climate factors are very important in shaping the dynamics of plant viral diseases in plants, with varied climatic conditions fostering the emergence of more virulent virus strains. Temperature, humidity and precipitation, directly and indirectly, influence vector abundance, virus replication and host susceptibility, thereby modulating PVY transmission dynamics. Managing PVY in potato crops requires a multifaceted approach due to its significant economic impact and complex transmission dynamics. Strategies include cultural methods, host-plant resistance, chemical interventions, vector control and emerging techniques like cryotherapy and nanomaterial applications. Understanding the profound impact of climate variables on the epidemiology and management of PVY underscores the urgent need for proactive measures. This study offers a comprehensive review of recent findings regarding the intricate relationship between climate variables such as temperature, CO₂ levels, light intensity, relative humidity, rainfall and wind velocity-and their significant influence on PVY infection severity and aphid vector population dynamics. Insights gleaned from this review will aid in formulating enhanced management strategies to combat the spread of this significant viral pathogen.

Keywords: Tomato, Temperature, CO₂, Light Intensity, Wind, Rainfall, Aphid

Introduction

The global population officially surpassed eight billion in November 2022 (Jain *et al.*, 2023). As the human population continues to rise, the imperative for more sustainable crop and food production methods becomes increasingly urgent, all while ensuring consistent crop productivity and quality. This poses ongoing challenges for scientists, agronomists and farmers worldwide. Plant viruses represent pivotal

pathogens that result in significant direct and indirect losses in crop production, thereby threatening global food safety and security (Rahman *et al.*, 2016; Hossain, 2024). Crop diseases caused by viruses are estimated to incur annual economic costs of nearly US\$60 billion (Manasseh *et al.*, 2023). The incidence of crop losses is thought to be notably higher in developing nations compared to developed countries.

The potato (*Solanum tuberosum* L.) is the fourth most crucial food source globally, following wheat, rice and

maize (Bajracharya and Sapkota, 2017). It is frequently affected by various viruses and diseases. *Potato virus Y* (PVY) is one of the diseases that makes growing potatoes difficult. PVY shows up as the most scientifically and economically significant plant virus, impacting solanaceous crops worldwide, including potatoes, peppers, tomatoes and tobacco (Scholthof *et al.*, 2011). PVY detrimentally affects potato tubers' yield and quality, leading to losses ranging from 10-90% (Valkonen *et al.*, 2017). Moreover, PVY can remain viable in potato tubers, contributing to increased initial inoculum levels in seed-producer fields for subsequent years' potato crops, thereby elevating the risk of rejection or downgrading of seed lots from affected fields (Flynn, 2013). So, the presence of PVY can result in shortages of certified seed and a reduction in farm revenue for seed growers.

PVY demonstrates extensive genetic variability and is known to manifest in various strains or variants (Gray *et al.*, 2010). The spread of infection and signs displayed may differ across these strains. These are also influenced by environmental factors, host cultivar and plant physiological stages (Nie *et al.*, 2012). The extent of losses is also very much affected by climatic conditions as extreme temperature, precipitation, RH, wind speed and rainfall significantly impact the severity of PVY. Additionally, the aphid population exhibits a positive correlation with climatic conditions, with early summer being more conducive than winter (Robert *et al.*, 2000). Hence, the weather plays a pivotal role in the initiation and progression of viral diseases, with climate variables uniquely influencing their interaction with hosts and vectors (Del Toro *et al.*, 2019).

Viral disease epidemics in suitable environmental territories are often extremely challenging to contain and prone to recurring outbreaks. Understanding the effects of climatic conditions on viral disease epidemics is critical for developing efficient plans for managing the vector and virus. Despite increasing studies, significant scientific gaps remain in our understanding of how various climate variables affect PVY, aphid vectors and their dynamics. Therefore, this review focuses on investigating the impact of climate variables, including temperature, CO₂ levels, light intensity, relative humidity, wind speed and rainfall, on the severity of PVY infection and the population dynamics of vectors. In addition to understanding the interplay between climatic factors and PVY dynamics, this study also addresses effective management strategies for mitigating the impact of PVY on potatoes and other susceptible crops.

Significance of *Potato virus Y*

Viruses of plants can completely damage thousands of different foods grown all over the world. The criteria determining these effects include the inoculum of a virus, features of the host plant (such as genotype and

developmental stage), number of vectors and weather circumstances (Anderson *et al.*, 2004). Potyviruses are responsible for causing reductions of up to 80% in tuber yield (Kreuze *et al.*, 2020). Considering its global reach and economic impact, PVY is among the top 10 plant viruses affecting crops (Lacomme *et al.*, 2017). The development of PVY isolates with characteristics of tuber necrosis was the primary factor in affecting tuber yield. The Potato Tuber Necrosis Ringspot Disease (PTNRD), caused by specific strains of PVY, inflicted substantial damage on potato crops in the 1980s and 1990s in the Middle East, particularly Lebanon, as well as in central European nations like Slovenia, Hungary and Germany. Numerous varieties of potatoes were infected, leading to a significant reduction in yield. The impact was substantial, affecting 18,000 hectares, which accounted for 60% of the potato crop, with over fifty percent of the tubers showing necrosis. PVY has been documented to cause significant damage to potato crops, leading to yield losses ranging from 10-100%. Additionally, tomato crops have been adversely affected, with reported yield reductions of 39-75% (Abbas *et al.*, 2020).

In the Brazilian potato production chain, PVY is a significant disease leading up to 80% of losses (Kreuze *et al.*, 2020). PVY infection affects different cultivars differentially. Some cultivars may be susceptible to PVY (symptoms emerge), tolerant (minimal yield losses may occur, but no symptoms appear), or resistant to PVY (Valkonen *et al.*, 2017). The vulnerability of several widely grown potato types, including Monalisa Igor, Hela, Lola and Rosalie, made up a significant portion of the farmed area in the affected countries (Le Romancer and Nedellec, 1997). A yield reduction of approximately 180 kg ha⁻¹, or total output loss of around \$18 ha⁻¹, was predicted for every 1% increase in PVY incidence in seed crops (Nolte *et al.*, 2004). In severe circumstances, plants that come in contact with a virus from seed tubers may show declines in tuber yield ranging from 10-80% (De Bokx, 1972). According to Valkonen (2007), an expected 30% prevalence of seed tubers infected with PVY in Spain is anticipated to result in a 10-15% loss in yield. In Finland, however, a study by Kurppa and Hassi (1989) indicated almost no yield losses in a crop with 10-20% PVY-infected seed potatoes. The economic consequences and potential food security implications make understanding and managing PVY crucial for sustainable agriculture and crop protection.

Geographical Distribution of *Potato virus Y*

The virus species' incidence, effects and geographic distribution are widely varied and mostly influenced by the presence of vectors, weather patterns and host crop/plant species (Lacomme and Jacquot, 2017). PVY exhibits a wide geographic distribution worldwide in different countries (Fig. 1). The PVY has been reported

in various regions of Argentina, China, Croatia, Ecuador, Egypt, Israel, Japan, Jordan, Kenya, Mexico, Pakistan, Portugal, Saudi Arabia, South Africa, South Korea, Switzerland, Syria, Tajikistan, Tanzania, United States, Zimbabwe (Table 1) (Tombion *et al.*, 2019; Wang *et al.*, 2012; Grbin *et al.*, 2023; Sivaprasad *et al.*, 2015; Elwan *et al.*, 2017; Avrahami-Moyal *et al.*, 2019; Chikh-Ali *et al.*, 2013; 2016a-b; 2019; Anfoka *et al.*, 2014; Quintero-Ferrer and Karasev, 2013; Abbas *et al.*, 2014; Serra *et al.*, 1997; Kisten *et al.*, 2016; Rigotti *et al.*, 2011; Alabi *et al.*, 2012; Chiunga and Valkonen, 2013; Crosslin *et al.*, 2002; Karavina *et al.*, 2016).

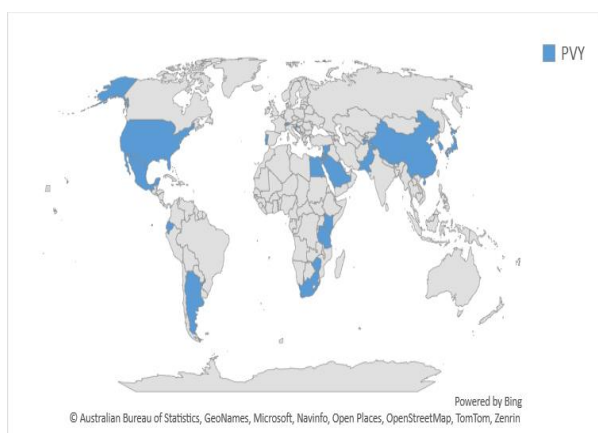


Fig. 1: Map showing the distribution of PVY across the globe

Table 1: Geographical distribution of PVY in various regions

Country	Crop	Reference
Argentina	<i>Calibrachoa</i>	Tombion <i>et al.</i> (2019)
China	<i>K. indica</i>	Wang <i>et al.</i> (2012)
Croatia	<i>Solanum lycopersicum</i>	Grbin <i>et al.</i> (2023)
Ecuador	<i>Solanum lycopersicum</i>	Sivaprasad <i>et al.</i> (2015)
Egypt	<i>Solanum tuberosum</i>	Elwan <i>et al.</i> (2017)
Israel	<i>Solanum tuberosum</i>	Avrahami-Moyal <i>et al.</i> (2019)
Japan	<i>Solanum tuberosum</i>	Chikh-Ali <i>et al.</i> (2019)
Jordan	<i>Solanum tuberosum</i>	Anfoka <i>et al.</i> (2014)
Kenya	<i>Solanum lycopersicum</i>	Chikh-Ali <i>et al.</i> (2016a)
Mexico	<i>Solanum tuberosum</i>	Quintero-Ferrer and Karasev (2013)
Pakistan	<i>Solanum tuberosum</i>	Abbas <i>et al.</i> (2014)
Portugal	<i>Solanum tuberosum</i>	Serra and Weidemann (1997)
Saudi Arabia	<i>Solanum tuberosum</i>	Chikh-Ali <i>et al.</i> (2016b)
South Africa	<i>Physalis peruviana L.</i>	Kisten <i>et al.</i> (2016)
South Korea	<i>Solanum tuberosum</i>	Chikh-Ali <i>et al.</i> (2019)
Switzerland	<i>Solanum tuberosum</i>	Rigotti <i>et al.</i> (2011)
Syria	<i>Solanum tuberosum</i>	Anfoka <i>et al.</i> (2014)
Tajikistan	<i>Solanum tuberosum</i>	Alabi <i>et al.</i> (2012)
Tanzania	<i>Solanum tuberosum</i>	Chiunga and Valkonen (2013)
United States	<i>Solanum tuberosum</i>	Crosslin <i>et al.</i> (2002)
Zimbabwe	<i>Capsicum annum L.</i>	Karavina <i>et al.</i> (2016)

General Characteristics of *Potato virus Y*

PVY was initially documented through Smith *et al.* (1931). PVY pertains under the genus Potyvirus and family Potyviridae, constituting the largest cluster of plant viruses encompassing 86 tentative species and 111 recognized species that affect more than 30 families of plants (Claude *et al.*, 2005). PVY is characterized as a monopartite virus, consisting of a single strand of positive-sense RNA (+ssRNA) with a length of approximately 9700 nucleotides, excluding the poly (A) tail (Abbas *et al.*, 2020). The PVY virion exhibits dimensions of approximately 730 nanometers in length (Delgado-Sanchez and Grogan, 1966) and a width of 11 nanometers (Varma *et al.*, 1968). Notably, the coat protein contributes significantly to the composition of Potyvirus virions, constituting approximately 95% of their mass (Hollings and Brunt, 1981). PVY infection is associated with the induction of non-crystalline amorphous inclusions in the cytoplasm of infected cells (Synková *et al.*, 2006). In the context of PVY infection, distinct inclusions known as "pinwheels" and "bundle-like" structures are typically observed (Shukla *et al.*, 1994). PVY "variants" can be categorized into at least 13 distinct subgroups, delineated through biological characteristics or phylogenetic analysis (Glais *et al.*, 2017; Gibbs *et al.*, 2017). PVY exhibits multiple strains that induce diverse symptoms in potato plant species. The extensive biological, serological and genetic variations among PVY isolates make categorizing them into distinct strains challenging. PVY is mainly classified into three different strains such as PVY^O, PVY^N and PVY^C. PVY^Z (Jones, 1990) and PVY^E (Kerlan *et al.*, 1999) are sometimes included in this group of historical strains. PVY^O is recognized as a common or ordinary strain with a global distribution (De Bokx and Huttinga, 1981). Despite being a molecular categorization, serotypes are only presently distinguished between PVY^O or PVY^N strains (Flynn, 2013). At least nine recombinant genomes have evolved from PVY^N and PVY^O (Hu *et al.*, 2009). PVY^{N:O}, PVY^{N:Wi} and PVY^{NTN} are the recombinant strain groups most frequently seen in potato production (Karasev and Gray, 2013). Regarding virus titer in infected plants, PVY^O demonstrated the highest ranking, followed by PVY^{NTN} and PVY^{N:O} across all three strains (Shrestha *et al.*, 2014) and PVY^O stands out as the most prevalent strain among the potato varieties (Haq *et al.*, 2016). Biological distinctions among PVY strains arise from the phenotypic responses observed in potato cultivars with specific hypersensitive HR resistance genes and the induction of necrotic symptoms in tobacco. Strain categories PVY^C, PVY^O and PVY^Z trigger HR phenotypes through hypersensitivity genes N^C, N^Y, or N^Z, respectively. In contrast, strain groups PVY^N and PVY^E can overcome all three hypersensitivity genes. PVY^N shows unique veinal necrosis in tobacco, while PVY^E differs in its elicited phenotypes (Kehoe and Jones, 2016; Jones and Vincent, 2018).

Symptomology of PVY

PVY spreads rapidly and affects mainly plants' leaves. Strong morphological and physiological changes are observed in virus-infected plants, including symptoms such as vein necrosis, leaf curling, and mosaic. These symptoms are associated with alterations in the structure and function of chloroplasts compared to healthy plants (Fig. 2) (Reinero and Beachy, 1989; Rahoutei *et al.*, 2000; Pompe-Novak *et al.*, 2001).

Discolored bands on the skin and necrotic tissue beneath them may extend into the tuber flesh, indicating signs of tuber necrosis (USDA, 2013). Depending on the cultivar, PVY^O symptoms in potatoes can range from mild to severe mosaic, necrosis of the leaves and stems, early leaf drop and occasionally early plant death (De Bokx and Huttinga, 1981; Nie *et al.*, 2012). Only a few isolates can cause potato tuber necrotic ringspot disease. Tobacco systemic mottling is caused by PVY^O (Loebenstein *et al.*, 2013). Certain varieties, such as shepody and russet Norkotah, can act as reservoirs for PVY, facilitating transmission by aphids because they are capable of displaying latent or symptomless foliar symptoms, even in plants with a substantial concentration of PVY (Draper *et al.*, 2002; Hamm *et al.*, 2010; Nie *et al.*, 2012). In numerous potato cultivars, the tobacco veinal necrosis strain PVY^N results in a mosaic ranging from almost symptomless to mild (Nie *et al.*, 2012). Depending on the cultivar infected, the majority of PVY^{NTN} isolates and some PVY^{N:O} isolates cause potato tuber necrosis disease (Piche *et al.*, 2004; Gray *et al.*, 2010; Nie *et al.*, 2012). In most potato cultivars, PVY^N typically results in relatively moderate leaf mottling, while in tobacco, it causes severe systemic veinal necrosis. Furthermore, hybrid genotypes like PVY^{N:O} and PVY^{NTN} can arise from mixed infections of common and necrotic strains, resulting in recombining genetic material (Lorenzen *et al.*, 2006). The symptoms of PVY^C and PVY^O strains in tobacco are comparable. Australia, India and certain regions of the United Kingdom and continental Europe are the major distribution areas (De Bokx and Huttinga, 1981). PVY^C appears in the leaf stipules of plants that carry the resistance gene Nc. Many cultivars of potatoes react hypersensitively to strains belonging to the PVY^C group (Calvert *et al.*, 1980).



Fig. 2: Typical PVY symptoms; (A) PVY infected potato plant; (b) healthy potato plant

Transmission of PVY

Plant viruses are obligatory parasites that need to spread to other plants in order to survive. Viral infections primarily transmit to plants through two pathways, e.g., vertical and horizontal pathways. Vertical transmission happens when the virus moves from contaminated planting material such as potato tubers to the growing plant and growing plants to tubers. Conversely, horizontal transmission occurs when a plant contacts the virus mechanically or via a vector, typically an insect or other animal. Both routes can lead to PVY infection in potatoes (Fig. 3). However, foliar symptoms of plants infected by vertical transmission are usually more severe than those infected through horizontal transmission (Lacomme *et al.*, 2017). PVY is transmitted mechanically through the use of contaminated instruments, such as by rubbing or coming into close contact with infected plants. As mechanical seed cutting can also disseminate PVY, it is important to sanitize equipment before utilizing it with various seed lots or types (Schramm *et al.*, 2011). Additionally, it can be transmitted intermittently by insect vectors. The viral infection rapidly begins and spreads within a few seconds following transmission by the vector (Burrows and Zitter, 2005). More than 65 aphid species, including potato-colonizing and non-colonizing species, are known to transmit PVY (Verbeek *et al.*, 2010). By aphid transmission, the maximum disease severity was 73.33% (Hussain, 1994). Studies have shown a relatively small number of particles present in the intracellular sap that the insect is probing (Powell, 2005). Through a competition system between infected and non-infectious PVY isolates, it was calculated that less than four PVY particles must be transmitted by an aphid for an infection to be effective and there were 0.5-3.2 virus particles per insect and per transmission for PVY in pepper plants (Moury *et al.*, 2007). In yellow traps, the Aphid appeared first at the end of October 1977, in mid-January 1978 and mid-December 1981 (Abbas *et al.*, 2020). In another research, the months of June and August had the highest aphid counts. The greatest number of insects was recorded in bug traps during the third week of August. The middle of August had the highest number of aphids captured on yellow traps and the highest likelihood of virus transmission during this month (Ahirwar and Pachaya, 2024). The effectiveness of aphid transmission varies between species. According to transmission assays, the aphids *Myzus persicae* and *Rhopalosiphum padi* are the most effective at transmitting the isolates of PVY^{NTN}, followed by the isolates of PVY^O and PVY^{N:O} (Mondal *et al.*, 2016).

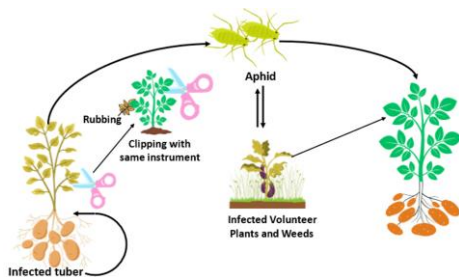


Fig. 3: Various modes of transmission of *Potato virus Y* in plants

According to Shrestha *et al.* (2014), plants infected mechanically with PVY^{N:O} exhibited greater mean tuber masses than plants infected with PVY^O or PVY^{NTN}, with non-substantially different tuber masses. This implies that the pattern of sensitivity of tuber mass to the three virus strains in mechanically infected plants differed from that observed in plants injected with aphids. Viral prevalence may also be impacted by the landscape's character, as natural enemies of the vector community may have an indirect effect. A decrease in species spillover may be the reason for the previously noted adverse association between landscape complexity and natural enemy abundance and diversity (Tschardtke *et al.*, 2012). Farms located in more complex landscapes showed minimal prevalence of PVY (*Potato virus Y*), whereas those in simpler landscapes had prevalences exceeding 30%. This shows that increasing landscape complexity, rather than cropland cover alone, may protect against PVY prevalence (Claflin *et al.*, 2017). In vertical transmission, a virus's infectious cycle in a plant host begins in one infected cell. PVY transmission will cause systemic infection of sink tissues above and below ground as it follows the source-sink partitioning of photo-assimilates throughout the plant. As a result, new tubers and other parts of plants will progressively get infected (Hull, 2002). PVY was shown to be four times more prevalent in a crop grown from seed potatoes in a field where plants exhibited symptoms of the disease compared to a crop where no symptomatic plants were observed (Fenton *et al.*, 2012). There is no evidence of PVY transfer by potato pollen or genuine seed (De Bokx and Huttinga, 1981). Weeds and volunteer plants can transmit PVY to healthy plants. For PVY to be effectively controlled in crops through the elimination of all inoculum sources (Jones *et al.*, 1996). In a crop, the capacity of aphids to transmit the disease and the host's vulnerability to infection play a role in the spread of PVY infection. Because older plants have physical barriers (such as hairs or waxes) that prevent insects from probing or feeding on them and spreading the virus. So, older plants frequently exhibit better resistance to infection than younger and more delicate plants. Stronger antiviral resistances are active against the transmitted viruses or volatile emissions, which repel insects and may also be responsible for resistance (Chung *et al.*, 2015; Fajinmi and Fajinmi, 2010).

Plant Physiological Changes Due to PVY

Virus-infected plants also display symptoms, possibly related to the activity or lack of plant hormones (Jameson *et al.*, 2000). The main causes of stunted plant growth rate in virus-infected plants are reduced activities of some photosynthetic enzymes, elevated levels of sugar or starch and impaired photosynthesis in virus-infected leaves with reduced Chlorophyll (Chl) content and maximum Chl fluorescence (Montalbini and Lupattelli, 1989; Funayama *et al.*, 1997; Osmond *et al.*, 1998; Funayama and Terashima; 1999). According to Synková *et al.* (2006), PVY infection greatly reduced the Photosynthetic rate (PN) in transgenic and shallow-rooted plants. In addition to stomata closure, other factors contributed to the reduction of photosynthetic rate, including a decline in ribulose-1,5-bisphosphate carboxylase/oxygenase activity, pigment contents in the chlorophyll and xanthophyll cycle and Photosystem II (PS II) activity. High irradiance treatment exacerbated the detrimental effects on PS II when infected with PVY. Lower levels of chlorophyll were noted in infected plants with symptoms and changes in chloroplast size and structure (Pompe-Novak *et al.*, 2001). When tobacco plants were infected with PVY, viral protein increased significantly in control plants but decreased in transgenic plants. Comparing transgenic plants to control plants, those with increased endogenous Cytokinin (CK) levels displayed reduced viral protein buildup and fewer PVY symptoms. Transgenic plants with PVY infection accumulated more xanthophyll, but healthy plants underwent a reduction in xanthophylls when exposed to strong light (Synková *et al.*, 2006). These findings point to the methionine cycle's primary transmethylation role as the determining factor of susceptibility or resistance (Spechenkova *et al.*, 2021). PVY^{NTN} infection had minimal effect on intercellular CO₂ concentration but drastically decreased net photosynthetic rate and stomatal conductance. According to Zhou *et al.* (2004), PVY^{NTN} mostly inhibited photosynthesis by interfering with the Calvin cycle's enzymatic activities, which led to a down-regulation of electron transport. A variety of potato cultivars with differing responses to PVY^{NTN} infection exhibited distinct activity of soluble, ionically and covalently bound peroxidases (Milavec *et al.*, 2008). Changes in the cytokinin level in inoculated leaves were seen in the susceptible interaction between potato and PVY^{NTN} (Dermastia, 1995).

Effect of Climatic Factors on PVY

Climate variables such as temperature, CO₂, light intensity, relative humidity, wind speed and rainfall significantly impact the severity of PVY and the population of aphids (Fig. 4). These factors play a crucial role in accelerating viral replication, increasing the risk of infection and facilitating virus transmission.

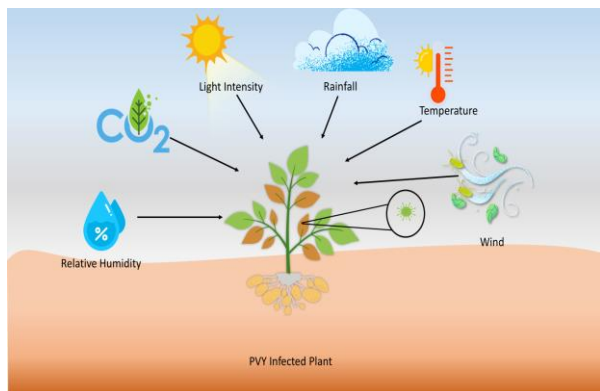


Fig. 4: Effect of different climatic factors on *Potato virus Y*

Effect of Temperature on PVY

Global average temperatures are expected to rise by up to 4.6°C by the year 2100, according to climate change models. The higher latitude regions are warming more quickly than lower latitude ones (Van Vuuren *et al.*, 2008). The direct effects of climate change, such as rising temperatures and the indirect effects, such as the quantity and activity of transmission vectors, are expected to significantly impact the dynamics of plant virus epidemics and the losses they generate (Jones, 2009). According to Del Toro *et al.* (2015), temperature is an environmental factor that influences the interaction of various RNA viruses with their hosts in different ways. Lower temperatures resulted in a more efficient hypersensitive resistance to PVY in potatoes (Valkonen, 1997). It was found that PVY isolates could inhibit the antiviral silencing defense even at relatively high temperatures, such as 30°C when they infected the solanaceous host *Nicotiana benthamiana*. Potato plants can experience widespread PVY infections between 16°C and 32°C. As the temperature increases, the duration of the infection decreases (Choi *et al.*, 2017). Another study demonstrated that the incidence of PVY infection in *Nicotiana benthamiana* plants was positively correlated with higher plant temperatures and the infection rates declined afterwards. The accumulation of PVY Coat Proteins (CPs) was lower at 10 or 15°C compared to 20°C during the early stages of infection. However, accumulation increased steadily throughout the infection period (Chung *et al.*, 2016). Symptoms of PVY in potato plants are more pronounced at higher temperatures (22/17 and 26/2°C) compared to lower temperatures (14/9 and 18/12°C) because decreased temperatures can have a detrimental impact on the spread of PVY and the development of symptoms. This could potentially explain why symptoms in potato plants infected with PVY^N (*Potato virus Y* Necrotic Strain) are frequently noticed towards the end of the growing season (De Bokx and Piron, 1977). The maximum regression value ($r = 0.90$) of the *Potato virus Y* disease trend incidence was recorded at

15-31°C maximum and 5-13°C minimum temperature. PVY exhibits strong expression in another experiment conducted between 24-28 and 9-12°C (Qamar *et al.*, 2016). Systemic PVY infection in potatoes is promoted at high temperatures. The high temperature promoted the development and expansion of necrotic spots on resistant cultivars carrying the Rychc gene (Ohki *et al.*, 2018). Temperatures affect the resistance reaction to *Potato virus Y* (PVY) strains in potato cultivars carrying the resistance gene Rychc. At 22°C, only a few small necrotic spots developed on inoculated leaves; however, at 28°C, distinct necrotic spots developed on inoculated leaves. Systemic infection and virus titers in resistant cultivars at 28°C were lower than in susceptible cultivars. Graft inoculation under high summer temperatures resulted in necrosis on leaves and stems, but PVY was barely detected in potato leaves carrying Rychc. Seedlings grown in a greenhouse at temperatures exceeding 30°C did not show PVY infection in cultivars carrying Rychc. These results indicate that Rychc confers extreme resistance to PVY strains occurring in Japan. On the other hand, the Ny-1 gene induces the Hypersensitive Response (HR) and restricts all PVY strains to the infection site at 22°C. Therefore, plants had no HR and were systemically infected at 28°C (Ohki *et al.*, 2018). Proteomic analysis showed that key enzymes of the Methionine Cycle (MTC) and MTC-related folate cycle were down-regulated at the protein level by PVY infection at the higher temperature of 28°C. The temperature-sensitive responses of potato plants to PVY indicate that the methionine cycle plays a role in plant-virus interactions (Spechenkova *et al.*, 2021). Elevated temperature can compromise the expression of Salicylic Acid (SA) markers in the sensitive cultivar Chicago, leading to increased susceptibility to *Potato virus Y* (PVY) infection. In contrast, the resistant cultivar Gala shows minimal temperature impact on resistance and suppression of the SA pathway, indicating a lower susceptibility to PVY (Makarova *et al.*, 2018). Heat waves of about 30°C can be harmful to aphid populations (Gillespie *et al.*, 2002; Jeffs and Leather, 2014). High temperatures can have a negative impact on the longevity and fecundity of adult females (Chiu *et al.*, 2012). The ideal temperature for the green peach aphid to multiply in population is 26.7°C.

Effect of CO₂ on PVY

Viruses have the capability to infect plants and depend on the physiological circumstances influenced by external elements, such as temperature or CO₂ levels, within the host. These conditions lead to alterations in the ratios of carbon to nitrogen, the rate and form of plant growth and the molecular pathways that regulate responses to both external living and non-living elements (Huang *et al.*, 2012; Matros *et al.*, 2006; Prasch and Sonnewald, 2013; Pritchard *et al.*, 1999; Zhang *et al.*, 2015). The impact of CO₂ as an environmental factor on viruses is complex and

gaining more recognition. Fluctuations in atmospheric Carbon dioxide (CO₂) levels can affect the interactions between viruses and their hosts, the dynamics of virus transmission and the stability of viral particles. eCO₂ increased plant above-ground biomass and did not significantly influence Total Non-structural Carbohydrates (TNCs) or nitrogen content. On the other hand, PVY infection adversely affected biomass, the TNCs and nitrogen content. Again, eCO₂ also increased soluble protein content, while PVY infection reduced chlorophyll content. The intercellular CO₂ concentration did not change upon infection with PVY^{NTN}. However, this infection markedly decreased the net photosynthetic rate and stomatal conductance (Zhou *et al.* 2004). Inoculation with *Potato virus Y* (PVY) demonstrated that elevated CO₂ levels reduced levels of viral coat protein in leaves, which indicated a lower virus spread. The accumulation of phenylpropanoids, such as CGA and coumarins, may contribute to the earlier confinement of the virus at high CO₂ (Matros *et al.*, 2006). According to Ye *et al.* (2010), elevated CO₂ (eCO₂) conditions have been found to alleviate damage from *Potato virus Y* (PVY) infection in tobacco plants. Interaction between eCO₂ and PVY infection was observed regarding free amino acid and nicotine content. Changes in peroxidase (POD) activity indicate that elevated CO₂ levels impair plant growth by reducing their resistance to the virus. The systemic titers of a PVY isolate in *Nicotiana benthamiana* plants were lower at elevated temperatures and CO₂ levels [30°C and 970 parts-per-million (ppm)], respectively, compared to typical circumstances (25°C, approximately 405 ppm CO₂) (Del Toro *et al.*, 2019). Overall, the results suggest that plants grown under eCO₂ have alleviated damage from PVY infection or eCO₂ delays the viral spread to some extent. Reust and Gugerli (1984) conducted a study in which dormant potato tubers were treated to induce sprouting and increase virus concentration. Tubers subjected to 40 O₂ and 20% CO₂ for 7 days sprouted nearly as effectively as those treated with rindite. Furthermore, O₂ with CO₂ treatments resulted in increased viral content in tubers, comparable to rindite-treated tubers, after 40 days.

This suggests that O₂ and CO₂-enriched atmospheres can effectively break tuber dormancy, facilitating the detection of PVY in tuber extracts due to the higher virus concentration. Elevated ambient CO₂ levels also impact several parameters related to aphid infestation of plants, including relative growth rate, colony growth rate, fecundity, development time, feeding efficiency, aphid colonization, susceptibility of host plant cultivars to aphids and interactions between aphids and plants (Hughes and Bazzaz, 2001; Ryalls *et al.*, 2015). Whereas, in another study showed that the atmospheric CO₂ concentrations did not directly impact the ability of aphids to spread PVY in the short term. Elevated CO₂ levels may indirectly affect the dynamics of virus transmission by influencing plant

defenses or aphid feeding behavior, ultimately resulting in more efficient viral transmission from the vector to the host plant (Bosquee *et al.*, 2018).

Effect of Relative Humidity on PVY

Relative humidity had a significant correlation with PVY disease severity in potato plants. Higher relative humidity levels were associated with increased disease severity of PVY (Qamar *et al.*, 2016). The range of 50-60% Relative Humidity (RH) was favorable for the development of PVY and PLRV infections (Iqbal *et al.*, 2023). Another study indicates that relative humidity of 78-84% increased and significantly correlated with PVY disease development, as indicated by higher *r* values (0.98) (Qamar *et al.*, 2016). The highest prevalence of the disease was observed at relative humidity levels ranging from 80-86%, alongside minimum temperatures of 11-13°C and maximum temperatures of 25-28°C, coinciding with pan evaporation rates of 2-2.9 mm (Abbas *et al.*, 2020). Haq *et al.* (2016) found in another investigation that the relative humidity of 82-83% is favorable to the severity of the disease. The transmission of PVY was increased by 30-35% when high temperature (25-30°C) and high relative humidity (80-90%) were combined. Even at 25°C or 30°C, transmission rates of PVY were roughly 50% lower if relative humidity was kept at 50% throughout the pre- or post-inoculation stages (Singh *et al.*, 1988). The whitefly population, a vector for PVY, was found to increase with relative humidity up to a certain level, after which the population decreased (Rahman *et al.*, 2009). Relative humidity may indirectly influence PVY incidence through its impact on aphid populations (Kumara *et al.*, 2017). However, further research is required to establish the direct relationship between relative humidity and PVY incidence.

Effect of Light Intensity on PVY

The intensity of light may indeed influence PVY symptoms. Although it is challenging to definitively state the impact of light intensity on plant viruses. Continuous fluorescent light (4000 lux) did not alter the rate of PVY transmission (Singh *et al.*, 1988). In comparison to high light intensity (100-200 uE/m²/sec), the low light intensity (270-330 uE/m²/sec) considerably exacerbated the severity of mosaic disease induced by PVY infection in potato cultivars Shepody and Red Lasoda (Draper *et al.*, 2002). Furthermore, light intensity also influences vector behavior. Aphids are attracted to shorter wavelength light, compelling them to ascend into the sky (Kennedy and Booth, 1963).

Effect of Rainfall and Wind Velocity on PVY

Rainfall indirectly affects PVY, while the direct impact of wind velocity on *Potato virus Y* (PVY) is limited. Establishing a correlation between rainfall and PVY

incidence is challenging due to variables such as significantly different sample collection methods across seasons. PVY is primarily transmitted through infected seed potatoes and aphids. Rain is a possible deposition route for aphids travelling on low-level jet streams (Flynn, 2013). However, Aphid populations on crops are eliminated by extreme weather events, particularly powerful winds and intense rainstorms (Jones, 1990; Ba-Angood and Stewart, 1980).

Management of PVY

PVY has inflicted enormous damage during the last few years. Managing PVY in potato crops is a continuous problem because of the non-persistent form of PVY transmission and the field expansion of seed potato tubers across several generations, which increases the probability of primary and secondary plant infections by PVY (Dupuis *et al.*, 2017a). Environmental factors have a great impact on PVY. As a result, it is necessary to handle viruses using environmentally friendly methods. Cultural, host-plant resistance, chemical, vector control, and Cryotherapy, using nano clay, are effective ways of controlling PVY (Fig. 5).

Cultural Methods

Cultural methods of disease control encompass a variety of practices aimed at managing plant diseases through manipulation of the growing environment and cultural practices. Planting virus-free seed potatoes or having a very low incidence of PVY tuber infection can minimize the number of inoculum sources within a crop and lower the danger of PVY spreading (Kerlan *et al.*, 1987; Rolot, 2005). A study conducted in Switzerland found that raising the altitude from 400-800 m reduced potato infection by 57%. This reduction was primarily due to the cooler average temperatures at higher altitudes (Steinger *et al.*, 2014). To lessen the chance of PVY spreading, planting and haulm removal should be done sooner rather than later (Dupuis *et al.*, 2017b). The crop's exposure to aphid flights will be shortened by early haulm destruction, lowering the crop's risk of infection (Basky and Almási, 2005; Kerlan *et al.*, 1987; Steinger *et al.*, 2014). Efficiently controlling PVY in crops requires the essential step of eliminating all sources of inoculum. Inoculum sources may be derived from weeds, unhealthy seed tubers, volunteer plants and potato plants produced from tubers or tuber segments left in the ground following the harvest of a previous crop (Jones *et al.*, 1996). Although rouging effectively reduces PVY spread. The degree of the effect varies, ranging from 0-20% (Broadbent *et al.*, 1950). For better results, border crops should only be planted with plant species resistant to PVY. Additionally, border plants can physically impede aphid flight by acting as a barrier (Simons, 1957).

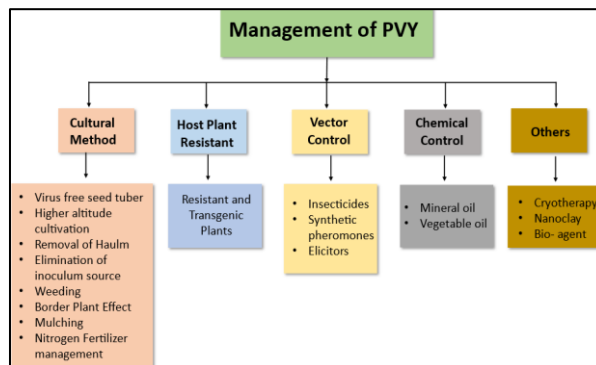


Fig. 5: The common practices used for managing *Potato virus Y* in potatoes

Furthermore, the spread of PVY can be effectively controlled by straw mulching (Udo *et al.*, 2004; Saucke and Doring, 2004; Kirchner *et al.*, 2014; Dupuis *et al.*, 2014). Various potato cultivars produced higher yields when mulched because it delayed the progression of PVY and PLRV infections (Iqbal *et al.*, 2023). Nitrogen fertilizer also has an impact on enhancing yield. However, Whitworth *et al.* (2006) revealed a significant yield reduction between PVY-negative and PVY-positive plots across all potato cultivars, irrespective of nitrogen levels. This suggests that although increased nitrogen affected total yield, it did not significantly mitigate the yield reduction caused by PVY infection.

Host-Plant Resistance

Host-plant resistance refers to plants' inherent ability to withstand or repel attacks from pests, pathogens, or other stressors. Host plant resistance offers an effective solution to pest problems, reducing the need for pesticides and lowering environmental contamination. Plants have evolved various defense mechanisms against phytopathogen attacks, which can be leveraged to create resistant cultivars (Sagredo *et al.*, 2009). Lawson *et al.* (1990) utilized the coat protein genes of PVX and PVY to transform a significant commercial potato cultivar known as Russet Burbank. Through mechanical inoculation, transgenic plants expressing both CP genes demonstrated resistance against PVX and PVY infection. When viruliferous green peach aphids were added to PVY, one line also showed resistance. In non-RYSC3 gene carrier plants, a substantial portion (22.5%) exhibited resistance, suggesting the presence of other R genes, such as hypersensitivity, affecting test efficacy. The Ryadg gene detection demonstrated high effectiveness (99.7%) in both parents and segregating progenies, underscoring its suitability as a marker for selecting PVY-resistant genotypes in potato breeding programs (Sagredo *et al.*, 2009). Three tetraploid somatic hybrid lines resulting from the fusion of protoplasts from a diploid potato, *Solanum tuberosum* cultivar BF15 and the wild potato species *Solanum berthaultii* were assessed for their

susceptibility to various soil-borne pathogens, specifically, *Fusarium solani*, *Pythium aphanidermatum*, *Rhizoctonia solani* and PVY. These hybrids exhibited enhanced resistance to the ordinary strain of *Potato virus Y* (PVY) in greenhouse conditions (Nouri-Ellouz *et al.*, 2016).

Chemical Control

Viruses are intracellular parasites and it is impossible to directly prevent their damage to crops through chemical interventions. However, several substances such as Ningnanmycin (NNM), cytosinepeptidemycin, Salicylic Acid (SA), flavonoids and terpenes show the potential to stop viral replication. In the net-house, (Van Chin *et al.*, 2022) observed that after 21 days of infection, dosing with Ditacin 8SL (NNM) three to six times prior to plant infection significantly reduced the infection of *Potato virus Y* (PVY) by 24-33%, *Tobacco Mosaic Virus* (TMV) by 28.9-50% and *Cucumber Mosaic Virus* (CMV) by 42.6-60%. After 21 days of inoculation in the net-house, Sat 4SL (Cytosinepeptidemycin) demonstrated effective control of TMV by 23.7-31.6%, CMV by 20.0-24.4% and PVY by 28.9-35.6%. In the field, NNM showed 93.5% effective control against PVY, 60.5% against CMV, 52.1% against TNRV and 100% effective control against TMV. Similarly, Sat 4SL demonstrated successful suppression of TMV (70.9%), CMV (58.3%), PVY (96.4%) and TNRV (36.9%). It has been suggested that one way to stop PVY from spreading is to spray oil on potato plants (Boiteau *et al.*, 2009; Bell, 1989; Boiteau and Wood, 1982; Wijs, 1980; Dupuis *et al.*, 2014; Hansen and Nielsen, 2012; Martín-López *et al.*, 2006; Steinger *et al.*, 2014). The exact mechanism of action of oils is not fully understood. It has been suggested that oil on aphid mouthparts might decrease aphids' acquisition and retention of PVY. Oil could potentially hinder the binding of virus particles to the stylet and reduce the duration of virus retention in the stylets (Bradley, 1963; Boquel *et al.*, 2013; Loebenstein *et al.*, 2001; Powell, 1992; Wróbel, 2009). Vegetable oil was shown to be less effective than mineral oil (Martín-López *et al.*, 2006; Rolot, 2005; Wróbel, 2012) and mineral oil has been observed to diminish virus replication and accumulation in inoculated plants, possibly by activating defense mechanisms within the plant (Loebenstein *et al.*, 2001; Peters and Lebbink, 1973; Al-Daoud *et al.*, 2014).

Vector Control

Vector control is a crucial strategy in mitigating the spread of viruses, particularly those transmitted by insects. Different kinds of pesticides may potentially impede the spread of viruses in three ways: Either by discouraging aphids (deltamethrin) (Rice *et al.*, 1983), modifying feeding habits with thiamethoxam, imidacloprid, pymetrozine and fluticamid (Morita *et al.*, 2007; Cho *et al.*, 2011; Boquel *et al.*, 2013) and limiting the mobility of an aphid (aldicarb) (Boiteau *et al.*, 1985).

In contrast, insecticides have a low effect on virus epidemiology, as the aphids often transmit PVY before they are killed (Boquel *et al.*, 2015). Insecticides such as pyrethroids can reduce PVY transmission under controlled conditions and have a near-instantaneous "knockdown" effect (Perring *et al.*, 1999; Gibson *et al.*, 1982; Collar *et al.*, 1997). (E)- β Farnesene (E β F) acts as the primary alarm pheromone (Zhang *et al.*, 1997), displaying repellent properties against aphid colonies and exerting influence on their development and fecundity (Gibson and Cayley, 1984). Laboratory studies have shown that E β F inhibits the acquisition and subsequent inoculation of PVY by *Myzus persicae* (Sulzer) (Gibson and Cayley, 1984). However, investigations carried out using tobacco plantlets and wingless aphids (*Myzus persicae* (Sulzer) and *Macrosiphum euphorbiae* (Thomas)) demonstrated that when exposed to E β F, there was an observed increase in the spread of PVY (Lin *et al.*, 2016). This may suggest that there was an enhanced movement of wingless aphids across plants. Apterous aphids can move between plants by walking on the soil surface, even without overlapping crop canopy (Alyokhin and Sewell, 2003; Narayandas and Alyokhin, 2006). Tomato leaves were treated with acibenzolar-S-methyl (Bion®), a functional analogue of Salicylic Acid (SA), as an elicitor. Subsequently, the leaves were inoculated with PVY. Treatment with BION alone provided protection against PVY, ranging from 72-86%. When additional elicitors were introduced, the results varied from 46-92% (Petrov and Andonova, 2012). Another study showed that Bion® was also evaluated in a field trial to prevent the spread of PVY in potatoes. The results showed a considerable reduction in PVY transmission, albeit a very small one at 14% (Dupuis *et al.*, 2014). PVY can be stopped from spreading using mechanical barriers, such as barrier crops and polythene sheeting. These are quick fixes for managing PVY and its vector (Abbas *et al.*, 2020).

Other Methods

There are other different methods of management PVY. Cryotherapy treatments have effectively eliminated *Potato virus Y* (PVY), including encapsulation-dehydration, encapsulation-vitrification and droplet, with virus-free plantlet frequencies ranging from 91-95% (Yi *et al.*, 2014). Nanomaterials can also manage PVY. Plant viral infections could be effectively and ecologically managed by using foliar sprays of nano clay against PVY infection (Aseel *et al.*, 2022). There are several potential uses for microbial secondary metabolites produced by bacteria in managing plant diseases. *Pseudomonas fluorescens*, *Rhodotorula* sp. and fermented neem extract were tested by Al-Ani *et al.* (2013) to determine their efficacy in protecting potato plants from the development of *Potato virus Y* disease in a field setting. The results demonstrated that employing a bio-agent to induce

systemic resistance is a viable alternative to insecticides for controlling *Potato virus Y* in potatoes. Treatments with *Klebsiella oxytoca* and biochar reduced the disease severity and concentration of PVY, while treatments with tobacco and potato plants in greenhouses showed a considerable increase in growth (Elsharkawy *et al.*, 2022). The fermentation filtrate of the *Streptomyces* SN40 successfully suppressed the systemic infection of the *Nicotiana benthamiana* by *Potato virus Y* (PVY) (Shu *et al.*, 2024).

Challenges and Future Prospects

One of the foremost challenges is the alteration of traditional pest and vector distribution patterns. Climate change poses significant challenges to the management of *Potato virus Y*, but there are also promising prospects for developing sustainable and resilient strategies. Future study in this field will be essential for ensuring sustainable, resilient and economically successful potato production in all potato-growing locations around the globe. This includes the development, adaption and use of integrated pest control. Emphasis should be placed on developing and applying biological techniques to manage pests. This will lessen the need for pesticides and lower the possibility that insect populations may become resistant to them (Kroschel *et al.*, 2020). Additionally, there is an increasing need for innovative technologies that enable the fast multiplication of healthy plants under regulated settings to produce high-quality seeds at a reasonable price (Kreuze *et al.*, 2020). Breeding for pest-resistant cultivars is typically one of the most cost-effective methods of disease management, even though it takes time. It is the first line of defense against viruses and other plant diseases (Neuenschwander *et al.*, 2023). The potential for diploid potato breeding and the use of more effective molecular markers might alter this in the future (Taylor, 2018). Long-term control of PVY can be achieved by genetically engineered resistance to field PVY isolates, as new strains lead to resistance breakdown regulated by R genes (Naveed *et al.*, 2017). Furthermore, climate-smart agricultural practices, such as crop rotation, diversification and agroforestry, can contribute to building resilient agroecosystems that are less susceptible to PVY outbreaks.

Conclusion

Viruses can cause significant diseases that threaten the sustainability of the world's food supply by inducing substantial direct and indirect losses in crop productivity. PVY is a primary obstacle in cultivating potatoes and other solanaceous crops, impacting yield and quality. Researchers, agronomists and farmers worldwide grapple with persistent challenges driven by

the expanding human population and the imperative to balance food production with sustainable practices, all while maintaining crop productivity and quality. Climatic elements such as temperature, CO₂ levels, humidity and precipitation play crucial roles in shaping the epidemiology of PVY viruses, influencing their transmission, replication and spread. Effectively managing and mitigating the impact of PVY necessitates a comprehensive understanding of these climatic factors. Therefore, climate-based management should be integrated into broader approaches, considering various factors that influence the spread and impact of PVY. Moreover, local conditions and specific potato varieties should be carefully considered when formulating management strategies.

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Author's Contributions

Mahabuba Mostafa: Drafted the manuscript, implemented the research, collected data and performed data analysis.

Md. Motaher Hossain: Conceived the study, secured funding, designed the research and reviewed the manuscript.

Ethics

This article is original and contains unpublished material. The corresponding author confirms that all co-authors have reviewed and approved the manuscript. Additionally, there are no ethical issues associated with this publication.

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