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REVIEW

Potato apical leaf curl disease: current status and perspectives on a disease caused by tomato leaf curl New Delhi virus

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Abstract

Potato apical leaf curl disease (PALCD) caused by a unique bipartite virus [tomato leaf curl New Delhi virus (ToLCNDV)] has emerged as a global threat. With the inception of ToLCNDV in 1995, it was causing curling/leaf mosaics in tomato, brinjal, chili, okra, papaya, cucurbits, etc., but under the changing climate, overlapping planting and boost-up in *Bemisia tabaci* populations, it shifted on potato crops. The first observation of PALCD as leaf curling/stunting of the potato plant was recorded in 1999 from northern India, and now it is spreading at an alarming rate in India. Recent outbreaks of ToLCNDV on various solanaceous, cucurbit crops, and weeds in other countries as well as the exchange of genetic and planting material of potato between the borders have made it a potential threat to potato production worldwide. To mitigate this disease, no antiviral products as well as resistant cultivars are known yet except Kufri Bahar; only planting of the healthy seed potato is the most appropriate method in the practice. The management of the disease mainly depends on diagnostics, control of insect vectors, rouging, and seed certification. These preventive measures are not enough to fulfill the food demand of the increasing population, and therefore, some concrete alternatives should be explored. In this context, the development of resistant varieties through conventional/molecular breeding or the use of advanced techniques like genome editing to edit susceptibility genes could be the future approach to combat the disease. This review highlights the current status of the pathogen and its genome, origin, evolution, and diversity, virus-vector relationship, disease symptoms, diagnostics, and management strategies.

Keywords Potato · Geminivirus · Whitefly · Detection · Leaf curl · Diagnostic · Management

Introduction

Potato (*Solanum tuberosum* L.) is a very important agricultural commodity that is consumed by the majority of populations across the world. It is considered as the most prominent accessible and economic crop after wheat and rice. A rapidly growing population and increasing hunger rates make potatoes a critical crop in ensuring food security. Globally, potato production is about 374 million metric tons, the outcome of greater than 4,500 varieties of potatoes. India is second in terms of total production after China and produces around 52.59 million metric tons of potatoes cultivated on a 2.18 million ha area with average productivity of 24.08 tons/ha (FAOSTAT 2019). The demand for potatoes will almost double by 2030 (Scott et al. 2019). In India, the potato crop is mainly grown in Uttar Pradesh, West Bengal, Bihar, Gujarat, Madhya Pradesh, Punjab, and Assam states of the country (Singh and Sharma 2018; Jeevalatha et al. 2018; Kumar et al. 2020). The sub-tropicalization of potatoes has resulted in its cultivation in diversified agro-climatic conditions that range from snowline to sea level (Kumar et al. 2019). However, when a crop is grown in diverse agro climates it faces severe biotic and abiotic stresses and potato is no exception (Tiwari et al. 2020). There are many biotic factors responsible for yield losses in potatoes, but viruses

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are a major concern. More than 50 viruses are reported worldwide to infect potatoes with variation in the intensity of yield losses (Kreuze et al. 2020; Kumar et al. 2020). In India, potato virus Y (PVY), potato leafroll virus (PLRV), potato virus X (PVX), potato virus S (PVS), potato virus A (PVA), and potato virus M (PVM) cause yield reduction up to 10–30% depending upon the intensity and vector pressure (Khurana and Singh 2003; Khurana 2004; Kaushal et al. 2007; Gawande et al. 2011; Kumar et al. 2017, 2020; Fox et al. 2017). During the year 1999, severe leaf curling on potato crop was observed in the northern part of India which quickly spread among almost all potato growing areas of the country. In the year 2001, the association of a begomovirus with this disease was proved by Garg et al. (2001) with the use of immune electron microscopy and named as potato apical leaf curl disease (PALCD). Later, the cause of this disease was confirmed as a variant of tomato leaf curl New Delhi virus (ToLCNDV) by Usharani et al. 2003. Since then, the incidence of this virus has immensely increased year by year and it has captured the top position in Indian potato viruses during the last two decades (Fig. 1). In Indo-Gangetic plains, the disease incidence is 40–100% which incurs heavy yield losses in potatoes (Lakra 2002; Venkatasalam et al. 2011). Up to 40% incidence of PALCD was reported from West Bengal (Saha et al. 2014). The yield losses were observed up to 60.8% with a significant reduction in size and number of tubers per plant in most prominent potato cultivars, i.e., Kufri Pukhraj and Kufri Khyati in India (Lakra 2003; Chandel et al. 2010). The numerous data on PALCD incidence have been documented and available in several published annual reports and research literature (Garg et al. 2001; Lakra 2002; Usharani et al. 2003; Jeevalatha et al. 2013, 2018; Saha et al. 2014; Kumar et al. 2020). The main factor behind the exponential increase in virus infection is a consistent rise in the population of whitefly (*Bemisia tabaci*), an efficient transmission vector of ToLCNDV (Chandel et al. 2010; Lakra 2010). Due to early planting, the regular exposure of potato crops to high temperatures leads to the buildup of a high population of whitefly which is one of the main reasons for the rapid outbreak of PALCD in India. This review of PALCD analyses the past and present research activities. We address the following topics: causal organism and its genome organization, the origin, evolution, and diversity of ToLCNDV and its vector (*B. tabaci*), vector transmission studies, symptomatology, diagnostics, and management strategies, etc.

Causal organism and its genome

The PALCD was first reported in the year 2001 from India, and the association of begomovirus as the causal organism of this disease was proved by Garg et al (2001). Within three years of its inception, based on the nucleotide sequence of one isolate of the associated virus from potato, this virus was reported as a new variant of a bipartite ToLCNDV (Usharani et al. 2003, 2004a, b). ToLCNDV, the causal agent of PALCD is a member of the *Geminiviridae* family of genus *Begomovirus*. It consists of two circular ssDNA components, named DNA-A and DNA-B of 2.7 kb and 2.6 kb, respectively (Fig. 2) (Jeevalatha et al. 2017a). DNA-A can replicate autonomously, while DNA-B is dependent on DNA-A for its replication and it is required for systemic infection and symptoms expression, nuclear localization, and systemic movement (Yadava et al. 2010; Nash et al. 2011).

In a phylogenetic analysis, the complete genomes of 12 representative ToLCNDV potato isolates were compared with selected ToLCNDV isolates from different crops and

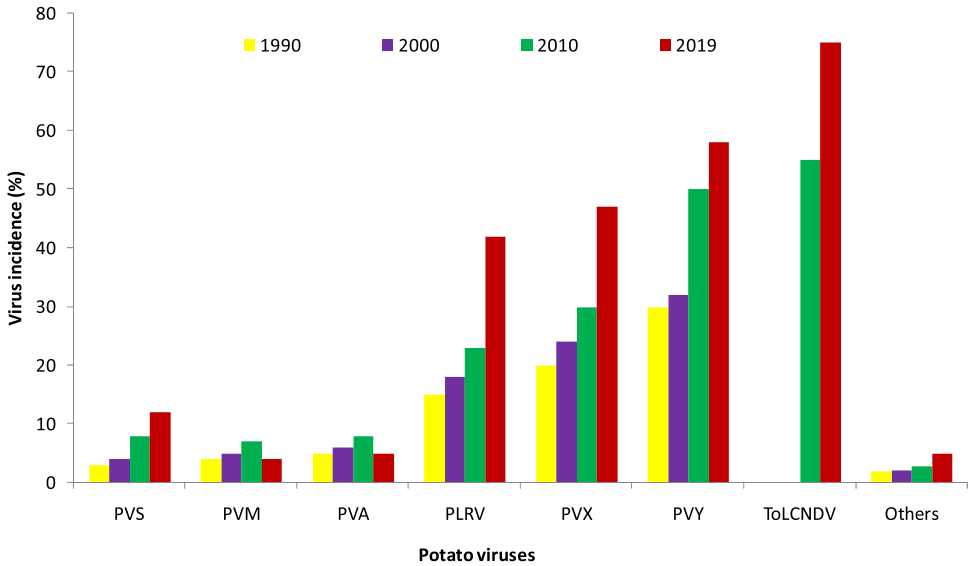


Fig. 1 Prevalence of ToLCNDV over other mosaic and leaf roll viruses during the past three decades. Modified and adopted from Singh et al. (2014) and based on data available in annual reports of last 29 years (All India Coordinated Research project on potato (AICRP-potato), Shimla, India and ICAR-Central Potato Research Institute (ICAR-CPRI), Shimla, India). Potato virus Y (PVY), potato leafroll virus (PLRV), potato virus X (PVX), potato virus S (PVS), potato virus A (PVA), potato virus M (PVM) and tomato leaf curl New Delhi virus (ToLCNDV)

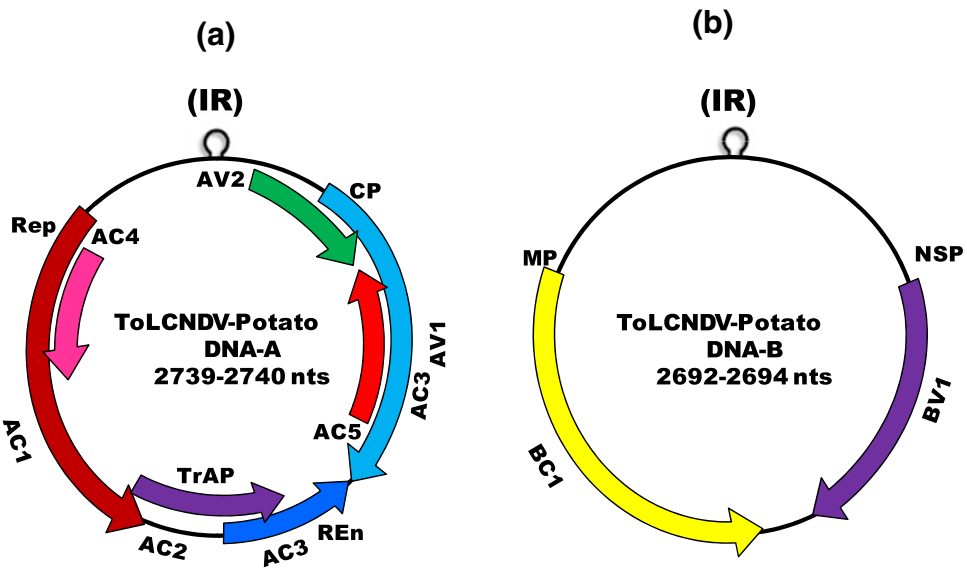
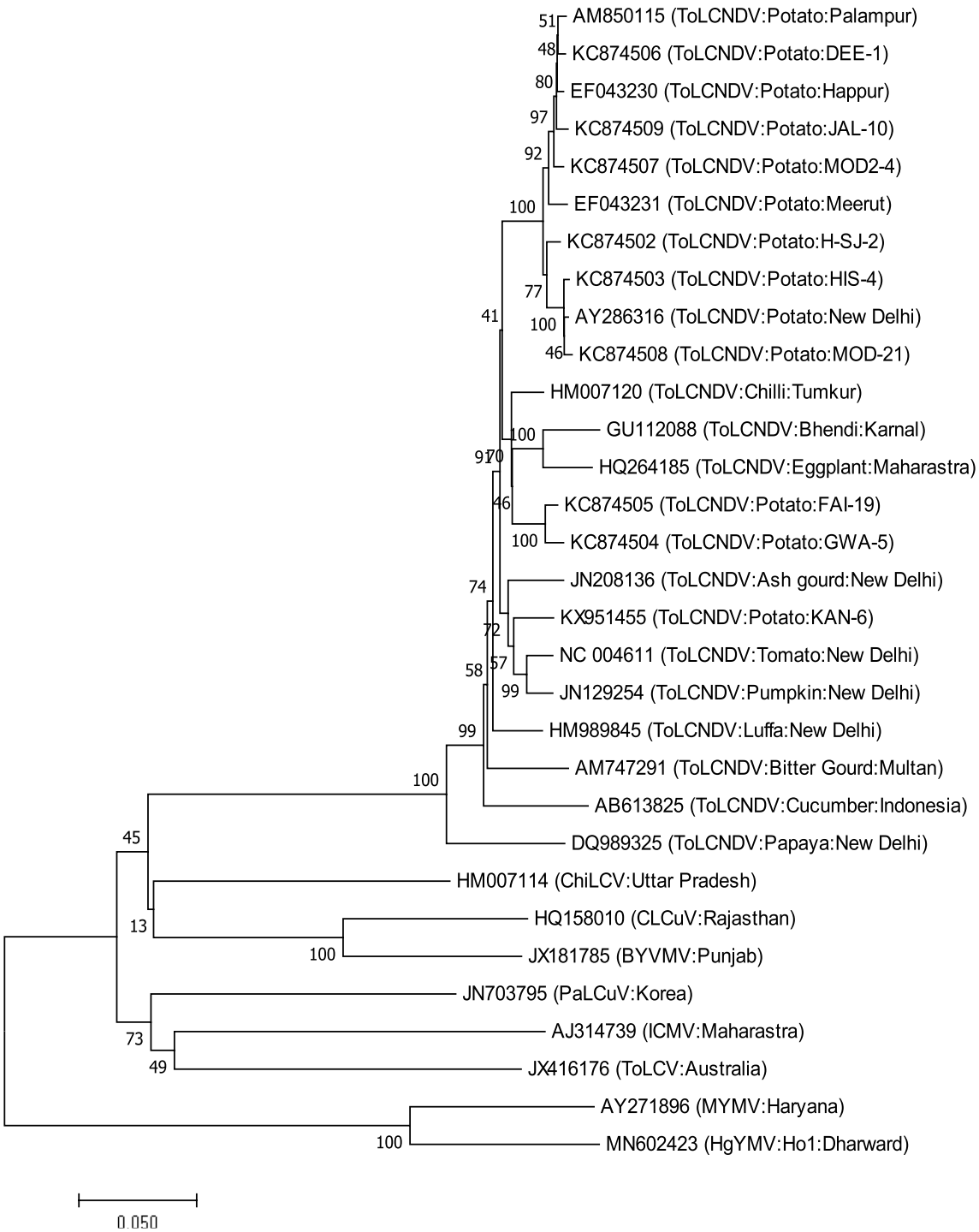


Fig. 2 Genome organization of ToLCNDV (genomic components DNA-A and DNA-B with arrows showing their respective genes). **a** Genes on DNA-A encode a replication-associated protein (Rep), a replication enhancer protein (REn), a transcriptional activator protein (TrAP), a coat protein (CP), AV1 and AV2 proteins and AC1, AC2, AC3, AC4, and AC5 proteins; **b** Genes on DNA-B encode a movement protein (MP) and a nuclear shuttle protein (NSP), BC1 and BV1 proteins. An Intergenic Region (IR) on DNA-A and DNA-B as the common region (CR). Modified and adopted from Jeevalatha et al. (2017a)

other leaf curling begomoviruses. Comparison of DNA-A of ToLCNDV potato isolates with other ToLCNDVs and leaf curling begomoviruses reported from India and worldwide showed the highest identity of 93.3–96.7% with ToLCNDV isolates of tomato, chili, pumpkin, ash gourd, and bitter gourd followed by 91.4–94.6% with ToLCNDV isolates of bhendi, 89.0–89.7% with ToLCNDV isolate of papaya and 70.4–74.0% with other begomoviruses. Evidence proved that all the 12 Indian ToLCNDV potato isolates are above the threshold cutoff value for species demarcation (≥ 91%) based on the recent begomoviruses taxonomy criteria (Brown et al. 2015; Fauquet et al. 2008). Similarly, ToLCNDV potato isolates were grouped in a single clade along with ToLCNDV infecting tomato, cucurbits, brinjal, chili, bhindi, papaya (100% bootstrap support). It is confirmed that begomoviruses that infect potatoes are variants of ToLCNDV (Fig. 3) (Jeevalatha et al. 2017a). However, initially, Usharani et al. (2004a, b) reported that begomoviruses infecting potatoes in India as a strain of ToLCNDV. There are reports which highlight that ToLCNDV originated because of genetic recombination between ToLCNDV and some other begomoviruses (Moriones et al. 2017). Several reports convey that mixed infection of different begomoviruses in the same host leads to recombination at the intra-species and inter-species level. The frequency of recombination in begomoviruses is high and therefore evolution in begomoviruses is fast due to recombination compare to mutation. The increasing genetic variability may be the driving force behind the adaptation of ToLCNDV to new agro-ecological zone and novel hosts (Seal et al. 2006; Padidam et al. 1999; Davino et al. 2009; Lozano et al. 2009).

Origin, evolution, and diversity of ToLCNDV and its vector *B. tabaci*

Begomoviruses are the most devastating viruses spread widely across the tropics and subtropics zones of the world. These viruses mutate very fast and get adapted to the new climate very quickly, and that is the reason why they are responsible for significant yield losses in many crops all over the world (Varma and Malathi 2003; Kumar et al. 2012; Pratap et al. 2011; Jyothsna et al. 2013; Kanakala et al. 2013). The high level of adaptation to changing climatic conditions is because of mixed infections, recombination, and mutations occurring at faster rates (Mansoor et al. 2006). ToLCNDV has drawn special attention to the whole world due to its significant damage to major vegetable crops. The whitefly-transmitted begomovirus was first described in 1995 on tomatoes (Padidam et al. 1995) and thereafter on other solanaceous crops (brinjal, chili pepper, and potato), cucurbits (gourds, melon), okra, and papaya (Kumar et al. 2012; Pratap et al. 2011; Jyothsna et al. 2013; Kanakala et al. 2013; Moriones et al. 2017; Juarez et al. 2019). After the discovery of ToLCNDV in India, it was confined to tropics and subtropics but during the last two decades, it is reported from temperate regions and becoming a serious menace to several economically important crops, (Castillo et al. 2011; Mnari-Hattab et al. 2015; Panno et al. 2016; Moriones et al. 2017; Juarez et al. 2019). ToLCNDV originated from India was detected in south-eastern Spain (Juarez et al. 2014), where it caused severe outbreaks in zucchini squash and significant yield losses to cucurbit crops. Interestingly in Spain, the ToLCNDV was detected in melon,



pumpkin, and cucumber crops, but not in tomatoes (Lopez et al. 2015). Similarly, in Tunisia and Italy, ToLCNDV was reported from cucurbit crops (Mnari-Hattab et al. 2015; Panno et al. 2016). Several reports of the occurrence of ToLCNDV on weeds like *Eclipta prostrata* and *Hibiscus cannabinus* and *Carica papaya* made it more important because, in absence of vegetable crops, these weeds favors the survival of *B. tabaci* (Pratap et al. 2011; Kumar et al. 2012; Jyothsna et al. 2013; Kanakala et al. 2013).

There is a consistent increase in the new hosts of ToLCNDV every year (European and Mediterranean Plant Protection Organization). Recently, several European and Asian countries reported the infection of ToLCNDV on several horticultural crops (Table 1). In India, the incidence of ToLCNDV, the causal organism of PALCD was initially

◂**Fig. 3** Neighbor-joining phylogenetic dendrogram constructed to describe the relationship between the DNA-A component of ToLCNDV and other begomoviruses. Numbers at nodes indicate percent bootstrap values. The following sequences were obtained from GenBank and used for comparisons and phylogenetic analysis: GU112088 (ToLCNDV: Bhendi: Karnal), NC_004611 (ToLCNDV: tomato: New Delhi), DQ989325 (ToLCNDV: Papaya: New Delhi), HM007120 (ToLCNDV: Chilli: Tumkur), JN208136 (ToLCNDV: Ashgourd: New Delhi), JN129254 (ToLCNDV: Pumpkin: New Delhi), AB613825 (ToLCNDV: Cucumber: Indonesia), HQ264185 (ToLCNDV: Eggplant: Maharashtra), HM989845 (ToLCNDV: Luffa: New Delhi), HM989845 (ToLCNDV: Luffa: New Delhi), AJ314739 (Indian cassava mosaic virus; ICMV: Maharashtra), HQ158010 (Cotton leaf curl virus; CLCuV:Rajasthan), JX181785 (Bhindi yellow vein mosaic virus; BYVMV: Punjab), HM007114 (Chilli leaf curl virus; ChiLCV: Uttar Pradesh), AY271896 (Mungbean yellow mosaic virus; MYMV: Haryana), EF043231 (ToLCNDV: Potato: Meerut), EF043230 (ToLCNDV: Potato: Happur), KC874506 (ToLCNDV: Potato: DEE-1), KC874507 (ToLCNDV: Potato: MOD2-4), KC874509 (ToLCNDV:Potato:JAL-10), KC874502 (ToLCNDV: Potato: H-SJ-2), AY286316 (ToLCNDV: Potato: New Delhi), KC874503 (ToLCNDV: Potato: HIS-4), KC874508 (ToLCNDV: Potato: MOD-21), KX951455 (ToLCNDV: Potato: KAN-6), KC874505 (ToLCNDV: Potato: FAI-19), KC874504 (ToLCNDV: Potato: GWA-5), MN602423 (HgYMV: Ho1: Dharward), AM747291 (ToLCNDV: BitterGourd: Multan), JX416176 (Tomato leaf curl virus; ToLCV: Australia), JN703795 (Papaya leaf curl virus; PaLCuV:Korea)

reported from Uttar Pradesh and later in Haryana (Garg et al. 2001; Lakra 2002). It is speculated that the virus shifted to potato from other solanaceous crops like tomato, sponge gourd due to overlapping planting period or early planting of potato or due to the nature of fast mutation within the begomoviruses group (Garg et al. 2001; Lakra 2002; Usharani et al. 2003; Jeevalatha et al. 2013; Tomar et al. 2018). There are reports that the virus came to potatoes in India from the cultivated sponge gourd and tomato (Sohrab et al. 2013; Saha et al. 2014). The transmission of viruses from cucurbit and tomato occurred due to overlapping in planting time and early sowing of potato. This early showing leads to exposure of potato with whitefly and high temperature which aggravates the disease. Now, this disease is widespread in major potato-growing states in India (Fig. 4) (Jeevalatha et al. 2012, 2013; Saha et al. 2014; Kumar et al. 2020; Kreuze et al. 2020).

ToLCNDV is transmitted by the whitefly *B. tabaci* (Gennadius) (genus *Hemiptera*, family *Aleyrodidae*). This vector is predominant in tropics, subtropics, and Mediterranean basin, and remains a major threat to agriculturally important crops (Sharma and Prasad 2017). *B. tabaci* is a complex destructive insect pest species that are reported to infest around 600 plant species in the world (Nombela and Muniz 2010; Chandrashekar and Shashank 2017). The begomoviruses are restricted mostly to phloem tissues of infected plants and transmit in circulative persistent manners in nature (Rosen et al. 2015). Although about 31 different species of *B. tabaci* are reported worldwide, nine genetic groups are found dominant in India. These groups are formed based on genetic makeup; host plant range and potential to transmit viruses within plant species (Ellango et al. 2015; Crowder et al. 2010). In India, the genetic group Asia I is the most widely distributed followed by Asia II-1. While Asia II-7, Asia II-8, and Asia II-5 genetic groups are also reported in a few locations (Reddy et al. 2012; Singh et al. 2012; Ellango et al. 2015). Distribution and incidence of *B. tabaci* in different parts of India are shown in Fig. 4. Garg et al. (2001) suspected that *B. tabaci* acts as a vector for ToLCNDV transmission in potatoes. Chandel et al. (2010) reported that *B. tabaci* not only sucks the sap from tender plants but also transmits the ToLCNDV in a circulative and non-propagative manner. In absence of regular hosts, weeds and other crops favor the survival of *B. tabaci*. In recent times, whitefly has created a big challenge to healthy potato seed production in India (Bhatnagar 2007).

Virus–vector interactions

It is important to know the transmission of viruses and their evolutionary tendency especially in contexts of intensive cultivation in the different agro-ecological zone to plan appropriate control measures. The potato is vegetatively propagated through tuber which is prone to a large number of pathogens, especially viruses. Potato degenerates at a very faster rate due to virus infection and therefore, it demands replacement of the seed potato every one or two years. However, the availability of healthy seed potato planting material has remained a constraint to potato farmers especially in developing countries. Most subsistence farmers in India either use their recycled seed potatoes or procure from other potato farmers, middlemen, or state agricultural departments. Due to this, farmers are forced to use deteriorated or degenerated seed potatoes and have to incur yield losses up to 40% (Singh et al. 2014; Singh and Sharma 2018). The continuous use of degenerated potato planting materials is also a leading cause of the spread of PALCD in India.

The primary source of infection of PALCD is diseased planting material. Further, the disease spreads through its vector, *B. tabaci* in a persistent circulative manner. Various weeds and field crops help in the survival of *B. tabaci* during the vegetables-free period (Singh et al. 1994; Tiwari et al. 2013). It is suggested that *B. tabaci* may be a species complex as many biotypes of *B. tabaci* have been reported from different countries (Oliveira et al. 2001). The infestation of whitefly was recorded in early crops planted in September than crops planted in November (Lakra 2003). In the Indo-Gangetic Plains of the country, the maximum whitefly population was observed in October–November, and thereafter sharp decline was recorded in December (Malik et al. 2005).

Table 1 Worldwide ToLCNDV reports on different cultivated host since its inception

Host species	Year	Reported place	References
Cucumber (*Cucumis sativus*)	2001	Indonesia	Mizutani et al. (2011)
Sponge Gourd (*Luffa cylindrical*)	2003	India	Sohrab et al. (2003)
Chili pepper (*Capsicum* spp.)	2004	Pakistan	Hussain et al. (2004)
Tomato (*Solanum lycopersicum*)	2004	New Delhi	Usharani et al. (2004a, b)
Tomato (*Solanum lycopersicum*)	2005	Bangladesh	Maruthi et al. (2005)
Daryai booti (*Eclipta prostrate*)	2005	Pakistan	Haider et al. (2006)
Bitter gourd (*Momordica Charantia*)	2005	Pakistan	Tahir and Haider (2005)
Chilli (*Capsicum annum*)	2006	India	Khan et al. (2006)
Papaya (*Carica papaya*)	2008	India	Raj et al. (2008)
Cucumber (*Cucumis sativus*), Bottle Gourd (*Lagenaria leucantha*), Muskmelon (*Cucumis melo*)	2008	Thailand	Ito et al. (2008)
Jute (*Corchorus capsularis*)	2010	India	Ghosh et al. (2010)
Oriental melon (*Cucumis melo*)	2010	Taiwan	Chang et al. (2010)
Bitter gourd (*Momordica charantia*)	2010	India	Tiwari et al. (2009)
Cucumber (*Cucumis sativus*)	2011	Indonesia	Mizutani et al. (2011)
Brinjal (*Solanum melongena*)	2011	India	Pratap et al. (2011)
Pumpkin (*Cucurbita pepo*)	2012	North India	Phaneendra et al. (2012)
Ash Gourd (*Benincasa hispida*)	2013	India	Roy et al. (2013)
Melons (*Cucumis melo*)	2013	Iran	Yazdani-Khameneh et al. (2013)
Zucchini (*Cucurbita pepo*)	2014	Spain	Juarez et al. (2014)
Bitter gourd (*Momordica Charantia*)	2015	India	Sharma et al. (2015)
Tomato (*Solanum lycopersicum*)	2015	Spain	Ruiz et al. (2015)
Cucurbits (*Cucumis spp.*)	2015	Tunisia	Zammouri et al. (2017)
Lentil (*Lens culinaris*)	2016	India	Naimuddin et al. (2016)
Opium poppy (*Papaver somniferum*)	2016	India	Srivastava et al. (2016)
Zucchini(*Cucurbita pepo*)	2016	Italy	Luigi et al. (2016)
Zucchini(*Cucurbita pepo*)	2016	Southern Italy	Panno et al. (2016)
Cucurbit (*Cucumis melo*)	2016	Iran	Yazdani-khameneh et al. (2016)
Ridge Gourd (*Luffa* spp.)	2017	Southern India	Patil et al. (2017)
Rubber bush (*Calotropis procera*)	2017	Pakistan	Zaidi et al. (2017)
Potato (*Solanum tuberosum*)	2017	Pakistan	Hameed et al. (2017)
Tomato (*Solanum lycopersicum*)	2017	Tunisia	Zammouri et al. (2017)
Soybean (*Glycine max*)	2017	Pakistan	Jamil et al. (2017)
Zucchini (*Cucurbita pepo*) and Water melon (*Citrullus lanatus*)	2018	Morocco	Radouane et al. (2018)
Tomato (*Solanum lycopersicum*)	2018	Seychelles	Scussel et al. (2018)
Pumpkin (*Cucurbita pepo*)	2018	Italy	Parrella et al. (2018)
Zucchini (*Cucurbita pepo*)	2019	Greece	Orfanidou et al. (2019)
Sweet Pepper (*Capsicum annuum*)	2019	Europe	Luigi et al. (2019)
Luffa (*Luffa* spp.)	2019	Indonesia	Wilisiani et al. (2019)

The thread-like mouthpart of the whitefly comes in contact with the phloem of the potato where the ToLCNDV is confined and after successful feeding on the host, virus acquisition occurs. A helper factor coded by the ToLCNDV was suspected to be involved in the acquisition from the diseased plants to whitefly (Capinera 2004). An acquisition period of 2–24 h followed by an inoculation access period of 2–3 days is sufficient for the successful transmission of the virus (Khurana 2004). However, normally around a single day feeding period is enough to acquire the geminiviruses (Schulten 1997). Under favorable weather conditions, *B. tabaci* can complete its life cycle within 20–30 days (Saini 1998). Minimum three complete generations of whiteflies are reported in potato crops (Chandel et al. 2010; Bhatnagar et al. 2017). To survive in adverse conditions, *B. tabaci* can reside under the leaves with reduced heat shock proteins and raised sorbitol levels in its body (Gerling 2002). Whiteflies generally

Fig. 4 Distribution map of ToLCNDV and *B. tabaci* in India. Modified and adapted from Singh et al. (2014) and Ellango et al. (2015) and based on data available in annual reports of last 19 years (All India Coordinated Research project on potato (AICRP-potato), Shimla, India and ICAR-Central Potato Research Institute (ICAR-CPRI), Shimla, India)

deposit their eggs in leaf tissues of the plants and remain there for 4–7 days (Arneja 2000). Whitefly goes through four nymphal instars stages (Dhawan et al. 2007). The first instar duration is usually 2–4 days, while the duration for second and third instars is about 2–3 days (Capinera 2004). The fourth instar duration is about 4–7 days (Arneja 2000; Dhawan et al. 2007). The final stage is adult and typically it can live from 10–20 days and can produce 50–150 eggs or even up to 300 eggs. Once the adult whitefly acquires the virus, it may remain viable for a long period and cause successful transmission (Chandel et al. 2010). In potato, it is reported that after the acquisition of ToLCNDV by whitefly, virus transmission is possible up to 5–20 days consistently (Kumar et al. 2020). A

latent period of 4–10 h is mandatory for the successful transmission of this virus by its whitefly vector. It is also a fact that female whiteflies are more efficient than adult male whiteflies in transmitting the virus (Boulehya et al. 1997). Hot and dry conditions with 26–32 °C temperature and 60–70% of relative humidity are optimal for whitefly development (Traboulsi 1995). An illustration is made in Fig. 5 for whitefly mediated transmission of ToLCNDV in potato.

Symptoms of PALCD

PALCD symptoms may range from foliar yellowing or spotting, necrosis or mosaic on leaves, leaf area reduction, and stunting. The most common symptoms of PALCD include leaf crinkling, apical leaf curling, chlorotic blotching, and stunting in plant parts. In northern India, symptoms of PALCD were first time noticed in early October planted crop showing stunting, chlorotic bloching, apically leaf crinkling with conspicuous mosaic and yellow mottling with purplish pigmentation on leaves (Garg et al. 2001).

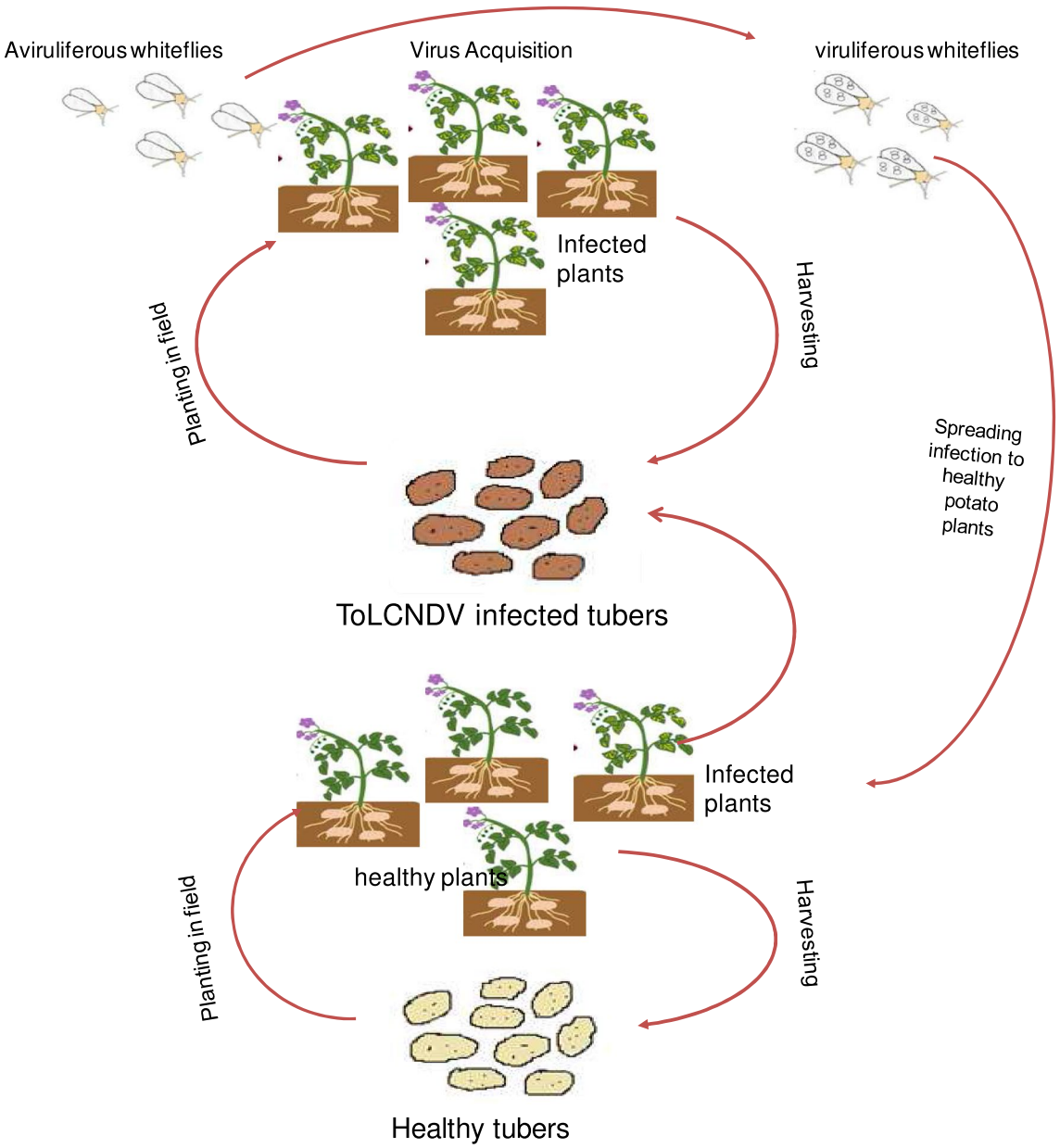


Fig. 5 Schematic diagram of the transmission of ToLCNDV from infected to healthy potato plants

Similarly, Usharani et al (2004a, b) performed inoculation of ToLCNDV on Kufri Anand cultivar of potato which shown peculiar symptoms of crinkling, yellowing, and mottling. An infected plant showed leaf crinkling, vein thickening, curling, and leaf distortion along with stunting symptoms on PALCD infected potato plants (Dhawan and Mandal 2008). In field conditions, the symptoms of upward and/or downward curling of leaves symptoms were also observed (Chandel et al. 2010).

The infectious clones of three different ToLCNDV isolates, viz., MOD-21, FAI-19, and KAN-6, were used for symptom expression studies through agro-inoculation in *N. benthamiana* and potato plants. These isolates produced different kinds of characteristic symptoms of PALCD on *N. benthamiana* and potato (Jeevalatha et al. 2017c). The isolate KAN-6 produces severe yellow mottling, downward curling, and stunted growth in *N. benthamiana*, while isolate MOD-21 produces downward curling and stunted growth, but yellow mottling was shown only in older leaves. The other isolate FAI-19 produced only downward curling symptoms. Typical symptoms of PALCD were observed in inoculated potato cultivar, i.e., Kufri Pukhraj with isolates MOD-21 and KAN-6, and the symptoms were the same as observed in infected *N. benthamiana* plant (Jeevalatha et al. 2017c). The other isolate FAI-19 produced only restricted yellow spots in Kufri Pukhraj. Primary symptoms of PALCD were recorded within 40–45 days from the date of planting under field conditions, and a severe reduction in the size of tuber was observed due to this disease. The secondary infected plant with PALCD showed crinkling, vein thickening, stunting, and leaf distortion (Chandel et al. 2010; Sohrab et al. 2013). The typical characteristic symptoms of PALCD on potato plants are shown in Fig. 6.

Diagnostic techniques for PALCD

Early diagnosis of virus disease is a critical step in its effective management. Since breeding for ToLCNDV resistance is in infancy, it becomes more important to quickly diagnose the disease. Garg et al. (2001) first observed virus particles under an electron microscope with an estimated size ca. 28×17 nm. Further, they reported that the virus does not trap with antisera of Indian cassava mosaic virus but shown excellent clumping in immune electron microscopy. Although ELISA is most commonly used for indexing the tubers against the potato viruses, it is not successful in the case of ToLCNDV. Tissue culture grown microplants are now mainly used as mother culture for seed potato production in which virus titer is very low and it is very difficult to detect such low titer using ELISA. In this context, more emphasis was given to the nucleic acid-based detection of this virus. Several modern detection methods have been developed which are quite useful for regular screening purposes (Garg et al. 2001; Gawande et al. 2007; Venkatasalam et al. 2011; Jeevalatha et al. 2013; Jeevalatha et al. 2014;

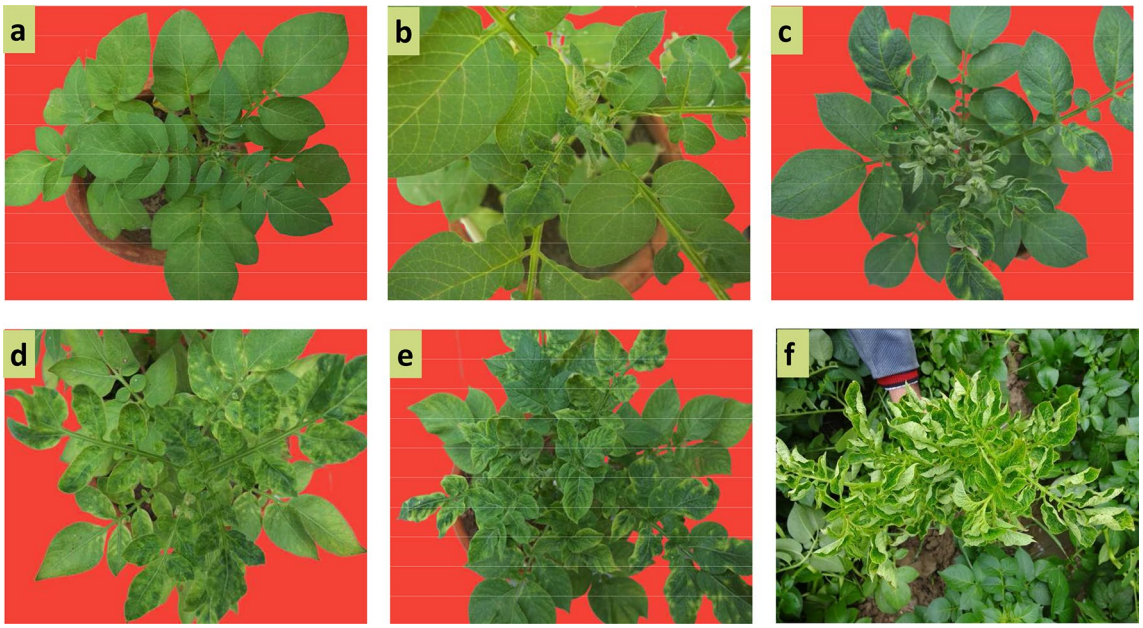


Fig. 6 Characteristic typical symptoms of potato apical leaf curl disease (PALCD) on potato in India. **a** Healthy plant-no symptoms; **b** initial apical leaf curling on potato plant (after 25 days of primary infection); **c** typical leaf curling symptoms (after 45 days of primary infection); **d** typical mosaic symptoms (due to secondary infection or after 60 days of primary infection); **e** severe mosaic symptoms (due to secondary infection or after 75 days of primary infection); **f** Mixed infection of PALCD with other mosaics in field conditions

Jeevalatha et al. 2018). Serological and molecular detection of ToLCNDV was also reported by Venkatasalam et al. (2005). Detection of ToLCNDV using nucleic acid spot hybridization (NASH) and polymerase chain reaction (PCR) has shown significant results. PCR was found more efficient than NASH for the detection of ToLCNDV (Gawande et al. 2007; Venkatasalam et al. 2011). However, the amplification was not satisfactory in samples having a very low titer of virus (Venkatasalam et al. 2011). Saha et al. (2014) performed PCR-based detection of ToLCNDV from West Bengal. Gawande et al (2007) developed a highly efficient and simple technique called print capture PCR for the successful detection of ToLCNDV. A uniplex and duplex PCR was developed using the coat protein gene and replicase gene for ToLCNDV detection in potatoes (Jeevalatha et al. 2013). They also performed a duplex PCR assay using the urease gene as an internal control to avoid any false-negative results. The detection limit for the PCR was as low as 2.4–0.24 pg of the total DNA of the infected plant. Jeevalatha et al (2014) developed highly sensitive and robust rolling circle amplification-based PCR detection for ToLCNDV to detect this virus in mother seed. An efficient qPCR assay has been reported for the detection of ToLCNDV (Jeevalatha et al. 2016). Sridhar et al (2016) developed a protocol for the detection of this virus in whitefly using print capture-PCR. They developed and validated the detection of ToLCNDV simultaneously in fresh and ethanol preserved whitefly. The method successfully detected 87 whitefly samples collected from Punjab, Haryana, Uttar Pradesh, and Madhya Pradesh. Presently, the large-scale testing of tubers demands a quick, sensitive, and equipment-free detection technique and therefore the LAMP method was evolved accordingly. The main advantage of this technique was visual detection without any gel electrophoresis, and also there is no need for thermal cycler as amplification occurs isothermally. Jeevalatha et al (2018) optimized loop-mediated isothermal amplification (LAMP) assay for the successful detection of ToLCNDV in infected leaf and tubers. This assay also successfully detected the virus in asymptomatic plants. This technique has the potential to reduce the cost and save time for large-scale testing of tubers.

Management of PALCD and its vector

Presently no appropriate management options are available for this disease and vector control is the only option through chemicals. Several management strategies mainly targeting the whitefly vectors control have been practiced in reducing this disease (Lakra 2003; Malik et al. 2005; Chandel et al. 2010). Most of the Indian potato cultivars are susceptible to both PALCD as well as whiteflies. However, cultivar Kufri Bahar is found resistant to this disease (Lakra et al. 2005; Jeevalatha et al. 2017b). Viruliferous whiteflies fed on Kufri Bahar do not carry the virus and thereby do not cause PALCD even under epidemic conditions (Lakra 2003). The mechanism of PALCD resistance and virus transmission inhibition in Kufri Bahar is very elusive. Recently, microarray analysis was performed in ToLCNDV inoculated and un-inoculated Kufri Bahar (resistant) and Kufri Pukhraj (highly susceptible) plants to study the gene regulation. About 1111 and 2588 genes were differentially regulated in Kufri Bahar and Kufri Pukhraj, respectively (Jeevalatha et al. 2017b). These include resistance gene analogues, cell cycle-associated genes, HSPs, F-box proteins, transcription factors, homeobox proteins, and genes with unknown functions. In the future, these identified genes could be used as markers in the breeding programs for virus resistance and as genetic sources in developing virus-resistant plants. The present progress of this disease demands a highly efficient host-based strategy to check virus multiplication and spread. RNA interference (RNAi) was also used for conferring resistance to ToLCNDV by Tomar et al. (2018). The AC1 gene is involved in the replication of geminivirus (Castillo et al. 2003) and therefore it was targeted. Here, three main strategies, viz., sense, antisense, and hairpin loop constructs, were used to develop resistance to ToLCNDV in two susceptible popular Indian potato cultivars, i.e., Kufri Badshah and Kufri Pukhraj. About 49 transgenic lines of Kufri Badshah and 33 lines of Kufri Pukhraj carrying these constructs were tested against ToLCNDV in the glasshouse. These transgenic lines were screened for resistance by grafting and a high degree of resistance was observed in one-third of the lines against ToLCNDV. The transgenic lines of Kufri Badshah and Kufri Pukhraj designated as GTLC2-127 and KPLC2-53, respectively, encoding the hairpin loop construct showed good immunity against the virus (Tomar et al. 2018). Historically, *B. tabaci* has been difficult to manage with traditional insecticides in horticultural and agronomic production systems (Palumbo et al. 2001). Therefore, the whiteflies vector must be controlled by a combination of environmental modifications, natural enemy enhancement, and area-wise control programs. Chandel et al (2010) reviewed the integrated management of PALCD and whitefly. Cultural management is vital for the whitefly vector. According to Dhawan et al (2007) continuous cultivation allows regular multiplication and spread of whiteflies. So creating a host-free period for population disruption by prompt destruction of hosts is very important. Elimination of weeds is also important as they act as bridge species during the host-free period (Dhawan et al. 2007). Late sowing of the potato when the climate is relatively cooler is also helpful in eliminating the whitefly buildup. Although several bioagents such as fungi, predators, parasitoids, and entomopathogenic nematodes are reported to control whitefly, most of these studies are confined to in vitro conditions. Under field conditions,

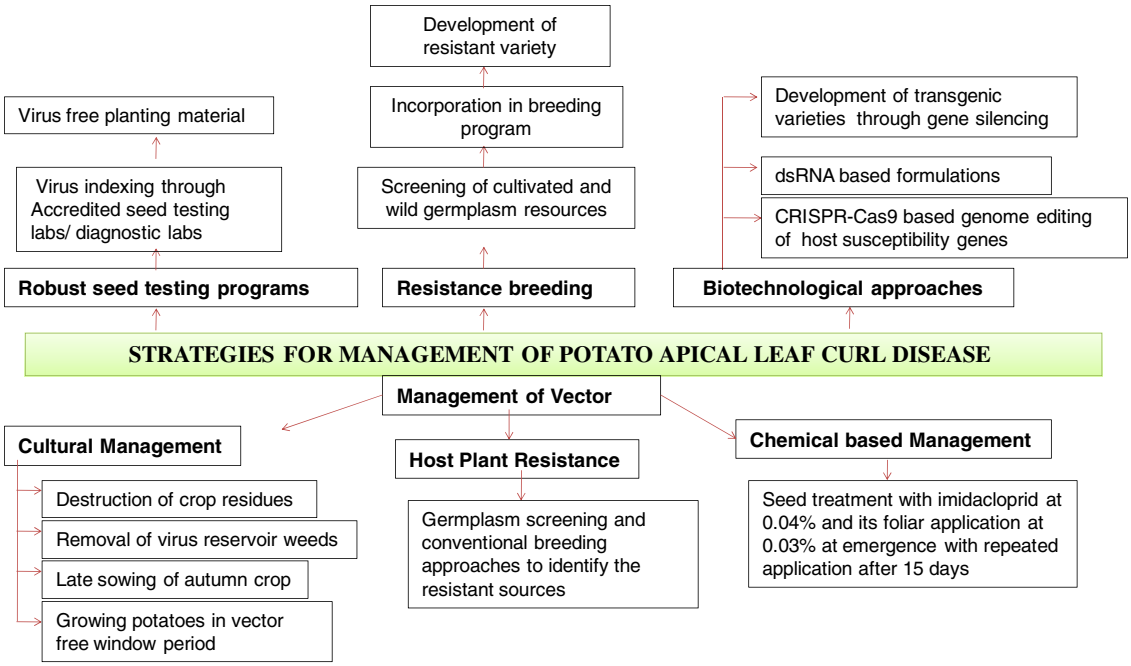


Fig. 7 Possible management strategies for PALCD and the associated whitefly

the parasitism is very limited and erratic (Capinera 2004). A depiction is made for possible management strategies of this disease in Fig. 7.

Conclusion and future thrust

It was a strange observation for plant pathologists as whitefly-transmitted begomovirus possesses a less chance of occurrence in potato as it is grown in winter months. But one cannot rule the possibility of whitefly buildup in potato because now it is sown much earlier in winters. So PALCD is one good example of how the change in the cropping system can lead to the emergence of a devastating disease. ToLCNDV is presently the most threatening virus in the Indian subcontinent, and recently it has spread to other regions. The emergence of ToLCNDV has incurred higher yield losses in potatoes. So far, the knowledge is limited about ToLCNDV and its epidemics, which is necessary to design the novel control approaches. Conventional control practices alone are not adequate to manage ToLCNDV. However, a unified management approach with appropriate knowledge of the disease epidemiology disease may facilitate the management of ToLCNDV epidemics. Currently, the management of PALCD and its vector includes the use of virus-free seed tubers, crop sanitation, manage whitefly populations below the threshold level through insecticides, and growing potato crops during the virus-free window. Future management strategies involve rigorous screening of germplasm against ToLCNDV through appropriate available diagnostic techniques and exploration of the possibility of disease resistance through a breeding program. To develop better management strategies a thorough knowledge about the tripartite virus–vector and host interaction and ecology of PALCD is required, which should be the focus of researchers in the future. The limited knowledge about pathogenomics of ToLCNDV and the precise interactions with the *B. tabaci* vector prohibit our strength to develop a sound management strategy. In the wake of changing climate, there will be profound effects on virus–vectors and we must have the ability to predict the nature and variation of ToLCNDV epidemics. Comprehensive knowledge of factors driving the evolution of ToLCNDV is essential for establishing more efficient and durable measures to control this disease. Some progress has occurred in developing ToLCNDV-resistant potato in past years, but much work should be done for resistant variety development using modern tools. Many variants of ToLCNDV exist in nature on variable hosts, and some of them are having the capacity to the adaptation to other host plants. An in-depth understanding of the host-adaptation will provide novel insights to protect potatoes against these viral infections.

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and SKC provided scientific feedback and critical comments to revise the content. All the authors read and approved the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical clearance No human subjects were used in the writing of the manuscripts.

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