Biology and Management of Aphids Infesting Potato

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Abstract

Aphids are the most important pests of potato worldwide. They are sap-feeding insects, but the major damage inflicted by aphids in potato crops is by transmission of numerous potato viruses limiting disease-free seed production with a progressive decline in yield. Potato crops are infested by a number of colonizing and noncolonizing species of aphids; the noncolonizing aphids are more important for the spread of nonpersistent viruses like *potato virus Y* (PVY), and the persistent viruses like *potato leaf roll virus* (PLRV) are mainly spread by colonizing aphids. More than 22 species of aphids are recorded worldwide that colonize potato plants, and more than 110 species are known to transiently visit the crops. Various attributes of aphid biology and ecology have contributed to their success as crop pests. The host-finding and feeding behavior of aphids predisposes them to being the predominant vectors of various viruses. Controlling the spread of PVY remains a challenge to the potato industry worldwide because of its nonpersistent mode of transmission and the evolution of new strains and variants. Various countries operate networks of traps to monitor the flight activity of aphid species in seed potato. It has been reported that aphids other than *M. persicae* are more important for the early-season spread of viruses like PVY. Currently, the aphid management

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methods in potato are mostly reliant on the use of various insecticides and mineral oils. Moreover, the use of infection-free seed, roguing, and use of cultural practices such as manipulation of planting and haulm-cutting dates are the most useful to keep the incidence of virus under control.

Keywords

Nonpersistent virus · Vector pressure · Aphid monitoring · Virus transmission · Host alternation · Parthenogenesis · Noncolonizing aphids

9.1 Introduction

Potato originated in the Andean highlands of South America and is now cultivated in a major part of the world across the temperate, subtropical, and tropical agroecologies. Its wide geographical distribution also exposes it to a plethora of diverse phytophagous arthropods. Kroschel et al. (2020) described a total of 49 species of insect pests infesting potato crops in different parts of the world. Out of these, 6 major and 32 minor species are prevalent throughout the temperate, tropical, and subtropical regions; 9 major species are prevalent in the tropical and subtropical regions; 2 major species affect potato crops in the temperate regions. Among the global pests of potato, aphids are the most important. Aphids are sap-feeding insects, but the major damage inflicted by aphids in potato crops is by transmission of numerous potato viruses. The resulting viral disease leads to considerable yield reductions, limits the production of disease-free seed potatoes, and causes a progressive degeneration of seed stocks.

Aphids (Aphididae: Hemiptera) are a diverse group of insects with more than 5000 species reported worldwide (Remaudière and Remaudière 1997; Favret 2014). They are distributed worldwide but are most abundant and most diverse in the temperate areas. Although many of these can infest the crop plants, only around 100 of them are of economic importance (Blackman and Eastop 2017). Aphids are generally recognized by a number of common morphological characteristics, e.g., soft body with head, thorax, and abdomen; siphunculi (secretory organs); five- or six-segmented antennae composed of two basal segments and a segmented flagellum with a terminal process; two-segmented tarsi, with the first segment much shorter than the second; and a cauda, which is often used for flicking away droplets of honeydew from the anus. These features have been modified, reduced, or secondarily lost in some species (Blackman and Eastop 2017).

Due to their remarkable ability to adapt and colonize diverse ecological situations, aphids are major pests of various crops, including potato. The cyclic parthenogenesis enables aphids to alternate sexual and asexual generations. The asexual reproduction leads to faster multiplication rates and quick colonization of the secondary hosts where they can cause severe crop damage. Aphids characteristically exhibit polyphenism, which is the production of different phenotypes from the same genotype. Polyphenism is the major reason for the success of the insects in general

(Simpson et al. 2011), allowing them to partition their life-history stages (larvae dedicated to feeding and growth and adults dedicated to reproduction and dispersal), to adopt different phenotypes in response to environmental change (seasonal morphs), and to cope with temporally heterogeneous environments (dispersal morphs) (Field et al. 2017). Aphids exhibit a range of continuous morphological variation, wider than in many other insect groups. Increases or decreases in size due to nutritional effects, for example, can accumulate over several generations, because the size of the mother can affect the size of her offspring. There may be large seasonal differences, with some species producing dwarf individuals when food quality is poor in midsummer.

Aphids can damage potato cops directly by feeding on sap and indirectly by transmitting various viral diseases. Although the direct damage inflicted by aphids is rarely of much significance, sap sucking by a large number of aphids can considerably weaken the plant, slow down the rate development, and reduce the tuber yield. Leaf deformation due to aphid feeding is also possible. Production of honey dew can promote the growth of sooty molds on foliage, potentially leading to reduced photosynthetic area and reduced yield. The most important damage caused by aphids in potato crops is due to the spread of viruses, which leads to reduced tuber yield and degeneration of seed stocks (Kroschel et al. 2020). The most important potato viruses transmitted by aphids are *potato virus Y* (PVY) and *potato leaf roll virus* (PLRV), which can cause losses worth millions of rupees (Loebenstein et al. 2001).

In this chapter, we provide an overview of the biology and ecology of the aphids with discussion in the context of potato. Separate sections dealing with virus transmission characteristics of aphids with emphasis on potato viruses are given, and the state of art with respect to transmission of potato viruses by aphids is provided. Finally, we provide a summary of the management methods generally adopted by potato farmers with concluding remarks.

9.2 Species Composition and Colonization

Potato crops are infested by a large number of colonizing and noncolonizing aphids. The colonizing species feed and breed on potato plants whereas the noncolonizing species are occasional transient visitors. More than 22 species of aphids are recorded worldwide that colonize potato plants (Blackman and Eastop 1994, 2000a, b, 2006) (Table 9.1; Fig. 9.1). Most of these aphids are polyphagous with worldwide distribution.

A large number of aphid species are reported on potato crops from different parts of India. Earlier, five major species infesting potato under Indian conditions were known, viz., *Myzus persicae* (peach potato aphid or green peach aphid), *Aphis gossypii* (melon aphid or cotton aphid), *A. fabae* (black bean aphid), *Rhopalosiphoninus latysiphon* (bulb and potato aphid), and *Rhopalosiphum rufiabdominale* (rice root aphid), in addition to two minor species *Rhopalosiphum nymphaeae* (water lily aphid) and *Tetraneura nigriabdominalis* (rice root aphid) (Pushkarnath 1959; Bindra and Sekhon 1971; Verma 1977; Sekhon and Bindra

Table 9.1 List of aphid species colonizing potato (after Blackman and Eastop 1994, 2000a, b, 2006)

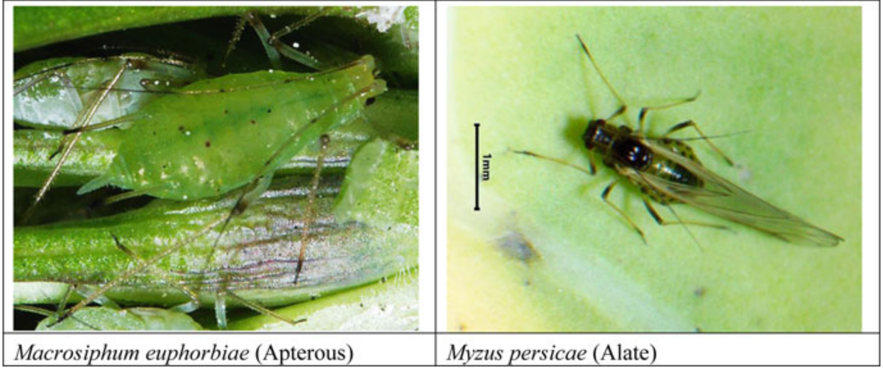
S. No.	Species	Common name	Life cycle
1.	*Acyrthosiphon malvae* (Mosley)	Geranium aphid; pelargonium aphid	Autoecious holocyclic
2.	*Aphis craccivora* Koch	Cowpea aphid, black legume aphid	Anholocyclic, sexual morphs recorded from India and Germany
3.	*Aphis fabae* Scopoli	Black bean aphid	Heteroecious holocyclic
4.	*Aphis frangulae* ssp. *beccabungae*	Alder buckthorn-potato aphid	Heteroecious holocyclic
5.	*Aphis gossypii* Glover	Melon aphid; cotton aphid	Anholocyclic/holocyclic
6.	*Aphis nasturtii* Kaltenbach	Buckthorn aphid; buckthorn-potato aphid	Heteroecious holocyclic
7.	*Aphis solanella* Theobold	Black bean aphid	Heteroecious holocyclic
8.	*Aphis spiraecola* Patch	Spiraea aphid; green citrus aphid	Anholocyclic/holocyclic
9.	*Aulacorthum solani* (Kaltenbach)	Glasshouse potato aphid; foxglove aphid	Anholocyclic/holocyclic
10.	*Brachycaudus helichrysi* (Kaltenbach)	Leaf-curling plum aphid	Heteroecious holocyclic/ anholocyclic
11.	*Macrosiphum euphorbiae* (Thomas)	Potato aphid	Heteroecious holocyclic/ anholocyclic
12.	*Myzus antirrhinii* (Macchiati)	–	Anholocyclic
13.	*Myzus ascalonicus* Doncaster	Shallot aphid	Anholocyclic
14.	*Myzus ornatus* Laing	Violet aphid	Anholocyclic, males recorded from India
15.	*Myzus persicae* (Sulzer)	Peach potato aphid; green peach aphid	Heteroecious holocyclic/ anholocyclic
16.	*Neomyzus circumflexus* (Buckton)	Mottled arum aphid	Anholocyclic
17.	*Pemphigus* sp.	–	Not clear
18.	*Pseudomegoura magnoliae* (=*Aulacorthum magnoliae*) (Essig and Kuwana)	–	Mainly anholocyclic
19.	*Rhopalosiphoninus latysiphon* (Davidson)	Bulb and potato aphid	Anholocyclic
20.	*Rhopalosiphum rufiabdominale* (Sasaki)	Rice root aphid	Heteroecious Holocyclic/ anholocyclic
21.	*Smynthurodes betae* Westwood	Bean root aphid	Heteroecious Holocyclic/ anholocyclic
22	*Uroleucon compositae* (Theobald)	Artichoke aphid	Anholocyclic

Aphis craccivora (Apterae)

Aphis spiraecola (Alate and nymphs)

Aphis fabae (Apterae)

Aulacorthum solani (Alate)



Macrosiphum euphorbiae (Apterous)

Myzus persicae (Alate)

Fig. 9.1 Common aphids infesting potato

1979; Kashyap and Verma 1982; Misra and Agarwal 1987; Kumara et al. 2017). Later, Bhatnagar et al. (2017) compiled information on 13 species of aphids recorded on potato crops in India, viz., *M. persicae*, *A. gossypii*, *A. fabae*, *A. spiraecola*

Table 9.2 A summary of studies on noncolonizing aphid species visiting potato crops from across the world

S. No.	Location	No. of species/ taxa reported	Period of study	Reference
1.	Harpenden, England	119	1984	Harrington et al. (1986)
2.	Wageningen, Netherlands	105	1983–1985	Piron (1986)
3.	Sweden	80	1976–1984	Sigvald (1987)
4.	New Brunswick, Canada	62	1984–1987	Boiteau et al. (1988)
5.	Southern Sweden	>20	1975–1979	Sigvald (1989)
6.	Southern and central Sweden	21	1975–1980	Sigvald (1990)
7.	Netherlands	122	1983–1987	De Bokx and Piron (1990)
8.	Minnesota and North Dakota, USA	34	1992–1994	DiFonzo et al. (1997)
9.	Hungary	28	1982–2001	Kuroli and Lantos (2006)
10.	Tunisia	103	2002–2004	Boukhris-Bouhachem et al. (2007)
11.	Tunisia	15	2001–2006	Boukhris-Bouhachem et al. (2010)
12.	Northern Finland	83	2007–2010	Kirchner et al. (2013)
13.	Idaho, USA	46	2012–2013	Mondal et al. (2016)
14.	Hokkaido, Japan	19	2016	Sano et al. (2019)
15.	Northwest Russia	43	2013–2017	Sukhoruchenko et al. (2019)

(spiraea aphid; green citrus aphid), *A. nerii* (oleander aphid), *A. craccivora* (cowpea aphid or groundnut aphid or black legume aphid), *Macrosiphum euphorbiae* (potato aphid), *Brevicoryne brassicae* (cabbage aphid or mealy cabbage aphid), *Aulacorthum solani* (glasshouse potato aphid), *Lipaphis erysimi* (mustard aphid or turnip aphid), *Hyadaphis coriandri* (coriander aphid), *Rhopalosiphum rufiabdominalis*, and *Rhopalosiphum maidis* (corn leaf aphid). In addition to these, *Myzus ornatus* Laing (ornate Aphid or violet aphid) and *Macrosiphum rosae* (Linn.) (rose aphid) are reported from potato in India.

A large number of aphid species are reported worldwide to transiently visit the potato plants while searching for their own host plant(s). The species composition is studied either based on sampling from potato foliage or with the help of Moericke yellow water pan traps or other types of impaction traps. In some of the studies, more than 120 species/specie groups have been collected from traps in potato fields (De Bokx and Piron 1990). In Table 9.2, a summary of studies on species composition of aphids visiting potato crops is given. Most of these aphids are the pests of other crops or originate from a large number of weed flora. Noncolonizing aphids are the major spreaders of nonpersistent viruses like PVY under filed conditions. Further discussion on the importance of noncolonizing aphids is given in other relevant sections.

9.3 Life Cycles and Dispersal

Aphids have complex life cycles characterized by host alternation and facultative parthenogenesis (Blackman and Eastop 2000a, b). Depending on their ability to host alternate, the life cycle may be heteroecious or autoecious. Aphids that practice host alternation are heteroecious; they live and sexually reproduce on a primary host, mostly woody perennials, during winter and colonize secondary hosts during the rest of the year before coming back to their primary host. Although heteroecy is considered a primitive life strategy in aphids, only about 10% of the modern-day aphid species are heteroecious. In contrast, majority of the species of aphids live on the same or a group of closely related herbaceous hosts throughout the year, commonly referred to as auto−/monoecious species (Williams and Blackman 2007).

Depending on their ability to undergo sexual reproduction, the aphid life cycle may be holocyclic or anholocyclic (Blackman and Eastop 2000a, b). Most of the aphid species alternate parthenogenesis and sexual reproduction and are called holocyclic. Such aphid species switch over to parthenogenesis from the first generation in spring to the appearance of sexual morphs in autumn. The asexual phase is spent partly on the primary host and mainly on the secondary hosts. The appearance of sexual morphs is induced by seasonal changes in temperature and photoperiod. In contrast, some species are anholocyclic; they do not produce sexual morphs or eggs and only reproduce by parthenogenesis (Fenton et al. 1998; Williams and Dixon 2007). Such species continue to utilize herbaceous hosts throughout the year, including winters. Although some species are strictly holocyclic or anholocyclic, certain populations in some holocyclic aphids can lose their sexual phase and become anholocyclic or generate only male populations (androcycly) during winter, mostly leading to production of abortive eggs (Blackman 1971; Margaritopoulos et al. 2002).

The viviparous mode of reproduction in aphids confers a rapid reproduction rate with short developmental times, resulting in population growth that is atypically high, even for insects. For instance, Dixon (1971) estimated that aphid populations in potato fields can reach densities of 2×10^9 individuals per hectare. Douglas (2003) suggested that such rates of population increase reflect nutrient allocation to the reproductive system. Energy is preferentially invested in embryo biomass and larval development rather than in maternal tissues. Aphids have telescoping generations, i.e., ovarian development and embryo formation start at the same time in embryonic mothers (Powell et al. 2006). Parthenogenetic reproduction results in clonal aphid colonies that have the same genotype. With this reproduction mode, an atypical characteristic can be amplified and become predominant in a given population after several generations. This can explain why aphids are able to quickly adapt to disturbances in their environment. Aphid populations may crash depending on the weather (Barlow and Dixon 1980), deteriorating resources, or pesticide treatments. However, parthenogenesis rapidly generates new populations that are adapted to their environment and, in some cases, resistant to pesticides.

Parthenogenesis generally occurs during the warmer months of the year and maximizes offspring production. In fall, it is interrupted and followed by sexual reproduction that produces overwintering eggs. Aphids produce both apterous (wingless) and alate (winged) morphs. Production of alate morphs is energetically costly (Dixon et al. 1993). Alates appear at different times during the year. They are considered to be colonizers and use winds to disperse and locate new hosts. Wingless fundatrices emerge from eggs laid on the primary host. Their alate progeny are the spring migrants. Alate production is completed within a 2-week period (Radcliffe 1982). These individuals fly to secondary hosts (e.g., potato) and, when conditions are favorable, generate apterous and parthenogenetic populations. During summer, overpopulation of aphids, degradation of host-plant nutritional suitability, or variations in light intensity, temperature, and precipitation induce the decline in aphid populations and the appearance of winged morphs that move to more suitable host habitats. In autumn, as day length and temperature decrease, the quality of secondary host plants is altered. These factors generate the appearance of a new generation of virginoparous alates that migrate to the primary host. After the second generation on the primary host, oviparous females appear and are fertilized by winged males (Radcliffe 1982). After reproduction, oviparous females lay their eggs on the primary host for overwintering (Powell et al. 2006). Timing of flight and the number of migrants is important for colonization, clonal fitness, and overwintering success. Aphids that colonize potato are mainly heteroecious and holocyclic, whereas as others switch from other herbaceous hosts to colonize potato or visit it transiently.

9.4 Ecology and Chemical Interactions

Other than rapid reproduction, alternation of sexual and asexual phases, and long-range migration, the most noteworthy feature of aphids is the adaptation to host-plant ecology and physiology. This includes host-plant and feeding-site discrimination using sensitive chemosensory cues, role of endosymbionts and chemical communication among the members of the species and between species.

9.4.1 Host-Plant Selection and Feeding

Host-plant selection in insects includes a sequence of behavioral responses. The sequence includes habitat location, host-plant location, host-plant acceptance, and host use. In general, a number of sensory cues, such as visual, olfactory, gustatory, and tactile stimuli as well as humidity and light intensity (Bernays and Chapman 1994), are used by insects during host selection. To locate a suitable host plant, winged aphids are confronted by various challenges, particularly depending on their host-plant range. Among the aphid species, only 5% are considered as polyphagous (Blackman and Eastop 2000a, b), and many others exploit not more than one or few closely related plant species and are highly specialized in their feeding preference (Dixon 1998).

A series of complex behaviors is involved in host-finding behavior by alate morphs of aphids, and these are closely linked with migration and function of dispersal. The sequence of host-selection behavior in aphids can be broadly categorized into three steps, (a) approach and landing on the plant, (b) leaf-surface exploration and brief probes, and (c) host acceptance, after assessment of the phloem sap, which leads to sustained sap ingestion (Niemeyer 1990; Caillaud 1999; Powell et al. 2006). The discrimination between host and nonhost plants involves perception of visual and volatile cues before landing (Nottingham and Hardie 1993; Powell et al. 1999) but also gustatory cues perceived during brief plant subepidermal probes (Bernays and Funk 2000; Caillaud and Via 2000; Powell and Hardie 2000; Funk and Bernays 2001) and during phloem sap ingestion (Van Helden and Tjallingii 1993). The relative importance of each of these steps is influenced by the aphid specialization with respect to the plant (Bernays and Funk 1999; Funk and Bernays 2001) and according to the aphid species (Tosh et al. 2003). Stylet penetration in the epidermis allows aphids to evaluate the phytochemistry of the plant and to detect antifeedant compounds, providing aphids with the information to decide whether to accept or reject the plant. Saguez et al. (2013) and Pettersson et al. (2007) have discussed the host-finding behavior, feeding, and nutrition in aphids in detail.

Since the past few decades, the research revealed that the host-finding and host-selection behavior of aphids are influenced by naturally occurring chemical compounds (Pickett et al. 1992; Pickett and Glinwood 2007; Webster 2012; Pickett et al. 2013). These comprise of (a) volatile organic compounds (VOCs) emitted by host and nonhost plants and (b) volatiles emitted by aphids (pheromones). The aphids' sensory receptor organs called rhinaria (Park and Hardie 2004), circular or oval structures located on the antennae (Shambaugh et al. 1978), perceive these small-molecular-weight lipophilic compounds (Pickett et al. 2013). A third method of chemical stimuli influencing the aphid host-finding and host-selection behavior is at the point when the aphid is making contact with the plant (Backus 1988; Powell et al. 1999, 2006; Alfaro-Tapia et al. 2007). In certain cases, specific VOCs are used by aphids as host cues. In some other cases, individual VOCs act as nonhost cues during host finding; further it depends on the host range of the aphid species. Apart from the effects of individual compounds, there are also specific effects of VOC blends (relative concentration of chemicals in a mixture of VOCs) on aphid choice behavior (Bruce et al. 2005). For example, VOCs that act as host cues in a blend can become nonhost cues when presented individually (Webster et al. 2010).

According to Powell and Hardie (2001), it is common that aphid species are able to respond to their primary host plant volatile cues, but there is variation in response to volatile cues by individuals from different developmental stages/phenotypes. Summer female aphids (virginoparae) do not show host-plant selectivity, whereas autumn return migrants (gynoparae and males) show olfactory responses to their primary host plant (Powell and Hardie 2001). Phenotypic differences were also identified by electroantennography among the different female phenotypes (virginoparae and gynoparae) and males of *A. fabae* (Powell and Hardie 2001). Wingless aphids of *Macrosiphum euphorbiae* is attracted to potato foliage, while winged aphids are not (Narayandas et al. 2006). A synergism between host-plant volatile and pheromone component has also been shown for aphids, for example, *A. fabae* primary host plant odors increase the response to the sex pheromone, released by mature oviparae aphids, when they return to their host in the autumn (Powell and Hardie 2001).

9.4.2 Endosymbiosis

Symbioses have evolved independently between various insect groups and microorganisms. Almost all of the insects harboring endosymbionts live through the life cycle on nutritionally unbalanced or poor diets. Majority of aphid species possess intracellular bacteria of the genus *Buchnera*, including the ones that colonize potato, namely, *Myzus persicae* and *Aphis gossypii*. *Buchnera* has an obligate association with aphids and are vertically transmitted via the aphid ovary. The *Buchnera aphidicola* benefits *M. persicae* by providing essential amino acids and vitamins that it cannot obtain in sufficient quantities from its diet (Douglas 1998; Prosser and Douglas 1991). Hence the presence of *B. aphidicola* is necessary for the survival and reproduction of the aphids, and the *Buchnera*-free aphids develop poorly and produce no or a few offspring. Disrupting this endosymbiotic bacterium of *M. persicae* can also change the feeding behavior, resulting in delayed host-plant acceptance (Machado-Assefh et al. 2015). The association of *Buchnera* also provides nonnutritional benefits like thermal tolerance and protection from the natural enemies to the aphids. The obligate endosymbionts limit the thermal tolerance of the host species. For example, the exposure of *Aphis gossypii* to elevated heat did not change *Buchnera* titer, resulting in enhanced fecundity. In contrast, heat suppressed the *Buchnera* titer in *A. fabae*; hence they suffered enhanced mortality, delayed development, and reduced fecundity (Zhang et al. 2019). Endosymbiotic bacteria also help *M. persicae* in the circulative transmission of PLRV. The endosymbiotic bacteria synthesize a predominant protein called symbionin and release it in the hemolymph. The symbionin interact with the coat protein of the virus and protect it from enzymatic breakdown in the vector hemolymph (Van den Heuvel et al. 1994).

Apart from the primary obligate bacteria, aphids harbor many facultative bacteria that are not necessarily required for aphid survival or reproduction but may give fitness advantages. Facultative secondary symbionts inhabit bacteriocytes, sheath cells, or hemocoel and are maternally or horizontally transmitted. Seven facultative endosymbionts have been reported from *M. persicae*, namely, *Hamiltonella defensa*, *Serratia symbiotica*, *Regiella insecticola*, *Wolbachia*, *Rickettsia*, *Arsenophonus*, and *Spiroplasma* (Vorburger et al. 2010; Xu et al. 2021). Among these facultative endosymbionts, *Regiella insecticola* have been reported in *M. persicae* to give protection against its two major parasitoids *Aphidius colemani* and *Diaeretiella rapae* (Von Burg et al. 2008; Vorburger et al. 2010).

9.4.3 Semiochemicals

Intraspecific communication in aphids is meant for attracting mates, aggregation, avoidance of competition, and warning against threats, like most other insects. Such signals are pivotal at different stages of the complex aphid life cycles, such as finding of correct primary and secondary hosts, finding mates before ensuing sexual reproduction, and evading predators and parasitoids who are able to respond to some of such cues. Therefore, aphids make extensive use of various semiochemicals at different stages of the life cycles.

The sex pheromones are produced in glandular epidermal cells on the tibiae of the hind legs of the sexual females and perceived by placoid sensilla, in the secondary rhinaria on the antennae of male aphids. During pheromone release, the female engages in typical “calling” behavior, with the hind legs raised (Hardie et al. 1991; Dewhirst et al. 2010). The pheromones usually comprise (4aS,7S,7aR)-nepetalactone and (1R,4aS,7S,7aR)-nepetalactol, monoterpenoids in the cyclopentanoid or iridoid series (Campbell et al. 2003). A further compound, (1S,2R,3S)-dolichodial, has been identified from oviparae of *Dysaphis plantaginea* (rosy apple aphid) (Dewhirst et al. 2008). Most aphids examined so far employ a limited range of pheromone components, but there are differences in relative and absolute compositions.

The asexual forms, and most often the apterae, release an alarm pheromone when disturbed. Nearby aphids exhibit a variety of behaviors, ranging from the removal of mouthparts from the plant and moving away to running, dropping off the plant, and even attacking the predator. Moreover, exposure to alarm pheromone can lead to an increase in the production of winged morphs in an aphid colony (Hardie et al. 1991; Vandermoten et al. 2012). The alarm pheromone is secreted along with the honeydew through siphunculi. The main component of the alarm pheromone of many aphids is the sesquiterpene hydrocarbon (E)-β-farnesene (Bowers et al. 1972; Edwards et al. 1973; Wientjens et al. 1973; Pickett and Griffiths 1980). Other components may also be present. For example, the alarm pheromone of *Megoura viciae* (vetch aphid) contains the monoterpenes α-pinene, β-pinene, (Z, E)-α-farnesene, and (E,E)-α-farnesene, in addition to (E)-β-farnesene, and these can synergize the activity of the latter.

A series of chemicals and their combinations have been demonstrated to have a role in the aggregation of aphid colonies and regulation of overcrowding. Similarly, semiochemicals from host plants are being identified that help the aphids to locate primary and secondary hosts (Pickett et al. 2017).

9.5 Virus Transmission by Aphids

9.5.1 Aphid Characteristics

Majority of the plant viruses are transmitted by arthropod, nematode, or fungal vectors, and among these, aphids are the most important family transmitting more viruses than any other group. More than 5000 aphid species have been described, and of these, over 190 have been reported to transmit plant viruses with many species able to transmit more than one virus (Remaudière and Remaudière 1997; Nault 1997; Hull 2002). Potato is infected by more than 30 RNA viruses (Salazar 1996), among which 13 are transmitted by aphids (Brunt and Loebenstein 2001). The two most important potato viruses transmitted by aphids are the PLRV and PVY. Other than these, *potato virus M* (PVM), *potato virus S* (PVS), *potato latent virus* (PLV), and *potato yellowing virus* (PYV) can become sporadically important (Brunt and Loebenstein 2001).

The virus transmission by an aphid consists of acquiring a virion from an infected plant, its retention in or on the aphid, and its inoculation in another plant to establish infection. The aphid may not be able to immediately release the virus and can do that only after some time has elapsed—the "latent period." Depending on the time for which the aphid can retain a virus in or on it to remain viruliferous, the modes of transmission are generally classified as nonpersistent, semi-persistent, or persistent. In nonpersistent transmission, virus acquisition and inoculation require few seconds to minutes, and there is no latent period involved in between. Such viruses are carried on the stylets of aphids and are retained for a very short time, e.g., potyviruses (*potato viruses A*, *Y*, and *V*), PVM (some strains), PVS (some strains), etc. The most important nonpersistent potato virus is PVY. For semi-persistent viruses, acquisition and inoculation take longer (usually 15 min), and there is no latent period in between. The aphids remain viruliferous for about 2 days. The persistent viruses take much longer for acquisition and inoculation, and there is a significant latent period involved. The aphids remain viruliferous for the lifetime after the latent period has passed, e.g., PLRV.

Several characteristics of aphids predispose them to being efficient virus vectors. Among the most important factors is the feeding behavior of aphids. After landing and tarsal contact with green surfaces, aphids tend to make brief stylet insertions ("probes") into the epithelial or parenchymal tissues. Probing behavior is a particularly important feature of host-plant selection by aphids, which provides information about host quality (Powell and Hardie 2000; Powell et al. 2006). Due to apparent lack of chemosensillae on the stylets, aphids need to ingest plant sap into the pharyngeal area of the foregut for chemosensory assessment. During the probing, the stylets puncture the epidermal cells for a very brief period of time and during which the virion of the nonpersistent virus are acquired. Aphids make several such probes on a plant before actual feeding on the phloem sap or rejection of the plant and moving on to the next plant. This phenomenon continues, and aphids tend to probe several plants before settling for feeding. This is perhaps the most important reason for quick spread of nonpersistent viruses by aphids and failure of chemical control to check such spread of viruses.

Molecular interaction of the aphid-virus-plant complex indicates a complex plethora of pathogenesis and defense reactions. For examples, the gelling saliva of aphids is known to contain phenoloxidases, peroxidases, pectinases, and glucosidases (Cherqui and Tjallingii 2000; Tjallingii 2006) whereas the watery saliva is a complex mixture of enzymes, e.g., those capable of degrading plant cell walls or preventing occlusion of sieve tubes and others capable of eliciting plant defense responses (Will et al. 2009, 2012; Bak et al. 2013). Proteome analysis of the saliva identified a wide range of secreted effectors with complex roles (Elzinga and Jander 2013; Pitino and Hogenhout 2013).

Virus infection of plants has been shown to increase the fitness of the aphids feeding on such plants. Viruses possibly affect the aphids directly or by manipulating the host plants to their advantage. This is further discussed in other sections of this chapter. Other than the host selection and feeding behavior of aphids, other biological characteristics help them spread viruses at alarming rates in crop plants, e.g., life cycle and dispersal, and host range, which are further discussed in other sections of this chapter.

9.5.2 Role of Colonizing and Noncolonizing Aphids

Broadbent (1948) was first to suggest that alatae of species that did not colonize potato could be potential vectors of PVY because of the brief probes they make when visiting potato crops. Till the 1990s, hundreds of noncolonizing aphids were evaluated for their ability to transmit potato viruses, PVY in particular. Among these, around 65 species are now established as vectors of PVY strains (Table 9.3). Although nonpersistent viruses are retained for a few seconds to minutes in their vectors, the retention times for PVY^N in its vectors can range from 4 h (Proeseler and Weidling 1975) to 17 h (Kostiw 1975). Therefore, it is to be expected that the noncolonizing aphids originating either from nearby or far locations can bring the viruses along and inoculate potato plants. In spite of this, the sources of virus within the crop fields (infected seed) are demonstrated to be more important in the spread of viruses in seed potato crops.

Although the colonizing species are more efficient at virus transmission compared with the noncolonizing species, the latter are the most important vectors of nonpersistent viruses because of their huge numbers (Halbert et al. 2003). Opposite to this, the spread of persistent viruses like PLRV is mainly accomplished by the colonizing species (Table 9.4). Persistent viruses are acquired when the aphids finally feed on phloem sap. Since the process of accepting a plant as host and locating the phloem takes a while, therefore, noncolonizing aphids are theoretically incapable of spreading persistent viruses like PLRV.

Table 9.3 List of aphid species known to transmit PVY (modified after Al-Mrabeh 2010; Lacomme et al. 2017)

S. No	Aphid species	Major host plants	PVY strain	Transmission efficiency (%)
1.	*Acyrthosiphon pisum*	Fabaceae, important pest of peas and alfalfa	PVY^{N}	14.0
2.	*Acyrthosiphon primulae*	*Primula* spp.	PVY^{N}	15.0
3.	*Anoecia corni*	Host alternation between *Cornus sanguinea* and roots of Poaceae	PVY^{O}	–
4.	*Aphis citricola* (=*Aphis spiraecola*)	Caprifoliaceae, Compositae, Rosaceae, Rubiaceae and Rutaceae, major pest of *Citrus*	PVY (pepper)	6.2
5.	*Aphis craccivora*	Fabaceae, major pest of leguminous crops	PVY (pepper)	4.0
6.	*Aphis fabae*	Host alternation between *Euonymus europaeus* and a variety of plants; *Aphis fabae* s. str. Colonizes *Vicia faba*	PVY^{O}, PVY^{N}	24.0
7.	*Aphis fabae cirsiacanthoides*	Host alternation between *Euonymus europaeus* and *Cirsium arvense*	PVY^{O}, PVY^{N}	39.3 for PVY^{O}, 80 for PVY^{N}
8.	*Aphis frangulae*	Sexual phase in Europe on *Rhamnus frangula*, host alternates to a wide range of plants depending on the subspecies		–
9.	*Aphis glycines*	Fabaceae, particularly *Glycine* spp., a major pest of soybean	PVY^{O}, PVY^{N}, PVY^{NTN}	14–75
10.	*Aphis gossypii*	On a very wide range of host plants, major pest of cotton and cucurbits, and in glasshouses in cold temperate regions	PVY^{O}	31
11.	*Aphis helianthi* (=*Aphis asclepiadis*, *A. carduella*)	Compositae/Asteraceae and Umbelliferae/Apiaceae		–
12.	*Aphis nasturtii*	Sexual phase on *Rhamnus* spp., on *Nasturtium officinale*, potato, *Veronica beccabunga*, *Drosera rotundifolia*, and *Rumex* spp.	PVY^{O}	7.1
13.	*Aphis pomi*	Rosaceae including *Chaenomeles*, *Cydonia*, *Malus*, and *Pyracantha*	PVY^{O}, PVY^{N}	2–9
14.	*Aphis rumicis*	On *Rumex* spp. and *Rheum* spp.		–

(continued)

Table 9.3 (continued)

S. No	Aphid species	Major host plants	PVY strain	Transmission efficiency (%)
15.	*Aphis sambaci*	*Sambucus* spp.; host alternation occurs in roots of plants such as *Cerastium*, *Dianthus*, *Silene*, *Melandrium*, *Moehringia*, and *Spergula* and also often on *Rumex*, *Capsella*, *Oenothera*, and *Saxifraga*	PVY^O, PVY^N	4.3–12
16.	*Aphis spiraecola*	See *Aphis citricola*		–
17.	*Aulacorthum solani*	Foxglove, extremely polyphagous	PVY^O, PVY^N	5
18.	*Brachycaudus cardui*	Compositae, e.g., *Arctium*, *Carduus*, *Cirsium*, *Cynara, Chrysanthemum*, *Tanacetum*, *Matricaria*), and Boraginaceae, e.g., *Borago*, *Cynoglossum*, *Echium*, *Symphytum*		–
19.	*Brachycaudus helichrysi*	Sexual phase on *Prunus* spp., host alternates to Compositae/Asteraceae and Boraginaceae	PVY^O, PVY^N	7.2 for PVY^O 0.9 to 5.9 for PVY^N
20.	*Brevicoryne brassicae*	Brassicaceae		–
21.	*Capitophorus elaeagni*	*Elaeagnus* spp. and sometimes on *Hippophae* migrate to Compositae (*Arctium*, *Carduus*, *Cirsium*, *Cynara*, *Gerbera*, *Silybum*)	PVY^O	2
22.	*Capitophorus hippophaes*	Elaeagnaceae (*Elaeagnus* spp., *Hippophae* spp.) migrate to Polygonaceae such as *Polygonum* and *Persicaria* spp.	PVY^N	3
23.	*Caveriella aegopodii*	Numerous genera and species of Umbelliferae, sexual phase on various *Salix* spp.	PVY, PVY^N	0.2–0.4
24.	*Caveriella pastinacae*	Host alternates from *Salix* to *Heracleum*, less commonly to *Pastinaca*		–
25.	*Cryptomyzus ballotae*	*Ballota nigra*	PVY	100
26.	*Cryptomyzus galeopsidis*	*Ribes* spp., migrating to *Lamium* and *Galeopsis*	PVY^N	17.4
27.	*Cryptomyzus ribis*	On *Ribes* spp., migrating to *Stachys* spp.	PVY^N	15.4

(continued)

Table 9.3 (continued)

S. No	Aphid species	Major host plants	PVY strain	Transmission efficiency (%)
28.	*Diuraphis noxia*	On grasses and cereals *Agropyron*, *Anisantha*, *Andropogon*, *Bromus*, *Elymus*, *Hordeum*, *Phleum*, *Triticum*	PVY pepper	4–7
29.	*Drepanosiphum platanoidis*	*Acer pseudoplatanus*, common on sycamores	PVY^N	0.6
30.	*Dysaphis plantaginea*	*Malus* spp., *Pyrus* spp., *Plantago* spp.		–
31.	*Dysaphis aucuparie*	On *Sorbus torminalis*, migrating to *Plantago* spp.		–
32.	*Hayhurstia atriplicis*			–
33.	*Hyadaphis foeniculi*	On *Lonicera* spp., migrating to various Umbelliferae	PVY^N	14.7
34.	*Hyalopterus pruni*	On *Prunus domestica*, migrating to *Phragmites* or sometimes to *Arundo donax*	PVY^N	13.9
35.	*Hyperomyzus lactucae*	On *Ribes* spp., migrating to *Sonchus* spp. and occasionally other Asteraceae	PVY^N	17.4
36.	*Hyperomyzus pallidus*	On Amaranthaceae, usually *Atriplex* and *Chenopodium* spp.		–
37.	*Lipaphis erysimi*	On various Brassicaceae (*Arabis*, *Capsella*, *Coronopus*, *Erysimum*, *Isatis, Lepidium*, *Matthiola*, *Sinapis*, *Sisymbrium*, *Thlaspi*, etc.) but not usually on field *Brassica* crops		–
38.	*Macrosiphum euphorbiae*	Sexual phase on *Rosa*, secondary hosts in more than 20 different plant families	PVY^N	29
39.	*Macrosiphum rosae*	On *Rosa* spp. in spring, migrating to Dipsacaceae (*Dipsacus*, *Knautia*, *Succisa*) and Valerianaceae (*Centranthus*, *Valeriana*)		–
40.	*Metopolophium albidum*	On grasses such as *Arrhenatherum elatius*	PVY^N	11
41.	*Metopolophium dirhodum*	On *Rosa* spp. in spring, migrating to numerous species of Poaceae and Cyperaceae.	PVY^N	3

(continued)

Table 9.3 (continued)

S. No	Aphid species	Major host plants	PVY strain	Transmission efficiency (%)
42.	*Metopolophium festucae*	Poaceae	PVY^{O}	0.5
43.	*Myzaphis rosarum*	Wild and cultivated *Rosa*	PVY^{O}	10
44.	*Neomyzus circumflexus*	*Sonchus oleraceus*	PVY^{O}, PVY^{N}	–
45.	*Myzus ascalonicus*	Polyphagous, Alliaceae, Caryophyllaceae, Compositae, Brassicaceae, Liliaceae, and Rosaceae		–
46.	*Myzus cerasi*	On *Prunus* spp., migrating to secondary hosts in Rubiaceae (*Asperula*, *Gallium*), Orobanchaceae (*Euphrasia*, *Rhinanthus*), Plantaginaceae (*Veronica*), and certain Brassicaceae (*Capsella*, *Cardamine*, *Coronopus*, *Lepidium*)	PVY^{O}, PVY^{N}	3.2
47.	*Myzus certus*	On Caryophyllaceae (*Cerastium*, *Dianthus*, *Stellaria*)	PVY^{N}	71.0
48.	*Myzus ligustri*	Privet hedges (*Ligustrum ovalifolium*, *L. vulgare*)	PVY^{O}, PVY^{N}	30.0 for PVY^{O}, 76.3 for PVY^{N}
49.	*Myzus myosotidis*	*Myosotis scorpioides* (*=palustris*)	PVY^{O}	100.0
50.	*Myzus persicae nicotianae*	Host alternates from *Prunus* to tobacco	PVY, PVY^{N}	15.3
51.	*Myzus persicae*	Host alternates from *Prunus* to a wide variety of plants.	PVY^{O}, PVY^{N}	50.0–71.0
52.	*Phorodon humuli*	On *Prunus* spp., migrating to *Humulus lupulus*	PVY^{N}	35
53.	*Rhopalosiphum oxyacanthae* (*=R. insertum*)	On Pyroideae (*Cotoneaster*, *Crataegus*, *Malus*, *Pyrus*, *Sorbus*) migrating to Poaceae (*Agropyron*, *Agrostis*, *Alopecurus*, *Dactylis*, *Festuca*, *Glyceria*, *Phalaris*, *Poa*, *Triticum*)	PVY^{N}	50
54.	*Rhopalosiphum maidis*	On *Avena*, *Hordeum*, *Oryza*, *Saccharum*, *Secale*, *Sorghum*, *Triticum*, and *Zea*, migrating to *Prunus* spp.	PVY^{O}	1.5
55.	*Rhopalosiphum padi*	On *Prunus* spp., migrating to numerous grasses and cereals	PVY^{O}, PVY^{N}	2–11.5

(continued)

Table 9.3 (continued)

S. No	Aphid species	Major host plants	PVY strain	Transmission efficiency (%)
56.	*Rhopalosiphum pseudobrassicae* (=*Lipaphis pseudobrassicae*)	Brassicaceae, including *Barbarea*, *Brassica*, *Capsella*, *Iberis*, *Raphanus*, and *Rorippa*		–
57.	*Schizaphis graminum*	Various species of Poaceae		
58.	*Sitobion avenae*	On numerous species of Poaceae, including all the cereals and pasture grasses	PVY^O, PVY^N	0.1–1.8
59.	*Sitobion fragariae*	Apterae on *Rubus* and other Rosaceae, migrating to Poaceae	PVY^O, PVY^N	0.5–10.1
60.	*Sitobion graminum*	Most probably *Schizaphis graminum*		–
61.	*Staphylae tulipaellus* (=*Rhopalosiphoninus staphyleae* ssp. *tulipaellus* Theobald)	*Beta vulgaris*, also recorded from the roots *Galium*, *Lycopersicon*, *Rumex*, *Tulipa*, and *Viola*		–
62.	*Therioaphis trifolii*	On many plants of Leguminosae/Fabaceae in the genera *Astragalus*, *Lotus*, *Medicago*, *Melilotus*, *Onobrychis*, *Ononis*, and *Trifolium*		–
63.	*Tetraneura ulmi*	Poaceae	PVY^N	–
64.	*Uroleucon* spp.	Compositae/Asteraceae	PVY^O, PVY^N	0.5–8.3
65.	*Uroleucon sonchi*	Mainly on *Sonchus* spp. and other genera in the tribe Cichoriaceae (*Lactuca*, *Cichorium*, *Hieracium*, *Ixeridium*, *Picris*, *Reichardia*)	PVY	–

9.5.3 Role of Apterae

The relative role of apterae in within-field spread of potato viruses continues to be a controversial topic. However, evidence has been slowly accumulating, which shows that apterae leave their host plants quite readily and can then play an important role in the local spread of virus within crops (Hodgson 1991). The voluntary movement of apterae could be particularly significant along the leaf blades of canopies of adjacent plants in touch, or by walking across soil from one plant to another (Ferrar 1969; Alyokhin and Sewell 2003). Major factors thought to affect dispersal by apterae include climatic effects (wind, rain), parasitoids and predators, host-plant

Table 9.4 List of reported aphid vectors of *potato leaf roll virus* (PLRV) (Source: https://aphmon.fera.co.uk/plrv_vector_info.cfm)

S. No.	Species	Relative efficiency factor
1.	*Aphis fabae*	0.30
2.	*Aphis gossypii*	0.50
3.	*Aphis nasturtii*	0.25
4.	*Aulacorthum circumflexum*	0.90
5.	*Aulacorthum solani*	0.30
6.	*Macrosiphum euphorbiae*	0.15
7.	*Myzus ascalonicus*	0.30
8.	*Myzus ornatus*	0.30
9	*Myzus persicae*	1.00
10.	*Phorodon humuli*	0.12
11.	*Rhopalosiphoninus latysiphon*	0.30
12.	*Rhopalosiphoninus staphyleae*	0.10

quality, and intra- and interspecific population interactions (summarized in Hodgson 1991). Hodgson (1991) found that apterous dispersal is frequent in *Myzus persicae* (Sulzer), *Brevicoryne brassicae* (Linnaeus), and *Megoura viciae* Buckton and arguably in other aphid species; the movement occurs at low population densities, mainly due to a reduction in the host-plant quality, and the main emigrants are young adults or fourth instar apteriform nymphs. Narayandas and Alyokhin (2006) reported that regardless of canopy overlap, most apterae of *Macrosiphum euphorbiae* (Thomas) moved within the rows of potato plants. Wind, rain, and mechanical raking significantly encouraged aphid movement between plants with overlapping canopies. Therefore, it is plausible to conclude that movement of apterae could have implications for within-field and along the row spread of viruses; however, the exact role needs to be ascertained for specified conditions (Narayandas and Alyokhin 2006).

9.5.4 Virus Induced Changes in Host Plant and Aphid

Plant viruses depend on both host plant and vectors for a successful infection and survival. Such vector-borne pathogens can modify their hosts and vectors in such ways that shape the frequency and nature of interactions between them, resulting in significant implications on transmission and spread of disease. In virus-induced host-plant manipulation, host odors are particularly probable targets for manipulation for the insect-borne pathogens as the insect uses host-released volatile compounds as key foraging cues, particularly host recognition and acceptance. *Cucumber mosaic virus* significantly increases the attractiveness of infected host plants by inducing elevated emissions of a plant volatile blend for *M. persicae* and *A. gossypii* (Mauck et al. 2010). Similarly *bean common mosaic virus* (BCMV), *bean common mosaic necrosis virus* (BCMNV), and *cucumber mosaic virus* (CMV) considerably reduce host-plant quality, inducing dispersal of *M. persicae* and *A. gossypii* from such plants but increasing the attractiveness of infected host plants to aphids via increased emissions of a plant volatile blend (Wamonje et al. 2020). Thus, these viruses appear to attract insect vectors deceptively to infected plants from which they then disperse rapidly; this is a pattern highly conducive to the nonpersistent transmission.

Viruses can also alter the host-plant metabolism or plant defense pathways that favor vector's attraction, settling, or feeding which, in turn, can be favorable for virus propagation and spread. Bak et al. (2019) reported that PVY and *turnip mosaic virus* manipulate host physiology by induction of ethylene signaling, which mediates *M. persicae* attraction to infected plants and hence virus spread. Similarly, PLRV infection attenuates the induction of jasmonic acid and ethylene using transient expression of three PLRV proteins (P0, P1, and P7) in potato and *Nicotiana benthamiana*. Attenuated induction of aphid-induced phytohormones manifests to alter host physiology and, in turn, aphid behavior and fecundity (Patton et al. 2020).

To understand the direct effect of the plant viruses on their vectors, Rajabaskar et al. (2014) carried out a study using *M. persicae*-PLRV pathosystem and observed that the viruliferous aphids prefer to settle on the healthy potato plants, whereas the non-viruliferous aphids preferred potato plants infected with PLRV. The direct effects on the vector upon acquisition of virus in terms of vector performance, behavior, or fecundity and longevity are also documented, which, in turn, could have implications for multiplication and spread of the viruses (Rajabaskar et al. 2014; Eigenbrode et al. 2018).

9.5.5 Virus Transmission Efficiency of Aphids and Vector Pressure

Numerous species of aphids visit potato crops transiently, and a number of species can breed on potato plants. Among these, the number of species that are physically capable of transmitting nonpersistent viruses like PVY is much higher compared with those that can transmit the persistent viruses like PLRV. The vectors are able to transmit PVY with variable efficacy (Kostiw 1979; Van Hoof 1980; Sigvald 1984; Harrington and Gibson 1989; De Bokx and Piron 1990). For instance, if a particular aphid species was found to transmit PVY 50 times out of the 100 times it fed, we would say that that species has a transmission efficiency of 50%. The peach potato aphid, *Myzus persicae*, is generally accepted as the most efficient vector of PVY. The virus transmission efficiency of all other species of aphids are expressed relative to the transmission efficiency of *M. persicae*, generally referred to as relative efficiency factor (REF); *M. persicae* is assigned an efficiency factor of 1. These REFs for the different aphid species are used to calculate the cumulative vector pressures of all the vector species present and contribute to PVY forecasting or control systems. Vector pressure is given by the product of the count of individuals of a particular species caught in traps in a particular period of time, mostly 1 week, and its corresponding REF. Vector pressure is considered as an important measure of estimating the risk the PVY spread in seed potato crops.

The virus transmission efficiency of aphids has been evaluated since the 1980s using different methods, mainly in Europe. In one method, the aphids were caught alive from potato fields, allowed to probe PVY-infected plants, and subsequently transferred to healthy potato plants. The resulting percentage of infected plants gave a measure of virus transmission efficiency of the aphids (Ryden et al. 1983; Sigvald 1984, 1986; De Bokx and Piron 1990). In the alternative method, the aphids caught alive from the potato fields were directly transferred to healthy plants (mostly tobacco) to determine their transmission efficiency (Harrington et al. 1986; Kostiw 1979; Katis and Gibson 1985; Woodford 1992; Boiteau et al. 1998; Halbert et al. 2003). Lately, the apterae from aphid cultures were used to assess their efficiency at transmitting PVY strains (Verbeek et al. 2010). The results most often differ among the studies mainly due to the use of different methods, biotypes of aphids, and host plants used (Verbeek et al. 2010). Earlier studies evaluated the transmission efficiency for strains like $\mathrm{PVY}^{\mathrm{O}}$ and $\mathrm{PVY}^{\mathrm{N}}$; the prevalence of recombinant strains like $\mathrm{PVY}^{\mathrm{NTN}}$ and $\mathrm{PVY}^{\mathrm{N\text{-}Wi}}$ has necessitated a fresh evaluation of the virus transmission efficiencies. It is reported that strains like $\mathrm{PVY}^{\mathrm{NTN}}$ and $\mathrm{PVY}^{\mathrm{N\text{-}Wi}}$ are transmitted at a higher rate than $\mathrm{PVY}^{\mathrm{O}}$ or $\mathrm{PVY}^{\mathrm{N}}$ (Verbeek et al. 2010; Mondal et al. 2016).

The REFs and the vector pressure are used for forecasting incidence of PVY and to take management decisions, particularly the timing of insecticide application, selection of the kind of pesticide to be applied, and decision on the time for cutting of haulms in seed potato crops. Many countries or regions producing seed potato operate trapping networks to monitor the flights of aphids and to alert farmers about the risk of virus spread in the current crop season. The transmission risk is mostly evaluated in terms of vector pressure (calculated by multiplying the abundance of each aphid species by its corresponding relative transmission efficiency factor (REF value) (van Harten 1983; Verbeek et al. 2010) and summing over the species (Basky 2002, 2006; Northing 2009; Kirchner et al. 2011).

During the early years, the population counts of aphids on potato plants were the determinants. However, from 1951 the flight activity of *M. persicae* became the main criterion, and this was recorded by using many Moericke (yellow water) traps. When an average of two or more *M. persicae* were caught in the yellow traps of one region on 1 day, this was taken as an indication that the summer flight of this species had started. The haulms of basic seed fields were usually destroyed within 10 days of that particular day (Hille Ris Lambers 1972). As long as PLRV was the most important virus disease in the Netherlands, this system functioned satisfactorily. However, in the 1950s, a new strain of $\mathrm{PVY}^{\mathrm{N}}$ invaded Europe, and the symptoms caused by it were mostly overlooked. As a result, roguing, which had been a good way to control other long known strains of PVY, was less effective, and there was a rapid spread of $\mathrm{PVY}^{\mathrm{N}}$. Since then $\mathrm{PVY}^{\mathrm{N}}$ has had to be taken into account in seed potato production (Van Harten 1983). Since 1976, much information has been published on early spread of $\mathrm{PVY}^{\mathrm{N}}$ in the Netherlands (van Hoof 1977, 1979) and on the ability and efficiency of many aphid species to transmit it (Kostiw 1979; Ryden 1979; van Hoof 1980).

By attributing relative efficiency factors to predominant vector species and considering their flights as recorded with suction traps in the Netherlands, values of vector pressure were obtained that correlate well with weekly infection of bait plants (Van Harten 1983). In Sweden, the relationship between occurrence of alate aphids and the proportion of PVY-infected progeny tubers has been studied since 1975. A dynamic simulation model for PVY has been designed for predicting the incidence of PVY. The simulation model describes a system which includes, e.g., healthy and PVY diseased potato plants, different aphid species as virus vectors and their efficiency as virus vectors, the susceptibility of the potato crop according to mature plant resistance, and date of haulm destruction. There was a good correlation between model output and samples of progeny tubers tested for PVY (Sigvald 1992). Basky (2002) conducted an aphid and virus survey in Hungary yearly between 1993 and 2000. Aphid flight was monitored using yellow pan traps, and virus infection in seed potato progeny tubers was tested with double-antibody sandwich ELISA and varied between 0.75% and 31.8% (PVY) and 0% and 13.25% (PLRV). A simple linear regression analysis showed that the factors examined, i.e., total aphid number, vector number, cumulative vector intensity, and age-corrected vector intensity, had significant effects on the proportion of PVY- and PLRV-infected progeny tubers in seed potato fields. Kirchner et al. (2011) modeled the seasonal increase in PVY incidence using aphid counts in traps, the relative vector efficiencies of the aphids, virus resistance of cultivars, and the initial infection rate of the seed tubers as explanatory variables in generalized linear mixed modeling in Finland. Results of this modeling approach showed that the incidence of seed-borne PVY infection and the early-season vector flights are the most important factors contributing to the incidence of PVY in the yield. Steinger et al. (2015) used a linear regression model including the cumulative sums (until mid-June) of two aphid species (*Brachycaudus helichrysi* and *Phorodon humuli*) as predictor variables for virus disease, which was remarkably well supported by the data ($R^2 = 0.86$). Remarkably, the abundance of *M. persicae*, often considered the main vector of PVY, was not correlated with virus incidence. Taken together, the analysis suggests that the early migrating aphid *B. helichrysi*, rather than *M. persicae*, is the main vector of PVY in Switzerland and that suction trap data are useful for the design of decision-support systems aimed at optimizing virus control in seed potato production.

Extensive aphid monitoring programs using suction traps have been running successfully in European countries, the USA, and New Zealand, for example. The oldest network is in the UK, which has been running for more than 50 years. In the United Kingdom, aphids relevant to seed potato protection are monitored by the Rothamsted/SASA suction-trap network and the FERA yellow water-pan trap network. Suction trap aphid data and weather data are used to forecast the start of aphid flights. Each week, results of trap catch (species composition and abundance) with a cumulative vector pressure index are published and made available to the farmers and others involved with this sector. This index is designed to give the user an assessment of the risk to their crop of PVY spread and helps in decision-making processes when considering the need for insecticide treatments and in deciding the best time to burn down/cut haulms of potato crops (https://secure.fera.defra.gov.uk/aphmon/index.cfm).

On similar lines, to monitor aphid flight, a national aphid-monitoring suction trap network has been established in South Africa in 2005. The network consists of nine 12.2-m-high Rothamsted-type suction traps, which are situated throughout major seed potato-growing regions. Each trap represents aphid samples over a radius of approximately 80 km. The aim of the South African network is to provide seed potato growers with aphid abundance data on a regional level to assess virus risk. The monitoring network and associated web-based database are to serve as an early warning system to assist growers in making management decisions regarding the location and timing of aphid control measures. To view long- and short-term trends in aphid abundance and keep track of aphid numbers and vector pressure, seed growers can apply for user registration on the website of Potatoes South Africa (Kruger and Laebscher 2012) (www.potatoes.co.za).

9.6 Management of Aphids in Potato Crops

Since the managements of aphids is the most important way to manage the incidence of aphid-transmitted viruses in potatoes, various tactics are adopted for the management of aphid-virus complex in seed potatoes. In ware potatoes, a comparatively less stringent pest management regime is adopted. Dupuis et al. (2017) and Pickup and Lacomme (2017) have discussed the subject in detail. The various aspects of the integrated management of aphids in potato cops are discussed as follows.

9.6.1 Monitoring of Aphids

The management of aphids in potato is principally the management of aphid-transmitted potato viruses. Aphids spread viruses when they move from an infected plant to a healthy one. Therefore, it is imperative to monitor the flight activity of aphids to assess the risk of virus spread under filed conditions. As described before, the flight activity of aphids is monitored using the yellow water pan traps or the section traps; each of these has its own merits and demerits. The information on abundance, species composition and flight activity, and ensuing risk of virus spread is made available to the farmers to decide the timings of pesticide/mineral oil applications or the timings for cutting of haulms (Pickup and Lacomme 2017). Various networks of suction traps and water pan traps are being operated in different parts of the world, as described in the earlier section.

9.6.2 Chemical Control

Various contact and systemic insecticides are used worldwide for the management of aphids in potato crops. Among the most commonly used ones are the neonicotinoids including imidacloprid, clothianidin, and thiamethoxam as seed treatment and foliar sprays. Other than these, dinotefuran and nitenpyram are also recommended. Due to their systemic ability and persistence, these are very popular among farmers (Dewar and Denholm 2017). Among the synthetic pyrethroids, cypermethrin, deltamethrin, esfenvalerate, lambda-cyhalothrin, and beta-cyfluthrin are effective due to their knockdown ability and ability to control nonpersistent viruses (Bedford et al. 1998). Among the new-chemistry insecticides, pymetrozine and flonicamid exert similar effects against aphids, causing irreversible cessation of feeding within a few hours of application, followed eventually by starvation and death, and are highly effective against aphids (Schwinger et al. 1994; Morita et al. 2007). Spirotetramat among the novel classes—the tetronic and tetramic acid derivatives—has shown promising results against aphids (Bruck et al. 2009). However, many aphids became resistant to insecticides (Radcliffe 1982; Devonshire et al. 1998; Foster et al. 2000). Various mechanisms have been shown to confer resistance to organophosphorus, carbamates, and pyrethroid compounds (Radcliffe 1982; Wheelock et al. 2005). Therefore, the use of insecticides should be strictly as per the resistance management guidelines, e.g., those of Insecticide Resistance Action Committee (https://irac-online.org/) (Nauen et al. 2019).

Petroleum-derived spray oils are long known to possess insecticidal activity. Mineral oils have been demonstrated to reduce the spread of PVY by more than 50% in comparison with untreated control on many occasions. The usual practice is to apply 5–10 L/ha with season-long spraying program at weekly intervals. Mineral oils possess direct toxicity toward the vector aphids, interfere with feeding behavior and binding of virions within the stylets of aphids, and impede the infection process post-inoculation. All these together or alone contribute to reducing the spread of nonpersistent viruses like PVY in field. Perhaps the most important limitation of mineral oils is the necessity for complete coverage of the foliage. Therefore, fresh foliage after treatment continues to be susceptible to probing by aphids and the consequent virus transmission. Therefore, mineral oils are applied more frequently in the early season and also when the aphid flight activity is higher (Yang et al. 2019; Shah et al. 2021).

9.6.3 Cultural Control

Weeding and general cleanliness in and around crop fields and removal of overwintering hosts can help reduce the incidence of aphids. Mulches including plastic reflective mulches and straw mulches have been demonstrated to considerably reduce the landing rate and population growth of aphids on potato (Summers et al. 2004; Shah et al. 2020). Similarly, intercropping with onion, garlic, or coriander is known to reduce aphid population (Lehmhus et al. 1996; Vidal 1997). Manipulation of planting and haulm-cutting dates to evade the periods of high aphid activity are practiced worldwide to reduce the incidence of aphid-borne viruses in seed potatoes (Pushkarnath 1959, 1967). Chang et al. (2017) have discussed the subject at length.

9.6.4 Natural Enemies and Microbials

Natural enemies of aphids belong to diverse taxonomic groups, from entomopathogenic fungi to parasitoids, and include generalist and specialist predators, many of which are commercially available (Hance et al. 2017). Most common among these are the braconid and aphelinid parasitoids, coccinellids, predatory bugs, lacewings, and syrphids. The natural enemies work better if their populations are conserved under field conditions by provision of food and refugia. Since the activity of natural enemies is slow, therefore, their role in the management of aphid-virus complex is limited.

Numerous biological control products that use one or more species of entomopathogenic fungi, e.g., *Beauveria bassiana*, *Lecanicillium* spp., are commercially available for aphid control. Proper timing of application is very important when these products are used because fungal spores are strongly influenced by environmental conditions, such as temperature and relative humidity (Kim et al. 2013).

Other than these, the extracts of many plants are known to reduce the aphid population through lethal or sublethal effects, e.g., garlic, neem, red chilli. Insecticidal soaps are used as a safer alternative in some occasions. Potassium silicate foliar sprays have been demonstrated to reduce the population of aphids by at least 60% with considerable reduction in the incidence of viruses in potato crops (Shah et al. 2019).

9.7 Conclusion and Future Outlook

The most significant type of damage inflicted by aphids in potato crops is through the spread of various potato viruses. Potato crops are infested by a number of colonizing and noncolonizing species of aphids, the noncolonizing aphids being more important for the spread of nonpersistent viruses like PVY. Various attributes of aphid biology and ecology have contributed to their success as crop pests. The host-finding and feeding behavior of aphids predisposes them to being the predominant vectors of various viruses. Controlling the spread of PVY remains a challenge to the potato industry worldwide because of its nonpersistent mode of transmission and the evolution of new strains and variants. The control strategies help reduce PVY transmission by aphids; however, each individual control strategy has its own limitations. Various countries operate networks of traps to monitor the flight activity of aphid species in seed potato. It has been reported that aphids other than *M. persicae* are more important for the early-season spread of viruses like PVY. Currently, the aphid management methods in potato are mostly reliant on the use of various insecticides and mineral oils. Besides, the use of infection-free seed, roguing, and use of cultural practices such as manipulation of planting and haulm-cutting dates are the most useful to keep the incidence of virus under control. Resistant cultivars (resistant to aphids and the viruses) with good agronomic traits and customer acceptance could go a long way in the sustainable management of vector-virus complex in potato.

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