Amer J of Potato Res (2002) 79:353-386

Invited Review

Aphid-transmitted Potato Viruses: The Importance of Understanding Vector Biology

Edward B. Radcliffe* and David W. Ragsdale

Department of Entomology, 219 Hodson Hall, 1980 Folwell Ave. University of Minnesota, St. Paul, MN 55108.
*Corresponding author: Tel: 612-624-977; Fax: 612-625-5299; Email: RADCL001@umn.edu

ABSTRACT

This review addresses some of the biological complexities presented by aphid-transmitted viruses of potato, *Solanum tuberosum* L., and their vectors and discusses the application of this knowledge to the management of potato viruses with particular emphasis on seed potato production.

INTRODUCTION

The disease cycle of insect-vectored pathogens represents a level of complexity beyond that of the classic disease triad of susceptible host, viable inoculum, and favorable environment (Ragsdale et al. 1994). The additional complication is the vector that must acquire and transmit the pathogen to enable progression of the disease. For most potato, *Solanum tuberosum* L., growers and their pest management advisors, the vector is the least understood component of this "disease tetrahedron." Sadly, in North America, research on aphid biology and ecology has been a largely neglected aspect of virus epidemiology and management. Some outstanding research has been done, but application of the science has lagged, and we have much more yet to learn. This deficiency is surprising since aphids are among the most important pests of temperate zone agriculture (Minks and Harrewijn 1987), and this is especially true for potato. Here we will review the biology and ecology of aphid vectors of potato viruses and discuss application of this knowledge in management of potato viruses.

Importance of Aphids

Aphids probably are of greater economic importance as potato pests worldwide than are defoliators or tuber pests. Aphids are important on potato primarily because of their role as virus vectors, but high aphid densities can cause direct plant injury and significant yield losses (Adams and Kelley 1950; Kolbe 1970; Shands et al. 1972c).

The most important aphid pest of potato is green peach (= peach-potato) aphid, *Myzus* (*Nectarosiphon*) *persicae* (Sulzer), (Hille Ris Lambers 1972; Radcliffe 1982; van Emden et al. 1969). *Myzus persicae* is a species complex that includes two other described species: tobacco aphid, *M. nicotianae* (Blackman) and *M. antirrhinii* (Macchiati) (Blackman and Paterson 1986; Blackman 1987). Genetic marker research cast doubt as to the validity of *M. nicotianae* as a distinct species, but confirmed validity of *M. antirrhinii* (Blackman and Spence 1992). Synonomy of *M. persicae* and *M. nicotianae* was indicated by analysis of populations from three continents and representing red and green color morphs. Random amplified polymorphic DNA-polymerase chain

---

Accepted for Publication May 3, 2002
ADDITIONAL KEY WORDS: *Myzus persicae*, *Aphis nasturtii*, *Macrosiphum euphorbiae*, *Rhopalosiphum padi*, Aphididae, *Solanum tuberosum*, seed potato, virus transmission, PLRV, PVY

reaction (RAPD-PCR), and mitochondrial cytochrome oxidase II (COII) and elongation factor 1 alpha (EF-1α) gene sequencing revealed few polymorphisms (Clements et al. 2000). Variants detected were not correlated with host plant or geographic origin. However, because *tobacco aphid* is economically important and biologically distinct it seems most appropriate to classify *nicotianae* as a subspecies of *M. persicae.*

North American potato specialists (mostly research and extension entomologists) surveyed in 1990 ranked *M. persicae* as either the first or second most important insect pest of potato in all production regions (Radcliffe et al. 1991). Other potato-infesting species of worldwide importance include potato (= green and pink potato) aphid, *Macrosiphum euphorbiae* (Thomas), buckthorn aphid, *Aphis nasturtii* (= *rhamni*) Kaltenbach, foxglove aphid, *Aulacorthum solani* (Kaltenbach), the melon (= cotton) aphid, *Aphis gossypii* Glover, complex (including *A. frangulae* [Kaltenbach]), bean (= black bean) aphid, *Aphis fabae* Scopoli, and the stolon-infesting, bulb and potato aphid, *Rhopalosiphoninus latysiphon* (Davidson) (Hille Ris Lambers and MacGillivray 1959; Raman and Radcliffe 1992; Robert and Bourdin 2001).

Aphid-transmitted Potato Viruses

Potatoes are subject to more than 30 virus diseases (Salazar 1996). All potato viruses contain single-stranded RNA. Viruses are obligate parasites and infection of new hosts depends upon assisted transmission. Depending upon the virus species, transmission can be mechanical through wounds, by a biological intermediary, or both. The most important vectors of potato viruses are aphids, and especially *M. persicae* (Eastop 1977; Ragsdale et al. 2001). Thirteen potato viruses are transmitted by aphids (Brunt 2001).

The most important virus diseases of potato are potato leafroll virus (PLRV, Genus *Polerovirus*, Family *Luteoviridae*) and potato virus Y (PVY = mosaic, Genus *Potyvirus*, Family *Potyviridae*), both aphid transmitted. Other aphid-transmitted viruses occurring in North America include potato virus A (PVA, *Potyvirus*), potato virus M (PVM, = paracrinkle, Genus *Carlavirus*), potato virus S (PVS, *Carlavirus*), potato latent virus (PLV, *Carlavirus*), alfalfa mosaic virus (AMV, = calico, Genus *Alfamovirus*, Family *Bromoviridae*), and cucumber mosaic virus (CMV, Genus *Cucumovirus*, Family *Bromoviridae*) (Brunt 2001; van Regenmortel et al. 2000).

Most viruses occur in nature as variants, which if they differ sufficiently from the type virus, are designated as strains (Salazar 1996). A number of strains of PVY have been described and vary in their symptomology in potato (Blanco-Urgoiti et al. 1998; Carnegie and van de Haar 1999; Nie and Singh 2002; Ohshima et al. 2000). Strains of PVY include PVY^{O} (ordinary or common strain), PVY^{N} (tobacco veinal necrosis), PVY^{C} (stipple streak strain), and PVY^{NTN} (potato tuber necrotic ringspot disease). PVY^{O} is worldwide in its distribution and produces severe mosaic, leaf drop, and stem necrosis in susceptible cultivars. PVY^{C} can produce hypersensitivity reactions. PVY^{N} first appeared in South America and Europe in the 1950s and more recently in North America. In potato, the symptoms caused by PVY^{N} are usually mild compared to PVY^{O}, and essentially asymptomatic in some cultivars, but PVY^{n} causes severe disease in tobacco. Worldwide, PVY^{N} appears to be increasingly common and is now predominant in much of Europe (Weidemann 1988). PVY^{NTN} was first identified in Europe in the 1980s and was recently found in North America (Singh et al. 1998). PVY^{NTN} causes a tuber defect that develops in storage, and makes the tubers unmarketable. All PVY strains are transmitted by aphids, but the PVY^{C} strain is transmitted only in the presence of a helper component the vector acquires feeding on PVY- or PVA-infected plants (Govier and Kassanis 1974a, 1974b).

Planting seed tubers with more than modest levels of virus infection (e.g., >10%) can result in yield and quality losses for the ware grower (Killick 1979; Reestman 1970; van der Zaag 1987). Viruses are of particular concern to seed potato producers because seed certification programs have low tolerances for virus infection (Allen et al. 1992; Gutbrod and Mosley 2001; Hiddema 1972). Tuber yields are rarely affected by current season inoculation of PLRV by aphids (= "primary infection") (Beemster and Rozendaal 1972), but infection can induce a tuber condition known as "net necrosis" in some cultivars, e.g., Russet Burbank, Green Mountain and Norgold Russet (Douglas and Pavek 1972). Net necrosis is expressed as a darkening of the vascular bundle that becomes more pronounced during storage (Roosen et al. 1997). Infection occurring mid to late season is more likely to induce net necrosis than is early season infection (Manzer et al. 1982). Primary infection with PVY can increase the number of undersized tubers (Hane and Hamm 1999). Potatoes are least susceptible to virus infection when plants are senescing and most susceptible during vegetative growth before flowering (DiFonzo et al. 1994; Whitworth et al. 2000).

Translocation of virus to tubers tends to slow as the plant matures, a phenomenon termed "mature plant resistance" (Beemster 1972, 1987; Sigvald 1985). Late-season tuber infection with PLRV can occur as soon as three days after inoculation (Storch and Manzer 1985), but typically few tubers become infected in the first week following inoculation (DiFonzo et al. 1994; Flanders et al. 1991; Whitworth et al. 2000). Mature plant resistance is cultivar specific for both PVY (Bagnall and Tai 1986a) and PLRV (Bagnall and Tai 1986b). Mature plant resistance to PLRV was pronounced in the cultivars Cascade and Abnaki (DiFonzo et al. 1995), but less evident in the cultivar Russet Burbank (Flanders et al. 1990). In the less-susceptible cultivars, mature plant resistance was more durable and more viruliferous aphids were needed to infect plants with PLRV.

In tubers, viruses are present in the vascular ring and buds. Germination of the bud permits virus multiplication and dispersal throughout the developing plant. The vascular ring connects the buds, but with some viruses not all sprouts may become infected if the titer is low or if there are obstacles to translocation, e.g., seedpiece decay.

Plants grown from seedpieces infected with PLRV or PVY (= "secondary infection") often produce no marketable tubers. Yield losses resulting from planting infected seed are variable, however, because of the complex nature of cultivar/environment interactions. Planting tends to disperse infected seedpieces throughout the field, and healthy plants growing next to gaps or diseased plants often yield more, partially offsetting any loss (Reestman 1970). Plants of cultivars that express only mild symptoms of infection can still be photosynthetically impaired and yield little, and because they are not stunted, compensation by adjacent plants is reduced.

Most seed potato certification programs use a limited generation production system (Allen et al. 1992; Franc 2001). Seed lots derived from tissue culture are required to be free of viruses. Tolerances are usually relaxed incrementally with successive generations in the program. If virus levels exceed tolerances, seed lots are downgraded to a more advanced generation or rejected outright if infection exceeds tolerance for certified seed. Typically, virus tolerances for seed lots to be increased another year range from 0% to 1%, and for seed used to plant ware fields from 1% to 5% infected tubers (Woodford 1988).

APHID SYSTEMATICS AND LIFE CYCLES

Aphids (Superfamily Aphidoidea) tend to be pests of temperate regions. About 4000 species occur in the superfamily. Aphid taxonomy is challenging with 20 recognized subfamily/family categories (Remaudière and Remaudière 1997). Our interest in this review is with Aphididae, species of which transmit 57% of known insect-vectored viruses (Blackman and Eastop 2000; Nault 1997).

Life cycles of the Aphididae are highly variable and often remarkably complex (Moran 1992). Clonal polymorphism is characteristic of and highly evolved in aphids (Kawada 1987; Miyazaki 1987). Polymorphism allows aphids to allocate resources efficiently to accomplish specific functions, but imposes constraints to performing other tasks (Dixon 1977). For example, resources allocated to developing flight muscles are not available for reproduction. In 97% of aphid species, reproduction is both asexual (parthenogenetic) and sexual, with multiple generations of asexual, viviparous reproduction between each occurrence of sexual reproduction (Blackman 1980). Aphids as a general rule have four larval instars (= nymphs), rarely five, before becoming adults.

The life cycle of *M. persicae* is heteroecious and typically holocyclic (van Emden et al. 1969; Blackman 1974). Eggs are deposited in fall on the primary host, certain *Prunus* (Rosaceae) species. In spring, these eggs hatch producing apterous, parthenogenetic, viviparous stem mothers (fundatrices). Winged progeny appear by the second generation, and the number and proportion of winged progeny peaks in the third generation on the primary host. Winged *M. persicae* invading potato can be true spring migrants from the primary host or alatae produced after several generations of parthenogenetic, viviparous reproduction (virginoparae) on secondary hosts, which include many common weeds and crops. Progeny of spring migrants are invariably apterous, but some proportion of each succeeding generation is winged. In late season, fall migrants are produced. These migrants are male and female. Female migrants that reproduce asexually on the primary host (gynoparae) give birth to apterous, sexual female progeny (oviparae). Oviparae mate with male migrants and produce fertilized eggs. In harsh climates, overwintering outdoors is not always possible. In the northern Midwest (e.g., 45°N) the time between appearance of fall migrants and leaf shed in *Prunus* appears insufficient to permit sexual reproduction (DWR personal observation). In milder climates and glasshouses, continuous asexual reproduction can occur. In some parts of the world, particularly in the tropics, clones can persist that have lost the ability to produce sexually. These "anholocylic" clones often retain the ability to produce some males.

In aphids, production of sexual morphs is influenced by photoperiod. Although the trigger appears to be short days, it is actually long nights (Lees 1959, 1966). This response is conditioned by many variables including temperature, crowding, and nutritional quality of the host plant. In northern climates, the advantage of sexual reproduction is obvious; the fertilized egg is the life stage most tolerant of cold. Anholcycly might seem advantageous where virginoparae can successfully overwinter outdoors. The fecundity cost of sexual reproduction is much greater than the proportion of males produced (Newton and Dixon 1988). Sexual reproduction occurs only once a year and even in temperate regions most aphid species show some tendency to abandon the sexual phase, but large populations increase the probability of a mutation occurring and becoming established (Blackman 1981). Sex must offer other advantages, however, since few aphid species are exclusively parthenogenetic. Possessing an egg stage can be an effective adaptation to declining host quality or temporal absence of foliage. Sexual reproduction may also serve to reset internal clocks that govern seasonal adaptations (Lees 1966).

Most aphid species are restricted in their host range to a single plant genus or even particular species (Eastop 1972). About 10% of aphid species, including all that colonize potato, show annual alternation of host plants (Eastop 1986). The primary (overwintering) host of heteroecious species is often a tree or woody shrub; the summer (secondary) hosts are commonly herbaceous and generally include a much broader range of host species. Only rarely is the primary host closely related to any of the summer hosts. *Myzus persicae* may be the most polyphagous of all aphid species: it is known to have more than 875 secondary hosts (Leonard et al. 1970, Tamaki 1981).

Dispersal to an alternate host generally requires production of winged progeny. In many species, contact stimulation from crowding appears to be the primary trigger inducing production of winged progeny that disperse to secondary hosts of the same or different species (Bonnemaison 1951). For example, in bird cherry-oat aphid, *Rhopalosiphum padi* (L.), and English grain aphid, *Sitobion avenae* (Fabricius), the proportion of offspring developing wings increases with crowding (Dixon and Glen 1971), and more so if both mothers and offspring experience crowding (Watt and Dixon 1981). Other cues that trigger or influence production of winged progeny can include deteriorating host quality (Sutherland and Mittler 1971), scotoperiod (Mittler and Matsuka 1985a, 1985b) or intrinsic maternal control mechanisms (Lees 1979).

The evolutionary success of aphids may be due to their flexible life cycles that enable them to track seasonal changes in host quality. Trees and shrubs can be excellent hosts early in the growing season, but most are poor or unsuitable hosts in summer (Dixon 1971a; Mordvilko 1928). Perhaps heteroecy evolved because environmental changes altered host plant physiology and weakened aphid specificity (Shaposhnikov 1987). It is assumed that woody hosts are the older association evolutionarily. Moran (1988, 1990) reasons that heteroecy is a complementary relationship because secondary hosts tend to be more nutritionally favorable, especially in summer. Returning to a single primary host may enhance mate finding (Ward 1987a, 1987b, 1991). Heteroecy also may enable aphids to escape natural enemies (Dixon 1998).

Alternation of hosts can benefit a species, but even in the Aphididae, heteroecy is the exception (Eastop 1986). Risk to the individual migrant is extreme. In one study, only 1 of 166 *R. padi* successfully migrated from the secondary to the primary host (Ward et al. 1998). Limited energy budgets dictate that the individual's opportunities to find a suitable host are "finite and few" (Dixon 1998). Moreover, production of winged forms is costly as winged morphs invariably take longer to complete their development and produce fewer progeny (Dixon and Howard 1986). Thus, host alternation can only be advantageous to a species if the migrating costs are offset by greater reproductive success on the secondary host. This may require several generations of reproduction on the secondary host.

APHIDS AS VIRUS VECTORS

Several authors have reviewed the role of aphids in transmitting potato viruses (e.g., Radcliffe 1982; Ragsdale et al. 2001; Robert and Bourdin 2001; Robert et al. 2000). A common theme of these reviews is that aphids possess biological attributes that make them especially effective in acquiring and transmitting plant viruses. Among the most important of these attributes are complex life cycles with specialized morphs adapted to different functions, alternation of host plants, and exceptionally short life cycles facilitated by parthenogenetic reproduction. Movement of virus into a potato field from an outside inoculum source is almost exclusively by winged aphids (Boiteau 1997; Broadbent 1950; Broadbent and Tinsley 1951). Within-field spread of PLRV is often by apterae walking from plant to plant (Flanders et al. 1991; Hanafi et al. 1989; Hodgson 1991; Ribbands 1963). Apterous *M. persicae* tend to be more efficient vectors of PLRV than winged morphs and nymphs more efficient than adults (Robert 1971). Apterae do not appear to play a significant role in within field spread of PVY (Ragsdale et al. 1994).

VIRUS TRANSMISSION CHARACTERISTICS

Aphid-transmitted viruses differ in how they are acquired, whether they circulate within the body of the vector, how they are transmitted to healthy plants, and how long a vector remains infective following virus acquisition. Once acquired, the aphid may be immediately capable of transmission, or a latent period may be required. With some viruses, the vector remains capable of transmission for only minutes to hours (Proeseler and Weilding 1975) or the first few feeding probes (Berger et al. 1987; Pirone and Harris 1977). With other viruses the vector remains capable of transmission for days or even its lifetime (Sylvester 1980).

Virus transmission patterns have been described using various classification schemes based on where virus is located in the vector, association of the virus with various internal organ systems, and how long the vector retains ability to transmit (Kennedy et al. 1962; Sylvester 1980). Nault (1997) proposed unification of these schemes recognizing four categories of virus transmission in Heteroptera: (1) nonpersistently transmitted, stylet-borne, (2) semipersistently transmitted, foregut-borne, (3) persistently transmitted, circulative, and (4) persistently transmitted, propagative. In categories 3 and 4, a latent period exists between acquisition and onset of ability to transmit. This lag occurs because the virus must pass through the gut into the hemocoel and enter accessory salivary glands before transmission can take place (Sylvester 1980). Once a vector acquires a persistently transmitted virus, it usually remains infective for life and capable of transmission even following a molt. PLRV is the only persistently transmitted, circulative potato virus (category 3). All other known aphid-transmitted potato viruses are nonpersistent, stylet-borne viruses (category 1). With nonpersistent viruses, e.g., PVY, no latent period occurs and the aphid remains viruliferous only for a few feeding probes following acquisition and never following a molt (Bradley and Rideout 1953). Clearly more dynamic processes are at work than mere contamination since not all aphids transmit all stylet-borne viruses (Nault 1997).

In secondarily infected plants, PLRV is found almost exclusively in phloem tissues, and most abundantly in companion cells (van den Heuvel et al., 1995). Thus, vectors must feed on phloem to acquire the virus. PLRV is only transmitted by aphids that colonize potato, and not by all colonizing species. PLRV has a latent period of 8 to72 h, but does not replicate in aphids (Eskandari et al. 1979; Tanaka and Shiota 1970). Both acquisition and transmission take minimum feeding times of 10-15 min (Miyamoto and Miyamoto 1966, 1971; Stegwee 1960) with maximum acquisition not occurring until about 12 h (Leonard and Holbrook 1978). *Myzus persicae* acquires more PLRV and tends to be able to transmit sooner when it feeds at higher temperatures (Syller 1994). PLRV is more readily acquired from the top leaves of young, secondarily infected plants than from older plants, but acquisition is not correlated with titer or feeding activity (van den Heuvel et al. 1993). Bacterial endosymbionts, *Buchneria* sp. (Cheilostomatida: Lepraliellidae), play a role in PLRV transmission (van den Heuvel et al. 1994). PLRV has a strong affinity for symbionin, the major protein synthesized and released into the hemolymph by *Buchneria* (Hogenhout et al. 1996, 1998; van den Heuvel et al. 1997). Mutant *M. persicae* lacking the endosymbiotic GroEL homolog cannot transmit PLRV. Treatment of the vector with antibiotics leads to rapid degradation of viral capsid protein and loss of infectivity. Unlike PVY, PLRV cannot be transmitted mechanically.

Myzus persicae is the most efficient, cosmopolitan, and commonly abundant vector of PLRV (Bradley and Rideout 1953; Hille Ris Lambers 1972; Robert 1971; Robert and Bourdin 2000; Woodford et al. 1995). Many populations of *M. euphorbiae* transmit PLRV poorly or not at all (MacKinnon 1969; Robert and Maury 1970; Tamada et al. 1984). In New Brunswick, however, *M. euphorbiae* has been implicated in early season spread of PLRV when *M. persicae* was not present (Singh and Boiteau 1986). *Macrosiphum euphorbiae* was also implicated as a consequential PLRV vector in Scotland (Howell 1974; Woodford et al. 1995). Other potential PLRV vectors that colonize potato in North America include *A. nasturtii* (Loughnane 1943), *A. solani* (Robert and Rouzé-Jouan 1971), and *A. gossypii* (Foster and Woodford 1997). In Europe, occasionally important PLRV vectors include *M. ascalonicus* (Hille Ris Lambers 1972) and *A. circumflexum* (Heinze 1960).

Most of the research on transmission of nonpersistent potato viruses has focused on PVY. More than 50 species of aphids have proven capable of transmitting PVY, including many species that cannot colonize potato (Boiteau et al. 1988; Harrington et al. 1986; Heimbach et al. 1998, Sigvald 1987, 1989; van Harten 1983). The nonpersistently transmitted stylet-borne viruses are relatively stable and reach high titers in epidermal and subepidermal plant cells. Acquisition and inoculation of PVY can occur in probes of just a few seconds duration (Bradley 1954). Puncture of the cell membrane is required for both acquisition and transmission (Pollard 1973).

Specificity of transmission varies greatly, not only at the species level, but differs among aphid biotypes and virus strains (de Bokx and Piron 1990; Harrington and Gibson 1989; Hinz 1966; Proeseler and Weidling 1975). A host plant previously infected with another virus can affect expression of host resistance to PVY and vector efficiency (Wilson and Jones 1993). We do not have sufficient information at this time to suggest that the transmission characteristics of PVY strains differ in ways likely to alter vector management strategies. It is, however, much more difficult to detect and rogue infected plants if infected plants are essentially asymptomatic.

Soybean aphid, *Aphis glycines* Matsumura, was discovered in North America for the first time in July 2000. This aphid is a known vector of a number of virus diseases including a variant of PVY, tobacco vein-banding mosaic virus (TVBMV, Genus *Potyvirus*) (Fang et al. 1985). *Aphis glycines* has not yet been implicated in the spread of PVY in potato, but its biology suggests cause for concern. *Aphis glycines* is a heteroecious, holocylic species. It is native to northern Asia where it overwinters on *Rhamnus davurica* Pall. In Minnesota, *A. glycines* has overwintered on *R. catharica* L. This aphid can reach exceptionally large populations in soybean, *Glycine max* (L.) Merrill, and shows a strong propensity to develop winged migrants.

Myzus persicae is the most efficient vector of PVY (MacGillivray 1981; Piron 1986), but the greater abundance of some less efficient vector species and their propensity to develop alatae can make them more important in PVY epidemiology, especially if migration occurs when potato plants are young (Boiteau et al. 1988; Harrington and Gibson 1989; Piron 1986; Sigvald 1987; van Hoof 1980; Weidemann 1988). PVY vectors common in North America include pea aphid, *Acyrthosiphon pisum* (Harris); *A. fabae*, *R. padi* (van Hoof 1977); *A. nasturii* (Harrington and Gibson 1989); *A. gossypii* (Raccah et al. 1985), *M. euphorbiae* (Singh and Boiteau 1986); and *Lipaphis erysimi* (Kaltenbach) (Sigvald 1989). In the U.K., leaf-curling plum aphid, *Brachycaudus helichrysi* (Kaltenbach), was one of the most abundant and efficient vectors of PVY (Harrington et al. 1986). Several cereal aphids are capable of PVY transmission (Harrington et al. 1986; Harrington and Gibson 1989; Kostiw 1979; Piron 1986; van Hoof 1980) and have sometimes been implicaticated as contributing to PVY epidemics (DiFonzo et al. 1997; Sigvald 1986; van Harten 1983).

HOST SELECTION/PROBING BEHAVIOR

An aphid's acceptance or rejection of a host plant is a complex process governed by visual, tactile, and chemical cues (Klingauf 1987a, 1987b). From contact with the leaf surface and probes lasting from a few seconds to several minutes in the epidermis, an aphid receives stimulatory cues communicating whether to continue probing. Excitatory gustatory stimuli tend to increase the frequency and duration of probes (Klingauf 1975). If the host provides appropriate cues, the aphid settles and probes deeper, the stylets eventually reaching the phloem (Pollard 1977). Most aphids are ultimately phloem feeders with final host acceptance dependent upon the qualitative and quantitative properties of the phloem (van Emden 1972). To reach the phloem can take from several minutes to more than an hour (Auclair 1963). In piercing plant tissue, the mandibles move alternately to channel a path for themselves and for the salivary and food canals formed between paired maxillae. Initial penetration is usually intracellular, and aided by hydrolytic enzymes. Aphids generally cause little cellular damage with their host exploring behavior, but their strategy of "sap sampling" by means of brief cell membrane penetrations to determine acceptance or rejection of a plant facilitates aphid transmission of nonpersistently-transmitted stylet-borne viruses. PVY acquisition is associated with intracellular ingestion and inoculation with salivation (Martín et al. 1997). Stylet paths that ruptured the cell wall behind the advance of the stylet tips and formation of the salivary sheath did not result in acquisition of PVY by *M. persicae* from tobacco, *Nicotiana tabacum* L., but acquisition occurred whenever the stylet tips came in contact with virus-laden cytoplasm (Lopez-Abdella et al. 1988).

The influence of plant chemistry on aphid feeding has been reviewed by Montllor (1991). Host selection in aphids appears closely linked to nutritional suitability and the absence of deterrent allelochemicals (Schoonhoven and Derksen-Koppers 1976). Phloem sap generally has low nitrogen concentrations; thus aphids tend to be sensitive to variations in the nitrogen content in their host plants. For example, reproduction of cabbage aphid, *Brevicoryne brassicae* (L.), and *M. persicae* on Brussels sprouts, *Brassica oleracea* L. var. *gemmifera*, was correlated with soluble nitrogen in the leaves of the same age and position (van Emden and Bashford 1969, 1971). Probing duration by *M. persicae* on artificial diets was longer when the diet included sucrose and amino acids (Mittler and Dadd 1965). Growth rates of *M. persicae* are correlated with amino acid concentrations, especially methionine and, to lesser degree, cysteine and histidine (Mittler 1970). The role of other amino acids and sucrose appears to be primarily as phagostimulants until the phloem is reached (Pelletier and King 1987).

MIGRATION AND LOCAL DISPERSAL

Migration enables spatial redistribution of insect populations (Taylor and Taylor 1983). Winged morphs can be considered obligate migrants (Dixon 1971b) with their production stimulated by environmental cues at least one generation in advance of appearance.

When the alatiform nymph becomes an adult, it is incapable of responding to flight stimuli until sclerotization is completed (Taylor 1957; Woodford 1969). Once this teneral period is completed, flight propensity gradually increases (Kennedy and Booth 1963a, 1963b). Each species has a minimum temperature threshold for flight initiation, e.g., 12.8 C for *M. persicae* (Broadbent 1949), and most species do not fly when temperatures are much above 30 C (Boiteau 1986; Robert 1979). Aphid flight requires a minimum light intensity threshold. Flight propensity is greatest in most species at intensities above 1000 lux (Robert 1987). Aphids are slow flyers (typically, 1-3 kmh^{-1}) and most inclined to take off at low wind speeds (e.g., <5 kmh^{-1}). Aphids, however, are capable of flight with winds of 12-13 ms^{-1} (>40 kmh^{-1}) and their tolerance of wind increases with age (Haine 1955).

In many aphid species, the maiden flight can be of extended duration (Johnson 1969; Moericke 1955). On taking off for the first time, aphids usually fly directly upward for several minutes in response to short-wavelength light (UV and blue) from the sky until that tendency is balanced by their response to reflection of long wavelength light (>500 nm) from foliage (Kennedy and Booth 1963a, 1963b). After reaching elevation, typically in the range of 8 m, their path of flight becomes horizontal. The aphid then engages in flight that can last for hours ("stratified migration") (Taylor 1965, 1974). When winds are below 5 kmh^{-1}, airflow tends to be laminar. Although an aphid's speed and flight direction are largely determined by wind, aphids actively terminate flight by flying down (repelled by UV or blue light). Thus, aphids have some control over the distance they travel and considerable control over their final destination. Many species, e.g., *M. persicae* and *M. euphorbiae*, autolyse their flight muscles within the first few days following their maiden flight (Johnson 1957, 1959).

Most days wind speeds exceed 5 kmh^{-1} and airflow is not laminar. Aphids flying in wind can become caught up in convection currents or air turbulence. Although relatively weak fliers, aphids can be lifted by convection currents to high altitudes (300-900 m) and transported long distances rapidly on upper air currents ("jet streams"). To remain aloft aphids must continue active flight as jet streams have little lift (Thomas et al. 1977). The vertical distribution profile of aphids in upper air is similar to that of dust or fungal spores indicating passive transport (Taylor et al. 1979). Migration is not directional; instead, the resulting distribution pattern and density gradient is dependent upon wind direction and the degree of air turbulence. In general, long-distance transport has less impact on population and genotype distribution than short-distance movement (Loxdale et al. 1993). For aphid pests that cannot overwinter in a particular location, annual variation in the pattern and success of migration may greatly influence pest status.

The distance that aphids fly has important implications for the epidemiology of plant viruses, especially those that are transmitted persistently. The maiden flight of aphids is not always of long distance. A release and recapture experiment under cloudy conditions using large numbers of radio-labeled *M. persicae* alatae revealed that few made maiden flights of greater than 100 m (Harrewijn et al. 1981). Thus, the pattern of within-field PLRV spread we usually associate with apterae could also result from spread by alatae. In locations with holocylic reproduction of *M. persicae*, e.g., the U.K. (Burt et al. 1964), the Columbia Basin of Washington (Thomas et al. 1997b), southern Idaho (Bishop 1967), and Maine (Shands et al. 1969), spread of PLRV tends to occur mostly in early and late summer, with little spread during mid-summer. Early summer spread might seem improbable. For that to occur, winged aphids originating from the primary host must make their maiden flight, land on a PLRV-infected host, settle and feed long enough to acquire the virus, then fly to a second host which they then inoculate. Some evidence suggests that spring migrants retain their flight worthiness longer than do alatae produced on summer hosts (Woodford 1968). In locations where anholocylic reproduction occurs, migrants may move directly into potato from secondary hosts infected with virus (Hanafi *et al.* 1995).

A variety of genetic markers have been used to deduce information about the origins of migrant aphid populations and subsequent spatial and temporal movement. *Myzus persicae* populations in Scotland are reestablished each spring from populations that overwinter in protected sites or winter crops and weeds in the south and east of England. Genetic analysis of clonal variation using an rDNA fingerprinting technique revealed numerous genotypes among *M. persicae* clones collected in Scotland, but one clonal type, apparently unique to Scotland, predominated in all locations sampled (Fenton et al. 1998). This contrasted with the finding of little clonal commonality among *M. persicae* populations in a similar sized area of Spain (Martínez-Torres et al. 1997a). The unique Scottish clone was found over successive years suggesting that it successfully overwintered in local protected sites. Clones with distinctive fingerprints were found to be widely distributed suggesting this molecular technique could be used to follow dispersal of individual clones.

POPULATION DYNAMICS

Aphids have potential population growth rates unmatched by other insect taxa. Pesticide-induced outbreaks of *M. persicae* on potato or sugar beet, *Beta vulgaris* L., can approach 2×10^9 aphids ha^{-1} and produce 1.5×10^6 winged emigrants ha^{-1} (Dixon 1971b). During periods of exponential growth, intrinsic rates of increase (r_m) in some aphid species can be greater than 0.4 per day (Barlow 1962; DeLoach 1974; Kindlmann and Dixon 1992). Under optimal conditions, aphids of most species develop from birth to reproductive maturity in about 1 wk, which is only a third of the time required for most similarly sized insects (Dixon 1990). For example, mean generation time for *M. persicae* is 130 DD, base 4 C (Whalon and Smilowitz 1979a). Aphid generations are, in effect, compressed ("telescoped") because reproduction is parthenogenetic and viviparous (Kindlmann and Dixon 1989). At maturity, developing embryos make up a large proportion of an aphid's weight and larger embryos themselves can have developing embryos. This enables aphids to achieve ratios of population growth to individual relative growth rates (r_m/RGR) of ~0.9, approaching the theoretical maximum, given energetic constraints, for mortal organisms (Kindlmann et al. 1992). Population growth rates in aphids are more dependent upon development rates than fecundity, and rate of reproduction in early adult life is more important than total reproductive capability in achieving reproductive potential (Dixon 1998). Within a season, aphid populations tend to grow exponentially and then crash as resources degrade (Dixon 1994). A small difference in reproductive success on an alternate host can quickly compensate for the huge risks associated with dispersing (Ward 1992a, 1992b). High intrinsic growth rates of aphids may have been the primary attribute that enabled the evolution of host alternation in aphids.

The population dynamics of aphids are difficult to study because aphids have overlapping generations and unstable age structures (Dixon 1998). Seldom do aphid populations show the seasonal cycling of density expected with regulation by natural enemies suggesting that the normal pattern is only weak regulation within a season. This counter-intuitive observation may simply reflect that ability to detect density-dependent mortality depends on what processes are involved and what methods of detection are used (Turchin 1990). Data from annual suction-trap surveys show that captures of many aphid species are cyclic and consistent with time-lagged density-dependent regulation (Bagnall 1992; Woiwod and Hanski 1992). These data, however, give no insight into the mechanisms of such regulation. Simulation modeling suggests that weather is a major disturbing factor and determinant of peak densities (Barlow and Dixon 1980).

Biological Control

Effective biological control of aphids on potato might seem unlikely given the current intensive use of pesticides by growers. Aphids on potato, however, seldom reach densities sufficient to cause direct plant injury except when outbreaks are induced by multiple applications of a foliar insecticide to which the aphid population is more refractory than are resident natural enemies (ffrench-Constant et al. 1988b; Harrington et al. 1989).

Aphids on potato are attacked by many parasitic Hymenoptera, mostly in the subfamily Aphidiinae (Braconidae, superfamily Ichneumonoidea) and Aphelinidae (superfamily Chalcidoidea) (Starý 1988a, 1988b). All Aphidiinae are aphid parasitoids with almost one third of the species apparently restricted to a single host species, but the evolutionary trend within the Aphidiinae appears towards oligophagy. Not all Aphelinidae are aphid parasitoids, but those that are tend to have a high degree of host specificity. Oligophagy is probably advantageous for these parasitoids since aphid populations tend to cycle between rapid increase and local extinction. Aphid population regulation by aphid parasitoids is often greatly diminished by hyperparasitoids (Sullivan 1988; Sullivan and van den Bosch 1971). Evidence exists that in some situations hyperparasitoids may actually be beneficial. In inherently unstable host/parasite systems, hyperparsitoids may help maintain a balance between the primary parasitoid and its host by preventing excessive buildup of parasitoid numbers (Beddington and Hammond 1977).

Typically, aphids are low-density pests on potato suggesting that generalist predators contribute more than parasitoids to holding newly established aphid populations in check (Mackauer and Way 1976). High parasitism rates are sometimes observed, especially at the end of aphid outbreaks, but more commonly parasitism rates on aphids in potato are low. For example, parasitism of *M. persicae* never exceeded 0.63% per year in Maine from 1941 to 1962 (Shands et al. 1965). During that period, predators were said to be responsible for 14 of 31 observed declines involving three aphid species on potato; entomopathogenic fungi were credited with the remaining 17 (Shands et al. 1972a, 1972b). Coccinellidae (ladybird beetles), Chrysopidae (lacewings), Anthocoridae (minute pirate bugs), Syrphidae (hover flies), Nabidae (damsel bugs), and Lygaeidae (big-eyed bugs) were the most important predators. On peach, generalist predators were much more important in regulating *M. persicae* than were parasitoids (Tamaki et al. 1967). Entomopathogenic fungi occasionally cause high levels of mortality of *M. persicae* fundatrices on peach in Washington State. It was suggested that irrigation could be manipulated to enhance this mortality (Kish et al. 1994). When aphids escape regulation by predators, their intrinsic growth rates tend to preclude within season recovery of regulation.

CULTURAL PRACTICES TO CONTROL VECTORS AND VIRUS SPREAD

Approaches to management of virus spread in potato can be categorized as preventive or therapeutic (Ragsdale et al. 2001). Prevention tends to focus on reducing inoculum, a primary objective of all seed certification programs (Franc 2001; Garrett 1986; Slack 1993), with therapeutic action focused on vector reduction. Certification programs are often so successful in eliminating inoculum that seed potato growers are tempted to become careless about vector management. Whenever seed lot rejections for virus rise, vector control therapies, especially insecticides, become a priority concern. Insecticides are the only practical means of suppressing vectors on the crop, but at best only minimize the spread of aphid-transmitted viruses. High levels of virus inoculum can negate any benefit of aphid control (Sigvald 1989). Often it can take several years to reduce the presence of virus inoculum in the seed production system sufficiently to end an epidemic (Harrison 1971). Unfortunately, whenever seed lot rejections increase or seed potatoes are in short supply, regulatory agencies are likely to be under pressure to relax phytosanitary standards, if only temporarily, but to do so will probably exacerbate the situation.

Spatial Isolation of Seed Potato Production

Ideally, seed potato increase should occur in areas well isolated from ware production, i.e., where sources of disease inoculum are unlikely to be present (Wurr 1978). To achieve this isolation, many U.S. states and Canadian provinces have established seed farms or designated geographic areas where potato production is limited to seed. In some countries, seed production is concentrated at high altitudes or along wind-swept coasts where few aphids occur. Seed potato production in Scotland is favored by harsh winters that generally prevent winter survival of aphids and volunteer potatoes that could harbor virus, and by cool, windy summers that keep the region comparatively aphid-free (Hollings 1955). In British Columbia, elite seed is grown in the Pemberton Valley, ~150 km from commercial potato production in the Fraser Valley (Frazer 1987). However, geographic isolation is never total, and the potential always exists for alate infective aphids to arrive from even a distant origin.

In most countries, and generally in North America, there is little isolation of late-generation seed and commercial production. The question is not what degree of isolation would be optimal, but what is the minimum separation required to reduce to an acceptable level the risk of virus spread from sources of virus inoculum or crops that produce large vector populations? In southeastern Scotland, spread of PLRV was found to be largely from inoculum sources within the crop (Cadman and Chambers 1960; Howell 1974; Woodford et al. 1983). Based on vector flight behavior as evidenced by captures in suction traps in eastern Idaho, Halbert et al. (1990) suggested 400 m to 5 km could provide effective isolation from known PVY sources, but that 30 km or more might be required for isolation from PLRV sources. Greater isolation distance is needed to limit PLRV spread because the persistent, circulative mode of transmission of this virus allows the vector to remain infective for life. In England, minimum separation of 800 m is recommended from potential sources of PVY (Harrington et al. 1986). In Denmark, a distance of just 40 m was shown to reduce spread of PVY (Hiddema 1972). Seed growers generally have limited flexibility in locating their seed fields, thus other cultural control methods and vector management assume greater importance. The regional nature of potato virus management problems is a compelling argument for industry-wide cooperation between growers and regions to effect inoculum reduction and vector management.

Temporal Isolation of Seed Potato Production

Isolation can also be achieved by modifying planting or harvesting dates. Early planting and haulm destruction ("vine-kill") dates have been recognized as an effective method of maintaining the health of elite seed stock in the Netherlands since 1810 (Hille Ris Lambers 1972). Early planting can be a useful strategy if the principal vector species do not begin colonization until late in the growing season. The more advanced the crop growth stage at the time of inoculation, the less likely daughter tubers will become infected. Unfortunately, in many northern temperate production areas, growers have limited flexibility in choosing planting dates because the growing season is short (Singh and Boiteau 1987). Preconditioning seed hastens plant emergence, but usually produces a lower leaf area index and often leads to earlier senescence; however, preconditioning can increase yields in potatoes harvested early (Allen et al. 1992).

A different temporal isolation strategy was used in the Netherlands in the early 1950s, with planting delayed so that plant emergence occurred after the colonization flight of *M. persicae* was over (Hille Ris Lambers 1972). This practice ended when a new strain of late blight made late planting impractical. In Maine, Shands et al. (1972c) found 50% less virus spread in late plantings compared to early plantings. They attributed this difference to late plantings missing early influxes of aphids, which resulted in a lower vector population developing in the field. Delayed planting was suggested as a PLRV control strategy for the spring-planted crop in one seed potato production area in Morocco (Hanafi et al. 1995) and in Cyprus (Ioannou 1989), where colonizing aphid flights persist for only a few weeks in the early-spring. In New Brunswick, late-planted potato plots had lower densities of *A. nasturtii* and *M. euphorbiae* suggesting that delayed planting could improve seed health (Boiteau 1984). Yield and tuber size were compromised, however, because haulms had to be killed before the mid-August migration of *M. persicae.* At the end of the growing season, rapid vine-kill is important to limit alate aphid production and reduce opportunity for virus movement to tubers in infected plants.

Many seed growers perceive that plants grown from minitubers are more susceptible to virus infection. The evidence suggests that when such differences occur they are not related to the origin of the seed lots, but to differences in the physiological age of the plants when vectors are active (Boiteau et al. 2000).

Roguing

Roguing, the physical removal of symptomatic plants from a field, is an important virus management tactic (Thresh 1988). This procedure is most practical when the incidence of virus infection is low and the field is small enough that every plant can be inspected several times during the growing season. Roguing should begin as soon as symptoms of secondary (tuber-borne) infection can be seen, typically when plants are 15-20 cm tall. Roguing is easiest to accomplish before the canopy closes (Woodford and Gordon 1990). The goal must be to remove all infected plants before winged aphids arrive. Many seed certification programs require roguing if virus infection is detected in field inspections. When roguing PLRV-infected plants after aphid colonization, plants surrounding the symptomatic plant should be removed because these neighboring plants may be infected, but not yet symptomatic (Mowry 1994). Virus spread can occur from these missed infected plants later in the season. If plants are rogued after aphids colonize the crop, viruliferous aphids may be dislodged in the process of plant removal. Treating a field with insecticide 1 wk before roguing did not reduce virus spread (Woodford and Gordon 1990). If the seed field is heavily infected (e.g., >~1% virus), roguing is often ineffective because infected plants will be missed. Tuber indexing, the practice of planting all seedpieces from a single tuber in a block, makes virus-infected plants easier to rogue (Franc 2001). Removing many infected plants can leave gaps in the field that increase the apparency of plants on the margins to immigrating winged aphids (Bell 1989). Late-season roguing is often impractical because symptom expression then tends to be less discernable (Woodford and Barker 1986) and chronically infected daughter tubers may be left after haulm removal.

Mechanical Barriers and Border Crops

Cultural manipulations that interfere with the phototactic responses of vector aphids can disrupt host plant selection and restrict virus spread (Antignus 2000). Aphids, particularly *M. persicae,* are attracted to yellow and repelled by highly reflective surfaces (Kring 1970). Ringing peppers, *Capsicum annuum* L., with sticky yellow polyethylene sheets reduced spread of PVY (Cohen and Marco 1973) and PLRV (Zimmerman-Gries 1979). Spraying whitewash also reduced PVY in peppers (Marco 1993). Similarly, mulches, e.g., aluminum foil (George and Kring 1971), white plastic (Wyman et al. 1979), and oat, *Avena sativa* L., straw (Setiawan and Ragsdale 1987) reduced the spread of insect transmitted pathogens in various crops.

Polymer webs can provide a high degree of protection against aphid-transmitted viruses (Avilla et al. 1997; Harrewijn et al. 1991; Hemphill et al. 1988). The cost and inconvenience of using row covers limit their application in seed potato production to high-value seed fields of small size such as the first field increase following propagation in the greenhouse or laboratory. Potato is particularly sensitive to shading and tuber yields are reduced even under coarse netting.

Barrier crops are more widely adaptable than mulches or floating row covers since they are easier to install and keep in place, and do not lose effectiveness due to weathering or as the canopy closes. Contrary to earlier preconceptions, barrier crops need not be taller than the crop protected (DiFonzo et al. 1996). Barrier crops of forage sorghum, *Sorghum bicolor* (L.) Moench), spring-planted winter wheat, *Triticum aestivum* L., or soybean reduced PVY spread equally. Routinely treating borders of spring-planted winter wheat and forage sorghum with insecticides to control cereal aphids did not increase their effectiveness in reducing PVY compared to untreated barrier crops. Barrier crops should have a fallow border to the outside with no gap between the barrier crop and the potatoes to take advantage of the tendency of winged aphids to alight at the interface of fallow ground and green crop. If immigrating alatae carrying PVY feed first on the border crop, they will probably lose their virus inoculum before moving into the potatoes (DiFonzo et al. 1996). Barrier crops need not be more than a few meters wide to be effective. In Lower Saxony, oat borders just 1 m wide lowered the number of winged aphids, and especially *R. padi*, caught in potato fields and was more effective in reducing PVY spread than the intensive use of insecticides in comparison plots (Thieme et al. 1998).

Small plots bordered by fallow are essentially targets for alighting aphids. That fact notwithstanding, it has been standard practice for seed growers to leave fallow strips or skip rows between seed lots to maintain varietal purity, and some seed certification programs mandate such gaps. Planting a border crop, or ground cover, e.g., spring-planted winter wheat, between seed lots would reduce apparency to immigrating aphids. Alternatively, growers could maintain the outer rows as a separate seed lot from the inner rows. In the Netherlands, the first 10-25 m of the seed field adjacent to a known virus source is either downgraded or rejected (Hiddema 1972).

Environmental Manipulations

The most vulnerable period in the life of a holocyclic aphid is passed on the primary host. Various environmental manipulations have been devised to exploit this vulnerability. *Myzus persicae* overwinters in northern Maine on Canada plum, *Prunus nigra* Aiton (Shands et al. 1969). A concerted effort was made over many years to eradicate this host. The program apparently met some success, delaying aphid infestation of potatoes by about two weeks (Hammond and Holbrook 1979). In the Columbia Basin, peach, *Prunus persica* L., is the overwintering host of *M. persicae*. Control measures used there include application of defoliants to peach before oviparae mature (Tamaki and Powell 1972; Tamaki and Weeks 1968), providing tree-bands to shelter predators (Tamaki and Halfhill 1968), pruning to remove overwintering eggs (Tamaki and Powell 1968) and eliminating weeds in orchards and irrigation ditches that serve as early season aphid hosts (Tamaki and Olsen 1979; Tamaki et al. 1980; Wallis and Turner 1969).

Castle and Berger (1993) found that plants infected with either PLRV or PVY were superior hosts of *M. persicae*, but that the aphids were not benefited by their host plants being infected with potato virus X (PVX, Genus *Potexvirus*), a virus not aphid transmitted. Virus infection can also affect host selection because *M. persicae* preferentially landed on PLRV-infected potato in a dark arena (Castle et al. 1998). Volatiles collected from PLRV-infected potato plants were more attractive and arrested *M. persicae* apterae longer compared to virus-free, PVY- or PVX-infected potatoes (Eigenbrode et al. 2002). Clearly, the association of aphids with their hosts is complex and this interaction becomes more so when plants are infected with aphid-transmitted viruses.

Weed Hosts of Potato Viruses

In temperate climates, most of the known weed hosts of PVY or PLRV are annuals, and transmission via true seed does not occur (Salazar 1996), effectively eliminating these species as virus sources. In Canada, no weed is considered a virus reservoir (Singh 1987), although a systematic survey has not been done. The winter annuals shepherd's purse, *Capsella bursa-pastoris* L., and Jim Hill mustard, *Sisymbrium altissimum* L., are known PLRV hosts, but appear unimportant in spread of the virus to potatoes (Thomas et al. 1997b; Woodford 1988). In the Souss Valley of Morocco, jimsonweed, *Datura stramonium* L., supports *M. persicae* populations before the winter potato crop emerges. This weed and volunteer potatoes were implicated as being principal sources of both viruliferous aphids and PLRV inoculum (Hanafi et al. 1995). Volunteer potatoes that emerge as weeds in rotation crops in the Columbia Basin are considered important PLRV reservoirs (Thomas 1983) and potatoes sprouting in cull piles have been implicated as a source of virus in Canada (Frazer 1987). In regions where winter frost extends below the root zone of potatoes, volunteer potatoes are rare and appear to be inconsequential sources of potato viruses (DiFonzo et al. 1997). Because ware producers often plant tubers with 1% to 5% virus (375 to 1800 infected plants per hectare), the crop itself generally overshadows perennial weeds as a source of potato viruses. Defoliants that prevent daughter tubers from sprouting, e.g., glufosinate-ammonium, may be an effective means of eliminating virus-infected volunteers.

Landscape Ecology

Changes in cropping patterns may change the effective isolation of a seed production area. For example, with increased production of winter rapeseed, *Brassica napus* L., in Scotland, virginoparous *M. persicae* successfully overwintered on this crop and resulted in earlier colonization of potato (Woodford 1988). The recent increase in hectarage of canola (a new crop derived from winter rapeseed) in Minnesota and North Dakota has been accompanied by a concomitant increase in the rejection rate of seed potato lots for excess virus (Radcliffe et al. 2002). In the northern Midwest, canola is an early spring-planted crop that matures in late July and appears to serve as a highly acceptable early season "bridging" host for migrant *M. persicae* that arrive before potatoes have emerged. Canola is also an excellent host for *L. erysimi*, a known vector of PVY (Heinze 1960; Sigvald 1989). *Lipaphis erysimi* was suggested as possibly contributing to a recent PVY epidemic in the Red River Valley (DiFonzo et al. 1997). In the Columbia Basin, three distinct flights of *M. persicae* occur (Thomas et al. 1997b). The spring migrants from peach appeared to be PLRV-free. The summer migrants, presumably from volunteer potatoes, winter rapeseed and weed hosts, were PLRV-infected. The fall migrants arrived so late they did not affect potato production. Winter rapeseed (Argentine) varieties and spring rapeseed (Polish), *B. campestris* L., varieties are not hosts for PLRV, but these crops were colonized in early season by *M. persicae*, producing migrants that dispersed to other hosts including potato in early summer (Thomas 1983).

PESTICIDES/INSECTICIDES

In 1972, the President of the United States coined the phrase Integrated Pest Management and committed the country to its development and implementation (Nixon 1972). Recently, considerable progress has been made in reducing the use of high-risk pesticides in the potato industry (Benbrook et al. 2002). However, dependence of North American potato producers on intensive pesticide inputs has not diminished. Much of the insecticide used on potato is targeted against pests other than aphids, but more than one third of all applications in the U.S. are specifically intended for aphid control (Guenthner et al. 1999; NASS 2000). Circumstances in which use of insecticides for aphid control is imperative in potato production are (1) to reduce abundance of colonizing virus vectors in seed production, (2) to prevent spread of PLRV in cultivars susceptible to net necrosis in ware production, and (3) where previously used insecticides targeted against other insect pests of potato have induced aphid outbreaks (Radcliffe et al. 1991).

The optimal timing of insecticide applications for control is regionally specific due to differences in time of aphid arrival with respect to crop maturity, whether immigrating alatae are carrying virus or must acquire it from sources within the field, and the ultimate use of the crop. In the Pacific Northwest, flights of *M. persicae* occur primarily in mid-June and mid-August with little flight activity between those dates. On potato, apterae peak in mid-summer with alates produced again in fall. Protecting the crop with insecticides in this situation has been most important in spring and fall. Recently, this area has seen an increase in production of an early season crop (typically the cultivar Shepody) grown for processing in mid-summer directly following harvest, before the storage crop (mostly Russet Burbank) is mature. Some growers vine-kill the early season crop by withholding irrigation. This management induces mid-summer production of winged aphids and has contributed to an increased incidence of PLRV in Oregon and Washington. In the northern Midwest, *M. persicae* does not overwinter locally (Mackauer and Way 1976). Summer populations are reestablished each spring, possibly from populations overwintering asexually on winter crops and weeds in the southcentral U.S. These migrants may arrive before potatoes have emerged, and presumably most colonize weeds and canola. Peak flight activity occurs in mid-summer. These alatae are assumed to be coming primarily from local secondary hosts, but many of the mid-summer immigrants to seed potato fields do carry PVY (DiFonzo et al. 1997) and PLRV (Radcliffe et al. 2002). Alatae moving into seed potato fields in late summer are likely to have originated in commercial potato fields. While this situation greatly increases the probability of their being viruliferous, their numbers are much lower than occur in mid-summer and potatoes are less susceptible because of mature plant resistance. In Eastern Canada, *M. persicae* flights occur late in the season making applications of insecticide against this species generally ineffective (MacGillivray 1972; Boiteau and Parry 1985).

Insecticides are of inconsistent benefit in controlling virus spread. Among reported successes of controlling virus spread by use of insecticides (all crops and insect vectors), 94 of 119 cases involved persistent and semi-persistent viruses (Perring et al. 1999). Most of the failures, 32 of 48 cases, involved nonpersistent viruses. Even when aphicidal residues are present, viruliferous alatae generally are not killed quickly enough to prevent virus transmission (Boiteau et al. 1985; Broadbent et al. 1957; Lowery and Boiteau 1988). Spread of PLRV from within field sources can be interrupted because of the extended post-acquisition latent period required before an aphid is able to transmit (DiFonzo et al. 1995; Flanders et al. 1991; Hanafi et al. 1989; Leonard and Holbrook 1978). Insecticides seldom kill quickly enough to prevent spread of PVY (Ragsdale et al. 1994; Shanks and Chapman 1965).

Insecticides Applied to Foliage

Insecticides applied as sprays to the foliage can be very effective in reducing resident aphid populations. Coverage is critical, particularly when targeting *M. persicae*, which tends to colonize leaves in the lower canopy. Spray applications tend to be much less effective against immigrating aphids because the persistence of aphicidal residues is often shorter than the interval between spray applications.

Movement of sprayers through the crop may promote interplant movement and aphid flight activity increasing virus spread (Klostermeyer 1959). This effect may be less important with fast-acting insecticides (Perrin and Gibson 1985). Certain insecticides, e.g., some pyrethroids, induce immediate hyperactivity and rapid incapacitation of vectors that can reduce potyvirus spread (Gibson et al. 1982a; Sawicki et al. 1983). Alternatively, insecticides that irritate aphids can increase spread of both PLRV (Klostermeyer 1959) and PVY (Gabriel et al. 1981; Gibson and Campbell 1986).

Methamidophos (an aliphatic organophosphate) has been used for aphid control on potatoes for 30 years and in North America is considered the standard for foliar application because of its consistent efficacy against *M. persicae*. Two thirds of the use of this insecticide in the U.S. is on potatoes, with 175,000 kg AI used in 1999. Annual economic benefit of methamiphos use on potato in the U.S. is estimated to be $281 million (NASS 2000). In North America, resistance to methamidophos has not been a problem in *M. persicae*; however, an 18-fold increase in methamidophos resistance was measured recently in populations from Washington State (M. Whalon, pers comm). Insecticide efficacy varies among species, e.g., *A. gossypii* tends to be tolerant of methamidophos, perhaps because the product has been used extensively to control this insect on cotton.

Imidacloprid (a neonicotinoid subclass chloronicotinyl) is used on potato as a systemic at planting or as a foliar insecticide. As a foliar insecticide, imidacloprid has a relatively slow mode of action on aphids that may reduce its effectiveness as a foliar insecticide for controlling PLRV spread by immigrating viruliferous aphids (Boiteau et al. 1997). Thiamethoxam (a neonicotinoid subclass thianicotinyl) reaches the mesophyll more rapidly than imidacloprid with aphids showing behavioral responses within 15 to 30 min (Harrewijn *et al.* 1998).

Pymetrozine represents a new class of insecticide chemistry (pyridine azomethine) and is an aphid-specific insecticide with unique mode of action. Pymetrozine is a central nerve poison, but does not kill directly. Instead, pymetrozine disrupts feeding behavior and interferes with stylet penetration (Harrewijn and Kayser 1997). Once exposed by contact or ingestion, aphids cease to feed within 20 min and apparently never recover ability to feed; however, death can take 5 days or more. When *M. persicae* viruliferous with PLRV were caged on pymetrozine-treated potatoes, transmission was reduced for up to 14 days following application (DWR et al. unpublished). The exceptional selectivity of pymetrozine suggests that it would be appropriate for early to mid-season use to conserve aphid natural enemies.

Use of certain insecticides can trigger massive aphid outbreaks by eliminating natural enemies or directly stimulating increased reproduction (Gordon and McEwen 1984; Lowery and Sears 1986a, 1986b). Most organophosphate, carbamate and pyrethroid insecticides registered for use on potato tend to flare outbreaks of potato-colonizing aphids, especially *M. persicae* (ffrench-Constant et al. 1988b; Foster 1986; Harrington et al. 1989).

Insecticides Applied at Planting or Plant Emergence

Systemic insecticides applied at planting or plant emergence can significantly reduce within-field spread of PLRV (Boiteau and Singh 1999; DiFonzo et al. 1995; Flanders et al. 1991; Hanafi et al. 1989; Woodford et al. 1983, 1988). The benefits of at planting or plant emergence application tend to be greatest in locations where migrant aphids are rarely viruliferous. However, in the Pacific Northwest, PLRV infection rates can approach 100% if *M. persicae* is not controlled with insecticides (Thomas et al. 1997b). The temporary suspension of aldicarb (a monomethyl carbamate) use (1988-1993) was estimated to have cost Washington State potato growers $36 million annually due to increased spraying of methamidophos and increased prevalence of net necrosis (Schreiber 1995). For 20 years, aldicarb at planting was considered the most effective means of controlling *M. persicae* on potato and of preventing spread of PLRV. Because of ground water considerations, aldicarb use on potato is now restricted in the U.S. to the Pacific Northwest, but in recent years use has declined greatly because of increasing resistance in *M. persicae.*

Electronic monitoring of *M. persicae* probing behavior on aldicarb-treated potatoes is instructive. Apterae were able to reach the phloem of aldicarb-treated plants before any impairment of feeding could be observed, which supported the conclusion that PLRV transmission by viruliferous alatae could not be entirely prevented by use of aldicarb (Holbrook 1977). Intoxicated aphids often dropped from a treated plant, recovered, and returned to feed several times before dying. Substantial sublethal effects of aldicarb were evident, however. More than half of alatae exposed to aldicarb-treated plants were unable to fly after 18 h exposure and <10% of those regained their ability to fly within 24 h after transfer to untreated plants (Boiteau et al. 1985). Naive aphids given access to PLRV-infected plants treated with various systemic insecticides were largely unable to acquire virus and transmission was significantly less than in the untreated control (Villacarlos 1987).

Imidacloprid has gained wide acceptance for control of Colorado potato beetle, *Leptinotarsa decemlineata* (Say), and when used at planting at the maximum labeled rate, provides aphid control for much of the growing season. Imidacloprid at planting reduced PLRV spread, but had no effect on PVY spread (Boiteau and Singh 1999). *Myzus persicae* made fewer long duration feeding probes on imidacloprid-treated potatoes (Woodford 1992). The frequency and duration of short probes by *M. eupborbiae* was not reduced, but intoxicated aphids travelled shorter distances and made fewer flights (Boiteau and Osborn-1997).

Insecticide Resistance

Insecticide resistance often severely limits a grower's choice of aphicides (Radcliffe et al. 1991). Insecticide resistance in *M. persicae* is a worldwide problem (Sawicki et al. 1978). *Myzus persicae*, like *L. decemlineata*, has developed resistance to all major insecticide classes (Devonshire and Moores 1982; Devonshire et al. 1998; Dewar et al. 1998) except the neonicotinoids. In Minnesota, *M. persicae* tends to be highly resistant to most currently registered foliar potato aphicides other than methamidophos, imidacloprid, pymetrozine, and thiomethoxam. In cage experiments with *M. persicae*, insecticide-resistance frequencies increased from 0.02 to almost 1.00, with just three applications of insecticide at 14-day intervals (ffrench-Constant et al. 1987). A mixture of deltamethrin (a pyrethroid) and heptenophos (an organophosphate) selected for resistance more strongly than demeton-S-methyl (an organophosphate) or pirimicarb (a carbamate). The more persistent the insecticide, the greater selection for resistance (ffrench-Constant et al. 1988a).

The evolution of insecticide resistance in *M. persicae* was recently reviewed by Devonshire et al. (1998). The first resistance mechanism reported in *M. persicae* was amplification of genes, *E4* or *FE4*, that code for production of the E4 and FE4 carboxyesterases that degrade or sequester organophosphate, carbamate, and pyrethroid insecticides (Devonshire 1977, 1989; Devonshire and Sawicki 1979). In highly resistant variants, these esterases can account for more than 1% of total body protein (Devonshire and Moores 1982). Resistance to endosulfan (a cyclodiene) (Unruh et al. 1996) and *cis* isomer pyrethroids revealed existence of other resistance mechanisms since these insecticides lack the highly specific binding sites required of carboxylesterase E4 (Büchi 1981). Insecticide-insensititive acetylcholinesterase (= modified AChE or MACE), an important resistance mechanism to organophosphorous and carbamate insecticides in many insects, was not identified in *M. persicae* until 1990 (Moores et al. 1994). Insensitive acetylcholinesterase imparts resistance to pirimicarb, a favored insecticide for controlling aphids with amplified esterase production. Recently, it has been shown that esterase-based resistance to pyrethroids in *M. persicae* is less important than a kdr-type mechanism (Martínez-Torres et al., 1997b). Aphids with R_3 levels of esterase show only a five-fold level of resistance to deltamethrin, whereas kdr alone conferred a 35-fold resistance. In U.K. populations of *M. persicae*, the kdr mechanism is strongly linked with amplification of the *E4* gene, but a survey of clones from other countries found that some with amplified *E4* lack kdr (Field et al. 1997). Analysis of genomic DNA from aphids reverting to susceptibility showed that the *E4* sequences were not lost, indicating that transcriptional control was involved, but superimposed over the underlying DNA amplification (Devonshire 1989). Control failure for aphids with neonicotinoid insecticides has not been reported, but differences in tolerance have been detected (Kerns et al. 1998).

It is commonly believed that in the absence of insecticides, resistant insects tend to be less fit, possibly due to resources being diverted from reproduction, or because of associated changes in physiology or behavior. In the field, insecticide-susceptible aphid clones tend to be more common in the spring and resistant clones suffer higher rates of mortality from low winter temperatures than do susceptible clones (Foster et al. 1996, 1997; Muggleton et al. 1996). Behavioral modifications associated with kdr resistance that lessen overwintering success in *M. persicae* may be due to alterations in the sodium channel gene reducing nervous system sensitivity to stimuli (Devonshire et al. 1998).

Insecticide-resistance management in aphids presents a challenge of exceptional complexity. Aphid pressure tends to vary greatly within and among years both in species composition and abundance. Much of the insecticide applied to potato is targeted against insect pests other than aphids, but these treatments can select for resistant aphids. *Myzus persicae, M. euphorbiae, A. nasturii,* and *A. gossypii* are species with exceptionally broad host ranges and are exposed to insecticides in many different circumstances including in greenhouses where the selection pressure may be intense. The mechanism or mechanisms of insecticide resistance in local aphid populations may not be known, except by inference from the performance of different insecticides. For virus vectors the recommended treatment thresholds are so low that it can be difficult to assess efficacy. Systemic insecticides applied at planting can be very effective against aphids, but this use presents continuous and maximum selection for resistance. Combining aphidical chemistries with different modes of action may assure control when the resistance mechanism is unknown, but also increases selection pressure. Rotating use of insecticides with different modes of action is recommended from the standpoint of resistance management (IRAC 2000). Because E4 and kdr resistance tend to be closely linked there is often cross resistance between organophosphates and pyrethroids (Devonshire 1998).

Non-target Impacts

Field populations of *M. persicae* can be readily increased for experimental purposes by application of selective insecticides. That pesticide-induced outbreaks are caused by suppression of natural enemies might seem intuitively obvious, but little published literature supports this notion. Most studies on the impact of natural enemies on aphid populations are conducted in small plots and may not be representative of what happens in production fields. It is reasonable to assume that parasitoids and predators must be greatly disadvantaged by the routine use of insecticides in the potato ecosystem. Insecticides targeted against other mid-season pests common to the midwestern and eastern U.S. such as the potato leafhopper, *Empoasca fabae* (Harris), can trigger aphid outbreaks. One strategy that can be employed to reduce the risk of flaring aphids is to use below-label rates of insecticides to control *E. fabae* (Suranyi et al. 1999). *Myzus persicae* is resistant to both esfenvalerate (pyrethroid) and dimethoate (organophosphate), but when these insecticides were used at one tenth to one quarter of the lowest labeled rates, leafhoppers were controlled and aphid numbers did not increase.

Crop Oils

Bradley et al. (1962) demonstrated in laboratory and greenhouse studies that nontoxic mineral oils applied to plants substantially reduced PVY transmission. In the field, mineral oils provided reductions of PVY spread as high as 88% (Bradley et al. 1966), but generally field control was not equal to that in laboratory studies (Bell 1989; Boiteau and Singh 1982; Boiteau and Wood 1982; Shands 1977). Reasons for lower efficacy in the field are unclear, but likely include weathering of oil deposits (Boiteau and Wood 1982), plant growth occurring in the interval between applications, and incomplete coverage. Some aphids, e.g., *M. euphorbiae*, prefer to land and probe on newly expanding leaves that may not be protected. *Myzus persicae* was unable to transmit PVY to plants 30 min after oil had been applied, but could do so, although with diminished ability, after 24 h (Gibson et al. 1988).

If high concentrations of oils are used (>3%) they can be phytotoxic, especially when mixed with fungicides or if applied when temperatures are high (Boiteau and Singh 1982). Adoption of the use of oils has been slow because of the risk of negative interactions with fungicides, cost, the need for repeated applications, and because control is not complete. The benefit of crop oils should not be discounted, however, as they are consistently more effective in controlling the spread of PVY than are insecticides. The use of crop oil is more commonly practiced in Europe than in North America. Combining oils with pyrethroids (Collar et al. 1997; Gibson and Cayley 1984; Gibson and Rice 1986), plant-derived antifeedants (Powell et al. 1998), and whitewashes (Marco 1986, 1993) improved PVY control over mineral oils alone.

The mechanism involved in control of PVY by mineral oil is not fully understood. Both acquisition and inoculation are inhibited by mineral oil, but this inhibition is not related to differences in feeding behavior that can be detected by monitoring stylet penetrations electronically (Powell 1992). When oil and purified virus are mixed, mechanical inoculation is inhibited (Loebenstein et al. 1964). Oils may interfere with a physiological process in the early stages of infection. Oils persist on sprayed leaves for 10-14 days, but weekly applications are required to protect new foliage (Simons and Zitter 1980).

Fungicides

Fungi in the order Entomophthorales are prevalent aphid pathogens and can cause epizootics resulting in spectacular collapse of aphid populations (Latgé et al. 1983; Shands et al. 1963, 1972c). The Entomophthorales are obligate entomopathogens and most species show a high degree of host and environmental specificity (Soper 1981). Infection results from contact with spores discharged from aphid cadavers. Epidemics tend to be associated with aphid crowding, high humidity, and reduced canopy temperatures. In Minnesota, predominant *M. persicae* pathogens are *Pandora* (*Erynia*) *neoaphidis* (Remaudière et Hennebert) Humber, *Entomophthora planchoniana* (Cornu), *Conidiobolus thromboides* (Drechsler), *C. obscurus* (Hall & Dunn) Remaudière & Keller, *C. coronatus* (Constantin) Batko, and *Zoophthora radicans* (Brefeld) Batko (Lagnaoui and Radcliffe 1998; Ruano-Rossil et al. 2001).

Use of fungicides on potato can interfere with Entomophthorales that infect *M. persicae* (Lagnaoui and Radcliffe 1998; Nanne and Radcliffe 1971). Potato entomologists once seemed inclined to believe that this interference was of little practical consequence because fungal epizootics generally are not observed until aphid densities are already much higher than recommended treatment thresholds. Initiation of epizootics requires a combination of favorable environmental conditions, well-distributed inoculum, and widespread spatial distribution of hosts (Remaudière et al. 1981; Robert et al. 1971). Shands et al. (1963) concluded that weather was of major importance in the initiation and spread of entomophthoran pathogens, but Missonnier et al. (1970) attached greater importance to a dense and uniformly distributed inoculum. Nevertheless, several researchers have noted that enzootic infections can prevent aphid outbreaks (Remaudière et al. 1981; Shands et al. 1963, 1972a; Soper 1981; Soper and MacLeod 1981).

In the early 1990s, exotic and more virulent strains of the potato late blight pathogen, *Phytophthora infestans* (Mont.) DeBary, became established and predominant in North America (Deahl et al. 1991; Goodwin et al. 1996; Peters et al. 2001). Most of these new strains are of the A2 mating type and resistant to the fungicide metalaxyl, formerly the only effective therapy (Daayf and Platt 1999; Deahl et al. 1995). To protect plants from late blight infection, potato growers now must rely on frequent application of protective fungicides (Goodwin et al. 1996). Since establishment of metalaxyl-resistant strains of late blight in North America, fungicide use on potato in the U.S. has doubled (NASS 2000). Concomitantly, *M. persicae* and aphid-transmitted potato viruses have become increasingly serious problems for growers.

Fungicides do not appear to induce *M. persicae* outbreaks, but interfere with the onset of mycoses (Ruano-Rossil et al. 2001). Wide differences in *M. persicae* density can result from exposure to various fungicide chemistries and application regimes. Control outcomes can be very different among locations and years. Rotation or combination of fungicides with different chemistries and modes of action was more disruptive to Entomophthorales than the season-long use of a single chemistry. The impact may depend upon which Entomophthorales species are the predominant. The first few weeks after *M. persicae* invades potato appear to be critical with respect to inoculum buildup of fungal pathogens. Mycoses were detected soon after aphid colonization and at host densities as low as 0.2 apterae per leaf which supported the notion that mycoses can occur at low aphid densities and prevent aphid outbreaks. Early season reduction in the frequency of fungicide applications based on potato late blight forecasts and introduction of biofungicides might conserve entomopathogenic fungi populations and improve biological control of aphids by these naturally occurring beneficial fungi.

Entomophthorales offer possibilities for exploitation as mycoinsecticides (Yeo et al. 1998). Entomophthorales present special problems in production because they are obligate entomopathogens and tend to have a high degree of host specificity. Past attempts to disseminate Entomophthorales for biological control have relied on the release of infected aphids or mycelia produced in submerged culture, but a new culture technique entraps vegetative cells in alginate granules (Shah et al. 1999).

Primary obstacles to the commercialization of mycoinsecticides have been cost of production, inconsistent product formulation, and limited shelf life.

Semiochemicals

Plants produce an amazing array of chemicals that influence aphid behavior (Herrbach 1992; Pickett et al. 1992). These semiochemicals (signaling chemicals) may offer potential as crop protectants. Two of the most successful classes of chemicals disrupting host selection and virus transmission are compounds derived from aphid alarm pheromone and plant-derived antifeedants (Griffiths et al. 1989).

When aphids are alarmed, e.g., by approach of parasitoids and predators, they can produce secretions from their cornicles that induce dispersal behavior among nearby aphids. The alarm pheromone of *M. persicae* has been identified as (*E*) β-farnesene (Bowers et al. 1972; Edwards et al. 1973). One approach for application could be to repel aphids before they settle and probe (Montgomery and Nault 1977). A second approach would be to combine alarm pheromone with a contact insecticide to increase probability of exposure (Griffiths and Pickett 1980). Derivatives of the alarm pheromone effectively inhibited acquisition of PVY by *M. persicae* although they had no discernable effect on probing or dispersal behavior (Gibson et al. 1984). Aphid alarm pheromone probably is a cue for some predators and parasitoids when searching for prey (Nakamuta 1991). Parasitized or diseased aphids tend to be less responsive to alarm pheromone, an adaptive suicidal behavior (McAllister and Roitberg 1987).

Allelochemicals are semiochemicals that affect a species other than the producer and many provide defense against herbivory. The sesquiterpene polygodial, a fast-acting aphid antifeedant, derived from the marsh pepper, *Polygonium hydropiper* L., reduced settling and acquisition of PVY by *M. persicae* (Gibson et al. 1982b; Powell et al. 1996). Systemic application of azadirachtin, extracted from the neem tree, *Azadirachta indica* A. Juss, did not affect survival of adult *M. persicae*, but interfered with acquisition and inoculation of PLRV (Nisbet et al. 1996). Exposure to azadirachtin reduced fecundity of *M. persicae* by increasing mortality of nymphs. Azadirachtin also interferes with the obligate, mutualistic, relationship of the vector and its *Buchneria* endosymbiont (van den Heuvel et al. 1998).

Site-specific Pest Management

Geographic Information System (GIS) technology can be used to describe within-field distribution of insects to target pesticide applications in space and time. This concept is known as Site-specific Pest Management or Precision Pest Management (MacRae 1998; Weisz et al. 1995). Global Positioning System (GPS) receivers with differential correction can locate positions within 1 to 5 m accuracy. Site-specific pest management could reduce the amount of pesticide needed to effect control. Such reduction would reduce environmental impact and grower exposure, decrease potential for development of insecticide resistance, preserve natural enemies in untreated portions of the field which might favor recolonization of the treated portions, and improve the economics of pest management.

Real-time site-specific pest managment is not yet established in low- or moderate-value cropping systems. The current strength of site-specific pest management techniques is that it enables researchers to establish within-field, spatio-temporal distributions of insect pests and formulate appropriate management recommendations. These techniques have been used to predict where wireworms are likely to be pests (Lefko et al. 1998) and to decrease pesticide inputs needed to control *L. decemlineata* (Weisz et al. 1995, 1996). Suranyi et al. (2002) demonstrated that site-specific pest management of *M. persicae* is possible in seed potato. Aphids were found aggregated at field edges during the initial colonization phase. Methamidophos applications targeting colonizing *M. persicae* at field borders reduced treatment costs ~70% compared to application across the entire field, but exposed >90% of aphids in the three fields. Winter "grow-outs" from border-treated fields had no more virus in the winter test than did those from adjacent fields entirely sprayed with methamidophos.

HOST PLANT RESISTANCE

Present day potato cultivars differ too little in aphid susceptibility for host plant resistance to be a useful control measure. Many wild potato species, however, are highly resistant to aphids. Studies to identify sources of aphid resistance in the NRSP-6 *Solanum* germplasm collection indicated resistance to be an evolutionarily primitive trait (Flanders et al. 1992, 1997). Accessions highly resistant to *M. pers*icae were identified in 36 of 86 potato species and to *M. euphorbiae* in 24 of 85 species. Potato species with greatest resistance to *M. persicae* were *S. trifidum* Correll, *S. brachistrichum* (Bitter) Rydb., *S. etuberosum* Lindl., *S. bulbocastanum* Dunal, and *S. canasense* Hawkes.

To date, only limited use has been made of wild potato species in developing insect-resistant cultivars (Flanders et al.

1999). *Solanum berthaultii* Hawkes is the wild potato that has received most attention as a potential source of aphid resistance (Tingey 1991; Tingey et al. 1982). Insect resistance in *S. berthaultii* is associated with the presence of two types of glandular trichomes. Type B trichomes are taller, tapering to their tip and exude a sticky secretion of sucrose fatty acid esters (King et al. 1986). Type A trichomes are short-stalked with a four-lobed head that when ruptured releases a sticky, viscous exudate of sesquiterpenes and polyphenol oxidase (Avé and Tingey 1986; Avé et al. 1987; Bouthyette et al. 1987). The acyl sugars of Type B trichomes are antifeedants for a number of insects including *M. persicae.*

When an aphid walks on the leaf surface or probes the plant, it can rupture the membrane-enclosed lobes of type A trichomes (Tingey and Laubengayer 1981). One of the predominant constituent sesquiterpenes is the aphid alarm pheromone (Gibson and Pickett 1983). Alarm pheromone excites the aphid, causing increased locomotion and the rupturing of more type A trichomes. When the tarsi are sticky with type B secretion, the rupturing of type A trichomes is even more likely. Release of the polyphenol oxidase causes an oxidation reaction resulting in eventual entrapment and death (Tingey 1991). Glandular trichomes impart a resistance that is effective against a wide range of insects including both *E. fabae* and *L. decemlineata.* The Cornell University potato breeding program released an advanced breeding line, NYL 235-4, said to be the first near cultivar-quality insect-resistant potato clone developed by traditional plant breeding (Plaisted et al. 1992). NYL 235-4 expressed high levels of resistance to *M. euphorbiae* when aphids were confined to the leaves, but aphid performance was restored when they had access to the entire plant and could feed on stems and apical buds (Ashouri et al. 2001).

Solanum etuberosum Lindl., a non-tuber-bearing species native to northcentral Chile, has high levels of resistance to PLRV, PVY, PVA, and PVX (Valkonen et al. 1992). Hybridization of *S. etuberosum* (EBN= 1) with *S. tuberosum* and with haploid US-W730 x *S. berthaultii* was accomplished by protoplast fusion (Novy and Helgeson 1994a). Progeny of *S. etuberosum* hybrids were resistant to PVY infection by mechanical inoculation (Novy and Helgeson 1994b). Resistance to PLRV and PVY was stable in field and cage experiments with large populations of viruliferous *M. persicae* (Novy et al. 2002). Two individuals in the second back-cross generation were identified as having the multiple resistances of *S. etuberosum* and enhanced tuberization.

Various *Agrobacterium*-mediated transformation procedures have been used to produce potato lines expressing genes that confer pathogen-derived resistance to viruses. Transgenic lines have been developed that are highly resistant, but not immune, to infection by PLRV, PVY, and PVX (Berger and German 2001; Brown et al. 1995). While aphids can still acquire virus from low titer plants, the efficiency of transmission is greatly reduced (Thomas et al. 1997a). Transgenic cultivars were released that expressed the δ-endotoxin from *Bacillus thuringiensis* Berliner, subsp. *tenebrionis* (*Bt*), for *L. decemlineata* control combined with PLRV replicase (Thomas et al. 2000), and others that expressed *Bt* and PVY coat protein (Berger and German 2001). These cultivars have since been withdrawn from the market because of the public backlash against genetically modified food. That not withstanding, this technology represents a novel means of reducing virus spread that is far more effective than presently used tactics.

Aldehydes produced in the cleavage of fatty acid hydroperoxides are thought to play a role in the defense of plants against herbivory. It has been proposed that aldehydes may regulate expression of defense-genes (Bate and Rothstein 1998). Consistent with that hypothesis, Desirée potatoes with antisense-mediated virus resistance had reduced hydroperoxidase lyases compared to nontransformed Desirée, and *M. persicae* were twice as fecund when reared on transgenic plants (Vancanneyt et al. 2001).

Some virus-susceptible cultivars do not express strong symptoms of virus infection. A recent epidemic of PVY in the Red River Valley of Minnesota and North Dakota was linked to the increased popularity of the cultivars Shepody and Russet Norkotah before it was widely recognized that absence of visual symptoms did not assure plants were virus free (DiFonzo et al. 1996). Potato breeding programs recognize the importance of understanding the range of symptom expression of PVY and PLRV and most routinely use serological tests (ELISA) to screen advanced breeding lines likely to be released as a named cultivar. In Minnesota, we now test for symptom expression of PVY^o and PLRV in the early stages of varietal selection. Serological tests are generally used by seed certification agencies to test asymptomatic cultivars in lieu of visual screening. Winter grow-outs remain the preferred method of post-harvest testing for virus because of problems achieving consistent performance with ELISA tests. Possible shortcomings of ELISA tests can include not having adequate controls, diluting plant sap too much to detect a low-titered virus like PLRV, and the necessity to test hundreds of tubers per seed lot. In virus-resistant cultivars, plant to plant spread in the field is less because of lower virus titer (Barker and Woodford 1992; Sigvald 1984; Souza Dias and Slack 1987; Thomas et al. 1997a). However, partial resistance can be overcome if vector pressure (numbers or duration of exposure) is increased (DiFonzo et al. 1995).

SAMPLING APHIDS

The distribution of aphids on plants is seldom uniform. Most aphids tend to feed and reproduce faster on young or senescent leaves (Kennedy and Booth 1951). On potato, *M. persicae* prefers older leaves; *A. nasturii* is more uniformly distributed, and *M. euphorbiae* prefers young leaves (Taylor 1955, 1962). Thus, unless one is willing to examine an entire plant, no single sampling procedure will be equally effective for all aphid species. For routine field sampling of aphids, e.g., to determine need to treat or to evaluate the success of previous control measures, random sampling from the lower to mid portion of the plant is the most efficient way to sample potato-colonizing aphids (Anscombe 1948). Stratified-leaf sampling in which equal numbers of leaves are taken from the upper, middle, and lower portions of the plant may be useful if the goal is to estimate aphid numbers per plant (Shands et al. 1954). Sweep net sampling is not useful for monitoring aphid populations because few are collected, and those that are may be crushed and unrecognizable. "Threshing" or shaking plants over ground sheets, paper, or trays can be used to sample young plants. Threshing has proven useful for early detection of invasion of seed fields by winged aphids (Halbert et al. 1990; Woodford et al. 1977).

Thresholds

Reliable and cost-effective sampling methods are essential in pest management. Estimating aphid densities on crops often presents special difficulties because colonizing populations tend to instability in their spatial distributions. Initial colonization by alatae is largely a random event, but field margins and windbreaks may contribute to pronounced infestation gradients. Colonies of apterae are established at these initial foci of infestation, resulting in a contagious distribution. These primary aggregations spread first by apterae walking and eventually by production of new alatae. Thus, initial colonization tends to follow a Poisson distribution, but typically within two to three weeks evolves to negative binomial distribution, and by the end of the season or during outbreaks to a log-normal distribution (Robert et al. 1988; Tamaki et al. 1973).

For purposes of aphid pest management decisions, and especially when concern focuses on preventing virus transmission, sampling is only required when aphids are at comparatively low densities. When an estimate of variance is known, the number of sample units required to make an estimate of desired precision can be determined from mean-variance models, e.g., Taylor's power law (Taylor 1961), Iwao's patchiness regression (Kuno 1969) or proportion-infested mean density models. Monte Carlo methods of evaluating these sampling methods have been devised (e.g., Nyrop & Binns 1991), but the underlying statistical distribution models might not represent actual field distributions. Recently developed software, Resampling for Validation of Sample Plans (RVSP), permits evaluation of the sample plan by resampling a portion of the actual field data (Naranjo and Hutchison 1997).

In seed production, monitoring aphid flight activity has proven useful in timing application of insecticides, crop oils, or defoliants (Boiteau and Parry 1985; Robert et al. 1988; Woiwod et al. 1984). Yellow water-pan traps of the design of Moericke (1951) have been used in the Netherlands for 50 years to monitor flight activity of *M. persicae.* The benefit to the Dutch seed industry from increased yields for each day that vine-kill could be safely delayed was estimated 0.6 t ha^{-1} (Hille Ris Lambers 1972). In the U.K., yellow sticky traps were preferred and used with great success for many years to sample *M. persicae* landing rates in potato and sugar beet (Watson and Heathcote 1966). Yellow in the range of 580 nm with a near absence of short-wave blue is highly attractive to *M. persicae*, but not equally so to other aphid species that may be important in transmission of PVY and other potyviruses (Baldy and Rabasse 1983). Since 1973, New Brunswick has monitored *M. persicae* flights with "topkill" mandated within 10 days once a cumulative five *M. persicae* have been collected in a yellow water-pan trap (Parry 1987).

In a study of aphid vectors of soybean viruses, a rugose-textured, lime green, ceramic tile trap provided a less biased estimate of landing rates than did yellow traps (Irwin 1980). In potato, however, these same green tiles provided a biased estimate of landing rates compared to similarly designed traps using potato foliage (Boiteau 1990). For most aphid species, green tile traps captured fewer aphids than did yellow traps (Eastop and Raccah 1988), but colored traps are rarely species specific (DiFonzo et al. 1997). Trap performance tends to have more to do with placement than color (A'Brook 1973). Green tile traps placed in a fallow field border caught significantly more aphids than traps placed in the middle of the field, while traps placed in the first potato row captured an intermediate number of aphids (DiFonzo et al. 1996). In Idaho, numbers of winged aphids captured in yellow water-pan traps placed on the edges of potato fields tended to be strongly correlated with immediate field populations, which was interpreted as suggesting that they measured aphids coming from the potato field rather than into it (Byrne and Bishop 1979a). Sticky fishing line traps have been used to obtain unbiased estimates of species composition and abundance over the crop canopy (Labonne et al. 1983).

Aphid captures provide only an indirect measure of risk of virus spread. One way of addressing this problem has been to expose indicator plants in the field at varying time intervals to relate virus spread to aphid flight activity (DiFonzo et al. 1997; Hanafi et al. 1995; Rydén et al. 1983; van Hoof 1977). Another approach has been to trap aphids alive and assay their ability to acquire and transmit virus (Harrington and Gibson 1989; Sigvald 1986; van Hoof 1980). Neither approach provides the real-time information needed to make pest management recommendations, and both are extremely labor intensive. Immunocapture RT-PCR technology makes it possible to test for specific viruses in individual field-collected aphids (Nie and Singh 2001; Singh 1999; Singh et al. 1995, 1997). Aphids can be collected in propylene glycol and stored in 95% ethanol until tested. RT-PCR does not indicate vector capability or efficiency of transmission and thus may overestimate risk of transmission (Leclercq-Le Quillec et al. 1995; Pirone and Thornbury 1988). RT-PCR data can be used to compare one field season to another and to relate risk of transmission to aphid landing rates.

Thresholds based on *M. persicae* apterae have been used widely by ware producers and by seed growers in areas where area-wide aphid flight activity is not routinely monitored. Static thresholds in the range of 20-100 aphids per 100 leaves have been proposed for ware producers (Byrne and Bishop 1979b; Cancelado and Radcliffe 1979; Davies 1934; Shields et al. 1984). A dynamic threshold model for *M. persicae* was developed in Pennsylvania in which the treatment threshold increased with accumulated day-degrees (Whalon and Smilowitz 1979b). There are cultivar differences in susceptibility to PLRV which suggests that higher thresholds may be appropriate for some cultivars (DiFonzo et al. 1995). Proposed action thresholds to minimize within-field spread of PLRV in cultivars susceptible to net necrosis and for use in seed potato production have ranged from 1-10 *M. persicae* apterae per 100 leaves (Cancelado and Radcliffe 1979; Flanders et al. 1991; Hanafi et al. 1989; Mowry 2001).

Aphid Trapping Networks

Association of virus spread in potatoes with aphid flight activity is well documented (Bacon et al. 1976; Boiteau and Parry 1985; Broadbent 1950; Hanafi et al. 1995; Hille Ris Lambers 1972; Thomas 1983; Thomas et al. 1997b). Initially, aphid-trapping networks focused on *M. persicae* because it was considered the most efficient vector of potato viruses. As the importance of PVY spread by less efficient but abundant vectors was recognized, aphid-trapping networks began routinely identifying these aphids (DiFonzo et al. 1997; Kurppa and Rajala 1986; Rydén et al. 1983; Sigvald 1984, 1986; Stufkens et al. 2000; van Harten 1983; van Hoof 1977).

By sampling aerial distributions of aphids at varying heights above the ground, it was determined that beyond a certain height aphids are randomly distributed and that the log density diminishes linearly as the log height increases (Johnson 1969). The high volume ($60 m^3 min^{-1}$), 12.2-m tall Rothamsted suction trap was designed for, and as a result of, studies of aphid flight behavior (Johnson and Taylor 1955). Since 1965, a network of 12.2-m suction traps has been deployed, first in the U.K, then in other European countries (Woiwod et al. 1984). The network, now known as EXAMINE (**EX**ploitation of **A**phid **M**onitoring systems **IN** **E**urope), presently operates 73 traps in 19 countries. The network has produced the most extensive and standardized, spatio-temporal database existing for any terrestrial invertebrate group. This long-term monitoring effort provides a unique resource for studies on the impacts of global change and has the potential to be analyzed in relation to other data sets such as those on climate, atmospheric composition, pollutants, and land use.

Trapping networks are intended to monitor aphid flight on a regional basis. At any particular location, e.g., an individual farm, the first spring migrants may not be detected because their occurrence is rare and the sample unit small. Another limitation is that the traps may not be monitored daily and expertise is required to identify the captured aphids. Nevertheless, on a regional basis, a network of traps can provide effective early warning of aphid flight activity. Captures later in the summer are likely to be predominantly of alatae from local weed and crop hosts. In Idaho, suction trap captures were predominantly of aphid species indigenous to host vegetation within a 30-60 km radius of the trap (Halbert et al. 1990).

An aphid trapping network, *Aphid Alert*, has been operated in the seed potato production areas of the northern Midwest since 1998 (Radcliffe et al. 2002). In 2001, we operated traps at 27 locations in five states: Minnesota, North Dakota, Nebraska, South Dakota, and Wisconsin. We used a suction trap and two green tile traps at each location. The *Aphid Alert* suction traps are 2.3-m tall, low volume (2.3 m^3 min^{-1}), and based on the design used to monitor Russian wheat aphid, *Diuraphis noxia* (Mordvilko), in the western U.S. (Allison and Pike 1988).

Regardless of the monitoring methodology used, a delay always occurs in processing the samples, summarizing data, and alerting growers to the findings. Woiwod et al. (1984) noted that it takes nearly 1 wk for suction trap samples to be processed and reports sent out for aphids that were trapped the preceding five to 12 days. Our experience with the *Aphid Alert* network is similar. *Aphid Alert* has been accepted by the region's seed producers as an important addition to their management of the crop. According to a reader survey conducted in 1999, 98% of respondents ranked the information in *Aphid Alert* as useful and 78% said they made pest management decisions based on information provided in the newsletter. Responding growers reported a preference for the traditional hardcopy newsletter, while consultants, extension specialists, and researchers overwhelmingly preferred the e-mail version. Survey respondents reported little use of the web-based version. We assume the proactive nature of the hardcopy and e-mail to be more convenient for our immediate clientele, especially during the growing season. However, the opening menu of *Aphid Alert* with links to archived back issues is accessed more than 300 times per month.

Clearly, by the time growers and pest management advisors receive reports, they are making management decisions based on aphid flight activity that occurred one to three weeks earlier. Additional post-trapping processing of the samples, for example, detection of PLRV by RT-PCR in the aphid itself, could make these data more valuable as a research tool, but would reduce its value as a management tool were that to further delay reporting.

Forecasting and Simulation Models

Forecasting disease incidence is particularly difficult when many potential vector species are involved. Thus, predicting the spread of nonpersistent viruses such as PVY is more problematic than predicting the spread of PLRV. In Sweden, a model was developed for predicting risk of PVY spread using aphid capture data weighted to reflect relative transmission efficiencies of the various vector species (Sigvald 1986, 1987, 1992). Other important variables and parameters of this model include proportion of PVY-infected source plants in the field, cultivar susceptibility, mature plant resistance, and date of vine-kill.

In the U.K. live trapping was used to identify 26 species as potential PVY vectors (Harrington and Gibson 1989). The date of first capture at Rothamsted from 1968 to 1988 of species that are largely anholocyclic, e.g., *M. persicae*, correlated with January-April mean temperatures. For species that are largely holocyclic, correlations with various mean winter temperatures were poor (Harrington et al. 1990). Total *M. persicae* captured in suction traps before 1 July correlated with December-June mean temperatures. Winter temperatures and resultant aphid mortality appears to be a primary determinant of the timing of *M. persicae* spring migration (Bale et al. 1988). A close relationship was found in the U.K. between the annual prevalence from 1951 to 1971 of sugarbeet yellowing viruses transmitted by *M. persicae* and the number of "frost days" (< -0.3 C) in January to March and mean April temperatures using Rothamsted weather data (Watson et al. 1975). Similarily, a model was developed to forecast incidence of PLRV in Scottish seed potatoes using virus incidence the previous year and number of *M. persicae* caught the previous year in 12.2-m suction traps (Pickup and Brewer 1994).

In New Brunswick, the average first date that the vine-kill threshold is reached can vary by a month from one year to the next, but is strongly correlated with the date of the first capture of the year in the province (Boiteau and Parry 1985). First captures tend to occur first in northern New Brunswick and typically in the narrow temporal window of July 22-27. These first arrivals are presumed to be long distance migrants since *M. persicae* seldom overwinters successfully on *P. nigra* in New Brunswick. If the immigrants are from the first agamic generation produced on *P. nigra* further south, then the average date that the threshold for vine-kill is exceeded, ~8 August, corresponds with development of the third agamic generation on the primary host in Maine.

Statistical modeling of aphid-vectored virus pathosystems presents problems of daunting complexity. Only a few have been developed, e.g., soybean mosaic virus in soybean (Irwin and Ruesink 1986), virus yellows in sugarbeet (Dewar and Smith 1999; Watson et al. 1975; Werker et al. 1998), and barley yellow dwarf (Burgess et al. 1999; Harrington et al. 1994). The vector is the black box for which adequate data are seldom available. In the U.K. and The Netherlands, a complex simulation model, EPOVIR, was developed that coupled crop growth and inoculum levels the previous season to forecast yield and PVY virus infection in seed potatoes (Nemecek et al. 1995, 1996). EPIVIT is a simulation model developed in Switzerland to predict incidence of contact transmitted and aphid-transmitted viruses in harvested tubers (Bertschinger et al. 1995a, 1995b). State variables of EPIVIT are autoinfection, primary infection of plants, and tuber infection of primarily infected plants. Input variables are daily minimum/maximum temperatures and aphid flight activity.

SUMMARY AND CONCLUSIONS

Control of aphid-transmitted viruses in potatoes is complex and a multitude of preventative and therapeutic tactics are required to minimize virus spread. At a minimum, the degree of isolation, the source of inoculum, the timing and intensity of aphid flights, along with identifying the predominant aphid species are needed to develop an integrated control program. Because vector management can never be entirely effective, the primary line of defense must be to minimize the amount of inoculum in seed potatoes. Insecticides are valuable tools for preventing spread of PLRV, but seldom effective in limiting spread of nonpersistently transmitted viruses. Cultural practices often are among the most effective and inexpensive of control measures that growers can implement. Cultural control practices are often not complicated, but like all pest management tactics require application of knowledge of vector biology and ecology.

ACKNOWLEDGMENTS

The authors are grateful for the many helpful suggestions and insights offered reviewers of previous drafts of this manuscript. We are particularly indebted to G. Boiteau, Agriculture and AgriFood Canada, Fredericton, N.B; R. Harrington, Institute Arable Crops Research (IARC), Rothamsted; Harpenden, U.K.; J.A.T. Woodford, Scottish Crop Research Institute (SCRI), Invergowrie, T.M. Mowry, University of Idaho, Parma, ID, and R.C. Venette, University of Minnesota, St. Paul, MN. Errors of fact, interpretation, or omission are the sole responsibility of the authors.

LITERATURE CITED

A'Brook, J. 1973. The effect of plant spacing on the number of aphids trapped over cocksfoot and kale crops. Ann Appl Biol 74:279-285.

Adams, J.B., and R.A. Kelley. 1950. Potato aphid control studies, 1946-1949, at Woodstock, N.B., Canada. Am Potato J 27:175-182.

Allen, E.J., P.J. O'Brien, and D. Firman. 1992. Seed tuber production and management. *In*: Harris, P. (ed), The Potato Crop, 2nd edition. Chapman & Hall, London. pp. 247-291.

Allison, D., and K.S. Pike. 1988. An inexpensive suction trap and its use in an aphid monitoring network. J Agric Entomol 5:103-107.

Anscombe, F. J. 1948. On estimating the population of aphids in a potato field. Ann Appl Biol 35:567-571.

Antignus, Y. 2000. Manipulation of wave length-dependent behavior of insects: an IPM tool to impede insects and restrict epidemics of insect-borne viruses. Virus Res 71:213-220.

Ashouri, A., D. Michaud, and C. Cloutier. 2001. Unexpected effects of different potato resistance factors to the Colorado potato beetle (Coleoptera: Chrysomelidae) on the potato aphid (Homoptera: Aphididae). Environ Entomol 30:524-532.

Auclair, J.L. 1963. Aphid feeding and nutrition. Annu Rev Entomol 8:439-490.

Avé, D.A., and W.M. Tingey. 1986. Phenolic constituents of glandular trichomes on *Solanum berthaultii* and *S. polyadenium*. Am Potato J 63:473-480.

Avé, D.A., P. Gregory, and W.M. Tingey. 1987. Aphid repellent sesquiterpenes in glandular trichomes of *Solanum berthaultii* and *S. tuberosum*. Entomol Exp Appl 44:131-138.

Avilla, C., J.L. Collar, M. Duque, P. Perez, and A. Fereres. 1997. Impact of floating rowcovers on bell pepper yield and virus incidence. HortSci 32:882-883.

Bacon, O.G., V.E. Burton, D.L. McLean, R.H. James, W.D. Riley, K.G. Baghott, and M.G. Kinsey. 1976. Control of the green peach aphid and its effect on the incidence of potato leaf roll virus. J Econ Entomol 69:410-414.

Bagnall, R.H. 1992. Epidemiology of potato virus Y in New Brunswick, Canada; a biennial rhythm and a 9-plus year cycle. Can J Plant Pathol 14:137-146.

Bagnall, R.H., and G.C.C. Tai. 1986a. Field resistance to potato virus Y in potato assessed by cluster analysis. Plant Dis 70:301-304.

Bagnall, R.H., and G.C.C. Tai. 1986b. Potato leafroll virus: evaluation of resistance in potato cultivars. Plant Dis 70:621-623.

Baldy, C., and J.-M. Rabasse. 1983. Caractéristiques spectrales de pièges jaunes utilisés pour la capture des aphides. Agronomie 3:161-166.

Bale, J.S., R. Harrington, and M.S. Clough. 1988. Low temperature mortality of the peach-potato aphid *Myzus persicae*. Ecol Entomol 13:121-129.

Barker, H., and J.A.T. Woodford. 1992. Spread of potato leafroll virus is decreased from plants of potato clones in which virus accumulation is restricted. Ann Appl Biol 121:345-354.

Barlow, C.A. 1962. The influence of temperature on the growth of experimental populations of *Myzus persicae* (Sulzer) and *Macrosiphum euphorbiae* (Thomas) (Aphididae). Can J Zool 40:145-156.

Barlow, N.D., and A.F.G. Dixon. 1980. Simulation of Lime Aphid Population Dynamics. Pudoc, Wageningen. 164 pp.

Bate, N.J., and S.J. Rothstein. 1998. C_6-volatiles derived from the lipoxygenase pathway induce a subset of defense-related genes. Plant J 16:561-569.

Beddington, J.R., and P.S. Hammond. 1977. On the dynamics of host-parasite-hyperparasite interactions. J. Anim Ecol. 46: 811-821.

Beemster, A.B.R. 1972. Virus translocation in potato plants and mature-plant resistance. *In*: de Bokx, J.A. (ed), Viruses of Potatoes and Seed-potato Production. Pudoc, Wageningen. pp. 144-157.

Beemster, A.B.R. 1987. Virus translocation and mature-plant resistance in potato plants. *In*: de Bokx, J.A., and J.P.H. van der Want (eds), Viruses of Potatoes and Seed-potato Production. Pudoc, Wageningen. pp. 116-125.

Beemster, A.B.R., and A. Rozendaal. 1972. Potato viruses: properties and symptoms. *In*: de Bokx, J.A. (ed), Viruses of Potatoes and Seed-potato Production. Pudoc, Wageningen. pp. 115-143.

Bell, A.C. 1989. Use of oil and pyrethroid sprays to inhibit the spread of potato virus Y^N in the field. Crop Protect 8:37-39.

Benbrook, C.M., D.L. Sexson, J.A. Wyman, W.R. Stevenson, S. Lynch, J. Wallendal, S. Diercks, R. Van Haren, and C.A. Granadino. 2002. Developing a pesticide risk assessment tool to monitor progress in reducing reliance on high-risk pesticides in Wisconsin potato production. Am J Potato Res 79:183-199.

Berger, P.H., and T.L. German. 2001. Biotechnology and resistance to potato viruses. *In*: Loebenstein, G., P.H. Berger, A.A. Brunt, and R.H. Lawson (eds), Virus and Virus-like Diseases of Potatoes and Production of Seed-potatoes. Kluwer Academic Publishers, Dordrecht. pp. 341-363.

Berger, P.H., R.J. Zeyen, and J.V. Groth. 1987. Aphid retention of maize dwarf mosaic virus (potyvirus): epidemiological implications. Ann Appl Biol 111:337-344.

Bertschinger, L., E.R. Keller, and C. Gessler. 1995a. Development of EPIVIT, a simulation model for contact- and aphid-transmitted potato viruses. Phytopathology 85:801-814.

Bertschinger, L., E.R. Keller, and C. Gessler. 1995b. Characterization of the virus X temperature interaction in secondarily infected potato plants using EPIVIT. Phytopathology 85:815-819.

Bishop, G.W. 1967. A leaf roll virus control program in Idaho's seed potato areas. Am Potato J 44:305-315.

Blackman, R.L. 1974. Life-cycle variation of *Myzus persicae* (Sulz.) (Hom., Aphididae) in different parts of the world, in relation to genotype and environment. Bull Ent Res 63: 595-607.

Blackman, R.L. 1980. Chromosomes and parthenogenesis in aphids. *In*: Blackman, R.L., G.M. Hewitt, and M. Ashburner (eds), Insect Cytogenetics. 10th Symp R Entomol Soc Lond. Blackwell, Oxford. pp. 133-148.

Blackman, R.L. 1981. Species, sex and parthenogenesis in aphids. *In*: Forey, P.L (ed), The Evolving Biosphere. Cambridge University Press, Cambridge. pp. 75-85.

Blackman, R.L. 1987. Morphological discrimination of a tobacco-feeding form from *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), and a key to New World *Myzus* (*Nectarosiphon*) species. Bull Entomol Res 77:713-730.

Blackman, R.L., and V.F. Eastop. 2000. Aphids on the World's Crops: an Identification and Information Guide, 2nd edition. John Wiley, Chitchester. 476 pp.

Blackman, R.L., and A.J.C. Paterson. 1986. Separation of *Myzus* (*Nectarosiphon*) *antirrhinii* (Macchiati) from *Myzus* (*N.*) *persicae* (Sulzer) and related species in Europe (Homoptera: Aphididae). Syst Entomol 11:267-276.

Blackman, R.L., and J.M. Spence. 1992. Electrophoretic distinction between the peach-potato aphid, *Myzus persicae*, and the tobacco aphid, *M. nicotianae* (Homoptera: Aphididae). Bull Entomol Res 82:161-165.

Blanco-Urgoiti, B., M. Tribodet, S. Leclere, F. Ponz, C. Pérez de San Román, F.J. Legorburu, C. Kerlan. 1998. Characterization of potato potyvirus Y (PVY) isolates from seed potato batches. Situation of the NTN, Wilga and Z isolates. Eur J Plant Pathol. 104:811-819.

Boiteau, G. 1984. Effect of planting date, plant spacing, and weed cover on populations of insects, arachnids, and entomophthoran fungi in potato fields. Environ Entomol 13:751-756.

Boiteau, G. 1986. Diurnal flight periodicities and temperature thresholds for three potato-colonizing aphids (Homoptera: Aphididae) in New Brunswick. Ann Entomol Soc Am 79:989-993.

Boiteau, G. 1990. Effect of trap color and size on relative efficiency of water-pan traps for sampling alate aphids (Homoptera: Aphididae) on potato. J Econ Entomol 83:937-942.

Boiteau, G. 1997. Comparative propensity for dispersal of apterous and alate morphs of three potato-colonizing aphid species. Can J Zool 75:1396-1403.

Boiteau, G., and W.P.L. Osborn. 1997. Behavioural effects of imidacloprid, a new nicotinyl insecticide, on the potato aphid, *Macrosiphum euphorbiae* (Thomas) (Homoptera, Aphididae). Can Entomol 129:241-249.

Boiteau, G., and R.H. Parry. 1985. Monitoring of inflights of green peach aphids, *Myzus persicae* (Sulzer), in New Brunswick potato fields by yellow pans from 1974 to 1983: results and degree-day simulation. Am Potato J 62:489-496.

Boiteau, G., and R.P. Singh. 1982. Evaluation of mineral oil sprays for reduction of virus Y spread in potatoes. Am Potato J 59:253-262.

Boiteau, G., and R.P. Singh. 1999. Field assessment of imidacloprid to reduce the spread of PVY^O and PLRV in potato. Am J Potato Res 76:31-36.

Boiteau, G., and F.A. Wood. 1982. Persistence of mineral oil spray deposits on potato leaves. Am Potato J 59:55-63.

Boiteau, G., R.R. King, and D. Levesque. 1985. Lethal and sublethal effects of aldicarb on two potato aphids (Homoptera: Aphidae): *Myzus persicae* (Sulzer) and *Macrosiphum euphorbiae* (Thomas). J Econ Entomol 78:41-44.

Boiteau, G., L.M. Moore, and D. Wattie. 2000. Comparative analysis of aphid vector behavior in response to potato plants grown from field tubers, minitubers or plantlets. Am J Potato Res 77:71-75.

Boiteau, G., W.P.L. Osborn, and M.E. Drew. 1997. Residual activity of imidacloprid controlling Colorado potato beetle (Coleoptera: Chrysomelidae) and three species of potato colonizing aphids (Homoptera: Aphididae). J Econ Entomol 90:309-319.

Boiteau, G., R.P. Singh, R.H. Parry, and Y. Pelletier. 1988. The spread of PVY^O in New Brunswick potato fields: timing and vectors. Am Potato J 65: 639-649.

Bonnemaison, L. 1951. Contribution à l'étude des facteurs provoquant l'apparition des formes ailées et sexuées chez les Aphidinae. Ann Épiphyties 2:1-380.

Bouthyette, P.-Y., N. Eannetta, K.J. Hannigan, and P. Gregory. 1987. *Solanum berthaultii* trichomes contain unique polyphenoloxidases and a peroxidase. Phytochemistry 26:2949-2954.

Bowers, W.S., L.R. Nault, R.E. Webb, and S.R. Dutky. 1972. Aphid alarm pheromone: isolation, identification, synthesis. Science 177:1121-22.

Bradley, R.H.E. 1954. Studies of the mechanism of transmission of potato virus Y by the green peach aphid, *Myzus persicae* (Sulz.) (Homoptera: Aphididae). Can J Zool 32:64-73.

Bradley, R.H.E., and D.W. Rideout. 1953. Comparative transmission of potato virus Y by four aphid species that infest potato. Can J Zool 31:333-341.

Bradley, R.H.E., C.A. Moore, and D.D. Pond. 1966. Spread of potato virus Y curtailed by oil. Nature 209:1370-1371.

Bradley, R.H.E., C.V. Wade, and F.A. Wood. 1962. Aphid transmission of potato virus Y inhibited by oils. Virology 18:327-329.

Broadbent, L. 1949. Factors affecting the activity of alatae of the aphids *Myzus persicae* (Sulzer) and *Brevicoryne brassicae* (L.). Ann Appl Biol 36:40-62.

Broadbent, L. 1950. The correlation of aphid numbers with the spread of leaf roll and rugose mosaic in potato crops. Ann Appl Biol 37:58-65.

Broadbent, L., and T.W. Tinsley. 1951. Experiments on the colonization of potato plants by apterous and by alate aphids in relation to the spread of virus diseases. Ann Appl Biol 38:411-424.

Broadbent, L., G.D. Heathcote, N. McDermott, and C.E. Taylor. 1957. The effect of date of planting and of harvesting potatoes on virus infection and on yield. Ann Appl Biol 45:603-622.

Brown, C.R., O.P. Smith, V.D. Damsteegt, C.-P. Yang, L. Fox, and P.E. Thomas. 1995. Suppression of PLRV titer in transgenic Russet Burbank and Ranger Russet. Am Potato J 72:589-597.

Brunt, A.A. 2001. The main viruses infecting potato crops, *In*: Loebenstein, G., P.H. Berger, A.A. Brunt, and R.H. Lawson (eds), Virus and Virus-like Diseases of Potatoes and Production of Seed-potatoes. Kluwer Academic Publishers, Dordrecht. pp. 65-67.

Büchi, R. 1981. Evidence that resistance against pyrethroids in aphids *Myzus persicae* and *Phorodon humuli* is not correlated with high carboxylesterase activity. Z Pflkrank Pflschutz 88:631-644.

Burgess, A.J., R. Harrington, and R.T. Plumb. 1999. Barley and cereal yellow dwarf virus epidemiology and control strategies. *In*: Smith, H.G., and H. Barker (eds), The Luteoviridae. CABI Publishing,Wallingford. pp. 248-261.

Burt, P.E., G.D. Heathcote, and L. Broadbent. 1964. The use of insecticides to find when leaf roll and Y viruses spread within potato crop. Ann Appl Biol 54:13-22.

Byrne, D.N., and G.W. Bishop. 1979a. Comparison of water trap pans and leaf counts as sampling techniques for green peach aphids on potatoes. Am Potato J 56:237-241.

Byrne, D.N., and G.W. Bishop. 1979b. Relationship of green peach aphid numbers to spread of potato leaf roll virus in southern Idaho. J Econ Entomol 72:809-811.

Cadman, C.H., and J. Chambers. 1960. Factors affecting the spread of aphid-borne viruses in potato in Eastern Scotland. III. Effects of planting date, roguing and age of crop on the spread of potato leaf-roll and *Y* viruses. Ann Appl Biol 48:729-738.

Cancelado, R.E., and E.B. Radcliffe. 1979. Action thresholds for green peach aphid on potatoes in Minnesota. J Econ Entomol 72:606-609.

Carnegie, S.F., and H. van de Haar. 1999. PVY^{NTN}, threats and possible solutions. UNECE, http://www.unece.org/trade/agr/meetings/ge.06/1999_09.r/pvyntn.doc.

Castle, S.J., and P.H. Berger. 1993. Rates of growth and increase of *Myzus persicae* on virus-infected potatoes according to type of virus-vector relationship. Entomol Exp Appl 69:51-60.

Castle, S.J., T.M. Mowry, and P.H. Berger. 1998. Differential settling by *Myzus persicae* (Homoptera: Aphididae) on various virus infected host plants. Ann Entomol Soc Am 91:661-667.

Clements, K.M., B.M. Wiegmann, C.E. Sorenson, C.F. Smith, P.A. Neese, and R.M. Roe. 2000. Genetic variation in the *Myzus persicae* complex (Homoptera: Aphididae): evidence for a single species. Ann Entomol Soc Am 93:31-46.

Cohen, S., and S. Marco. 1973. Reducing the spread of aphid-transmitted viruses in peppers by trapping the aphids on sticky yellow polyethylene sheets. Phytopathology 63:1207-1209.

Collar, J.L., C. Avilla, M. Duque, and A. Fereres. 1997. Behavioral response and virus vector ability of *Myzus persicae* (Homoptera: Aphididae) probing on pepper plants treated with aphicides. J Econ Entomol 90:1628-1634.

Daayf, F., and H.W. Platt. 1999. Assessment of mating types and resistance to metalaxyl of Canadian populations of *Phytophthora infestans* during 1997. Am J Potato Res 76:287-295.

Davies, W.M. 1934. Studies of aphides infesting the potato crop. II. Aphis survey: its bearing upon the selection of districts for seed potato production. Ann Appl Biol 21:283-299.

de Bokx, J.A., and P.G.M. Piron. 1990. Relative efficiency of a number of aphid species in the transmission of potato virus Y^{N} in the Netherlands. Neth J Plant Pathol 96:237-246.

Deahl, K.L., S.P. De Muth, S.L. Sinden, and A. Rivera-Peña. 1995. Identification of mating types and metalaxyl resistance in North American populations of *Phytophthora infestans*. Am Potato J 72:35-49.

Deahl, K.L., R.W. Goth, R. Young, S.L. Sinden, and M.E. Gallegly. 1991. Occurrence of the A^{2} mating type of *Phytophthora infestans* in potato fields in the United States and Canada. Am Potato J 68:717-725.

DeLoach, C.J. 1974. Rate of increase of populations of cabbage, green peach, and turnip aphids at constant temperatures. Ann Entomol Soc Am 67:332-340.

Devonshire, A.L. 1977. The properties of a carboxylesterase from the peach-potato aphid, *Myzus persicae* (Sulz.), and its role in conferring insecticide resistance. Biochem J 167:675-683.

Devonshire, A.L. 1989. Insecticide resistance in *Myzus persicae*: from field to gene and back again. Pestic Sci 26:375-382.

Devonshire, A.L., and G.D. Moores. 1982. A carboxylesterase with broad substrate specificity causes organophosphorus, carbamate, and pyrethroid resistance in peach-potato aphids (*Myzus persicae*). Pestic Biochem Physiol 18:235-246.

Devonshire, A.L., and R.M. Sawicki. 1979. Insecticide-resistant *Myzus persicae* as an example of evolution by gene duplication. Nature 280:140-141.

Devonshire, A.L., L.M. Field, S.P. Foster, G.D. Moores, M.S. Williamson, and R.L. Blackman. 1998. The evolution of insecticide resistance in the peach-potato aphid, *Myzus persicae*. Phil Trans R Soc, Lond, B, 353:1677-1684.

Dewar, A., L. Haylock, S. Foster, A. Devonshire, and R. Harrington. 1998. Three into one will go – the evolution of resistance in the peach-potato aphid, *Myzus persicae*. British Sugar Beet Rev 66:14-19.

Dewar, A.M., and H.G. Smith. 1999. Forty years of forecasting virus yellows incidence in sugar beet. *In*: Smith, H.G., and H. Barker (eds), The Luteoviridae. CABI Publishing, Wallingford. pp. 229-243.

DiFonzo, C.D., D.W. Ragsdale, E.B. Radcliffe. 1995. Potato leafroll virus spread in differentially resistant potato cultivars under varying aphid densities. Am Potato J 72:119-132.

DiFonzo, C.D., D.W. Ragsdale, E.B. Radcliffe, and E.E. Banttari. 1994. Susceptibility to potato leafroll virus in potato: effects of cultivar, plant age at inoculation, and inoculation pressure on tuber infection. Plant Dis 78:1173-1177.

DiFonzo, C.D., D.W. Ragsdale, E.B. Radcliffe, N.C. Gudmestad, and G.A. Secor. 1996. Crop borders reduce potato virus Y incidence in seed potato. Ann Appl Biol 129:289-302.

DiFonzo, C.D., D.W. Ragsdale, E.B. Radcliffe, N.C. Gudmestad, and G.A. Secor. 1997. Seasonal abundance of aphid vectors of potato virus Y in the Red River Valley of Minnesota and North Dakota. J Econ Entomol 90:824-831.

Dixon, A.F.G. 1971a. The life-cycle and preferences of the bird cherry-oat aphid, *Rhopalosiphum padi* L., and their bearing on the theories of host alternation in aphids. Ann Appl Biol 68:135-147.

Dixon, A.F.G. 1971b. Migration in aphids. Sci Progr 59:41-53.

Dixon, A.F.G. 1977. Aphid ecology: life cycles, polymorphism and population regulation. Annu Rev Ecol Syst 8:329-353.

Dixon, A.F.G. 1990. Evolutionary aspects of parthenogenetic reproduction in aphids. Acta Phytopathol Entomol Hungarica 25:41-56.

Dixon, A.F.G. 1994. Individuals, populations, and patterns. *In*: Leather, S.R., A.D. Watt, N.J. Mills, and K.F.A. Walters (eds). Individuals, Populations and Patterns in Ecology. Intercept, Andover. pp. 449-476.

Dixon, A.F.G. 1998. Aphid Ecology: An optimization approach, 2nd edition. Chapman and Hall, London. 300 pp.

Dixon, A.F.G., and D.M. Glen. 1971. Morph determination in the bird cherry-oat aphid, *Rhopalosiphum padi* L. Ann Appl Biol 68:11-21.

Dixon, A.F.G., and M.T. Howard. 1986. Dispersal in aphids, a problem in resource allocation. *In*: Danthanarayana, W. (ed), Insect Flight: Dispersal and Migration. Springer, Berlin. pp. 145-151.

Douglas, D.R., and J.J. Pavek. 1972. Net necrosis of potato tubers associated with primary, secondary, and tertiary infection of leafroll. Am Potato J 49:330-333.

Eastop, V.F. 1972. Deductions from the present day host plants of aphids and related insects. *In*: Insect-Plant Relationships. Symp R Entomol Soc Lond 6:157-178.

Eastop, V.F. 1977. Worldwide importance of aphids as virus vectors. *In*: Harris, K.F., and K. Maramorosch (eds), Aphids as Virus Vectors. Academic Press, New York. pp. 3-61.

Eastop, V.F. 1986. Aphid plant associations. *In*: Stone, A.R., and D.L. Hawksworth (eds), Coevolution and Systematics. Clarendon Press, Oxford. pp. 35-54.

Eastop, V.F., and B. Raccah. 1988. Aphid and host plant species in the Arava Valley of Israel: epidemiological aspects. Phytoparasitica 16:23-32.

Edwards, L.J., J.B. Siddall, L.L. Dunham, P. Unden, and C.J. Kislow. 1973. Trans-β-farnesene, alarm pheromone of the green peach aphid, *Myzus persicae* (Sulzer). Nature 241:126-127.

Eigenbrode, S.D., H. Ding, P. Shiel, and P.H. Berger. 2002. Volatiles from potato plants infected with potato leafroll virus attract and arrest the virus vector, *Myzus persicae* (Homoptera: Aphididae). Proc R Soc Lond 269:455-460.

Eskandari, F., E.S. Sylvester, and J. Richardson. 1979. Evidence for lack of propagation of potato leaf roll virus in its aphid vector, *Myzus persicae*. Phytopathology 69:45-47.

Fang, H.-S., H.-H. Nee, T.-G. Chou. 1985. Comparative ability of seventeen aphid species to transmit tobacco vein-banding mosaic virus. Bull Tobacco Res Inst, Taiwan Tobacco and Wine Monopoly Bureau 22:41-46.

Fenton, B., J.A.T. Woodford, G. Malloch. 1998. Analysis of clonal diversity of the peach-potato aphid, *Myzus persicae* (Sulzer), in Scotland, UK and evidence for the existence of a predominant clone. Mol Ecol 7:1475-1487.

ffrench-Constant, R.H., A.L. Devonshire, and S.J. Clark. 1987. Differential rate of selection for resistance by carbamate, organophosphorus and combined pyrethroid and organophosphorus insecticides in *Myzus persicae* (Sulzer) (Hemiptera: Aphididae). Bull Entomol Res 77:227-238.

ffrench-Constant, R.H., S.J. Clark, and A.L. Devonshire. 1988a. Effect of decline of insecticide residues on selection for insecticide resistance in *Myzus persicae* (Sulzer) (Hemiptera: Aphididae). Bull Entomol Res 78:19-29.

ffrench-Constant, R.H., R. Harrington, and A.L. Devonshire. 1988b. Effect of repeated applications of insecticides to potatoes on numbers of *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) and on the frequencies of insecticide-resistant variants. Crop Protect 7:55-61.

Field, L.M., A.P. Anderson, I. Denholm, S.P. Foster, Z.K. Harling, N. Javed, D. Martínez-Torres, G.D. Moores, M.S. Williamson, and A.L. Devonshire. 1997. Use of biochemical and DNA diagnostics for characterising multiple mechanisms of insecticide resistance in the peach-potato aphid, *Myzus persicae* (Sulzer). Pestic Sci 51:283-289.

Flanders, K.S., S. Arnone, and E.B. Radcliffe. 1999. The potato: genetic resources and insect resistance. *In*: Clement, S.L., and S.S. Quisenberry (eds), Global Plant Genetic Resources for Insect-resistant Crops. CRC Press, Boca Raton. pp. 207-239.

Flanders, K.L., E.B. Radcliffe, and J.G. Hawkes. 1997. Geographic distribution of insect resistance in potatoes. Euphytica 93:201-221.

Flanders, K.L., E.B. Radcliffe, and D.W. Ragsdale. 1991. Potato leafroll virus spread in relation to densities of green peach aphid (Homoptera: Aphididae): implications for management thresholds for Minnesota seed potatoes. J Econ Entomol 84:1028-1036.

Flanders, K.L., D.W. Ragsdale, and E.B. Radcliffe. 1990. Use of enzyme-linked immunosorbent assay to detect potato leafroll virus in field grown potatoes, cv. Russet Burbank. Am Potato J 67:589-602, and 67:811 (errata).

Flanders, K.L., J.G. Hawkes, E.B. Radcliffe, and F.I. Lauer. 1992. Insect resistance in potatoes: sources, evolutionary relationships, morphological and chemical defenses, and ecogeographic associations. Euphytica 61:83-111.

Foster, G.N. 1986. Effects of two insecticidal spray programmes on aphids and the spread of potato leafroll virus. Ann Appl Biol 108 (Suppl Tests Ag Chem Cultivars):24-25.

Foster, G.N., and J.A.T. Woodford. 1997. Melon and cotton aphid (*Aphis gossypii* Glover: (Homoptera: Aphididae)) as a potential new virus vector of potatoes in Scotland. The Entomologist 116:175-178.

Foster, S.P., R. Harrington, A.L. Devonshire, I. Denholm, S.J. Clark, and M.A. Mugglestone. 1997. Evidence for a possible fitness trade-off between insecticide resistance and the low temperature movement that is essential for survival of UK populations of *Myzus persicae* (Hemiptera: Aphididae). Bull Entomol Res 87:573-579.

Foster, S.P., R. Harrington, A.L. Devonshire, I. Denholm, G.J. Devine, M.G. Kenward, and J.S. Bale. 1996. Comparative survival of insecticide-susceptible and resistant peach-potato aphids, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), in low temperature field trials. Bull Entomol Res 86:17-21.

Franc, G.D. 2001. Seed certification as a virus management tool, *In:* Loebenstein, G., P.H. Berger, A.A. Brunt, and R.H. Lawson (eds), Virus and Virus-like Diseases of Potatoes and Production of Seed-potatoes. Kluwer Academic Publishers, Dordrecht. pp. 407-420.

Frazer B.D. 1987. Aphid and virus management in potatoes in British Columbia. *In:* Boiteau, G., R.P. Singh, and R.H. Parry (eds), Potato Pest Management in Canada. Proc Symp Improv Potato Pest Protect, Fredericton, NB. pp. 23-29.

Gabriel, W., J. Szulc, and M. Wislocka. 1981. Influence de la distance des sources d'infection sur l'effet de traitements à l'aide d'insecticides systémiques sur la propagation des virus Y et M de la pomme de terre. Potato Res 25:1-11.

Garrett, R.G. 1986. Prologue: a basis for control. *In:* McLean, G.D., R.G. Garrett, and W.G. Ruesink (eds), Plant Virus Epidemics: Monitoring, Modelling and Predicting Outbreaks. Academic Press, Sydney. pp. 1-10.

George Jr., W.L., and J.B. Kring. 1971. Virus protection of late-season summer squash with aluminum mulch. Conn Agr Exp Stn, Circ 239.

Gibson, R.W., and C.C. Campbell. 1986. Investigations into how cypermethrin controls the spread of potato virus Y by aphids. 1986 British Crop Protect Conf — Pests Dis 997-1000.

Gibson, R.W., and G.R. Cayley. 1984. Improved control of potato virus Y by mineral oil plus the pyrethroid cypermethrin applied electrostatically. Crop Protect 3:469-478.

Gibson, R.W., and J.A. Pickett. 1983. Wild potato repels aphids by release of aphid alarm pheromone. Nature 302:608-609.

Gibson, R.W., and A.D. Rice. 1986. The combined use of mineral oils and pyrethroids to control plant viruses transmitted non- and semi-persistently by *Myzus persicae.* Ann Appl Biol 109:465-472.

Gibson, R.W., R.W. Payne, and N. Katis. 1988. The transmission of potato virus Y by aphids of different vectoring abilities. Ann Appl Biol 113:35-43.

Gibson, R.W., J.A. Pickett, G.W. Dawson, A.D. Rice, and M.F. Stribley. 1984. The effects of aphid alarm pheromone derivatives and related compounds on non- and semi-persistent plant virus transmission by *Myzus persicae.* Ann Appl Biol 104:203-209.

Gibson, R.W., A.D. Rice, and R.M. Sawicki. 1982a. Effects of the pyrethroid deltamethrin on the acquisition and inoculation of viruses by *Myzus persicae.* Ann Appl Biol 100:49-54.

Gibson, R.W., A.D. Rice, J.A. Pickett, M.C. Smith, and R.M. Sawicki. 1982b. The effects of the repellents dodecanoic acid and polygodial on the acquisition of non-, semi-, and persistent plant viruses by the aphid *Myzus persicae.* Ann Appl Biol 100:55-59.

Goodwin, S.B., L.S. Sujkowski, and W.E. Fry. 1996. Widespread distribution and probable origin of resistance to metalaxyl in clonal genotypes of *Phytophthora infestans* in the United States and western Canada. Phytopathology 86:793-800.

Gordon, P.L., and F.L. McEwen. 1984. Insecticide-stimulated reproduction of *Myzus persicae*, the green peach aphid (Homoptera: Aphididae). Can Entomol 116:783-784.

Govier, D.A., and B. Kassanis. 1974a. Evidence that a component other than the virus particle is needed for aphid transmission of potato virus Y. Virology 57:285-286.

Govier, D.A., and B. Kassanis. 1974b. A virus-induced component of plant sap needed when aphids acquire potato virus Y from purified preparations. Virology 61:420-426.

Griffiths, D.C., and J.A. Pickett. 1980. A potential application of aphid alarm pheromones. Entomol Exp Appl 27:199-201.

Griffiths, D.C., J.A. Pickett, L.E. Smart, and C.M. Woodcock. 1989. Use of insect antifeedants against aphid vectors of plant virus disease. Pestic Sci 27:269-276.

Guenthner, J.F., M.V. Wiese, A.D. Pavlista, J.B. Sieczka, and J.A. Wyman. 1999. Assessment of pesticide use in the U.S. potato industry. Am J Potato Res 76:25-29.

Gutbrod, O.A., and A.R. Mosley. 2001. Common seed potato certification schemes, *In:* Loebenstein, G., P.H. Berger, A.A. Brunt, and R.H. Lawson (eds), Virus and Virus-like Diseases of Potatoes and Production of Seed-potatoes. Kluwer Academic Publishers, Dordrecht. pp. 421-438.

Haine, E. 1955. Aphid take-off in controlled wind speeds. Nature 175:474-475.

Halbert, S.E., J. Connelly, and L.E. Sandvol. 1990. Suction trapping of aphids in western North America (emphasis on Idaho). Acta Phytopathol Entomol Hungarica 25:411-422.

Hammond, D., and F.R. Holbrook. 1979. Maine finds methods to control leaf roll: results of pilot research program. Spudman 17:18-20.

Hanafi, A., E.B. Radcliffe, and D.W. Ragsdale. 1989. Spread and control of potato leafroll virus in Minnesota. J Econ Entomol 82:1201-1206.

Hanafi, A., E.B. Radcliffe, and D.W. Ragsdale. 1995. Spread and control of potato leafroll virus in the Souss Valley of Morocco. Crop Protect 14:145-153.

Hane, D.C., and P.B. Hamm. 1999. Effects of seedborne potato virus Y infection in two potato cultivars expressing mild disease symptoms. Plant Dis 83:43-45.

Harrewijn, P., and H. Kayser. 1997. Pymetrozine, a fast-acting and selective inhibitor of aphid feeding. *In-situ* studies with electronic monitoring of feeding behaviour. Pestic Sci 49:130-140.

Harrewijn, P., W.J. de Kogel and P.G.M. Piron. 1998. CGA 293'343 effects on *Myzus persicae*: electrical penetration graph studies and effect on non-persistent virus transmission. Proc Brighton Crop Protect Conf — Plant Dis 813-818.

Harrewijn, P., H.D. Ouden, and P.G.M. Piron. 1991. Polymer webs to prevent virus transmission by aphids in seed potatoes. Entomol Exp Appl 58:101-107.

Harrewijn, P., H.A. van Hoof, and J.P.W. Noordink. 1981. Flight behaviour of the aphid *Myzus persicae* during its maiden flight. Neth J Plant Pathol 87:111-117.

Harrington, R., and R.W. Gibson. 1989. Transmission of potato virus Y by aphids trapped in potato crops in southern England. Potato Res 32:167-174.

Harrington, R., N. Katis, and R.W. Gibson. 1986. Field assessment of the relative importance of different aphid species in the transmission of potato virus Y. Potato Res 29:67-76.

Harrington, R., G.M. Tatchell, and J.S. Bale. 1990. Weather, life cycle strategy and spring populations of aphids. Acta Phytopathol Entomol Hungarica 25:423-432.

Harrington, R., E. Bartlet, D.K. Riley, R.H. ffrench-Constant, and S.J. Clark. 1989. Resurgence of insecticide-resistant *Myzus persicae* on potatoes treated repeatedly with cypermethrin and mineral oil. Crop Protect 8:340-348.

Harrington, R., J.A. Mann, R.T. Plumb, A.J. Smith, M.S. Taylor, G.N. Foster, S.J. Holmes, A.J. Masterman, S.J. Tones, J.D. Knight, J.N. Oakley, I. Barker, and K.F.A. Walters. 1994. Monitoring and forecasting for BYDV control — the way forward? Aspects Appl Biol. 37:197-206.

Harrison, B.D. 1971. Potato viruses in Britain. *In*: Western, J.H. (ed), Diseases of Crop Plants. MacMillan, London. pp. 123-159.

Heimbach, U., T. Thieme, H.-L. Weidemann, R. Thieme, R. 1998. Transmission of potato virus Y by aphid species which do not colonise potatoes. *In*: Nieto Nafría, J.M., and A.F.G. Dixon (eds), Aphids in Natural and Managed Ecosystems. Universidad de León, León, Spain. pp. 555-559.

Heinze, K. 1960. Versuche zur Übertragung nichtpersistenter und persistenter Viren durch Blattläuse. NachBl dtsch PflSchDienst 12:119-121.

Hemphill Jr., D.D., G.L. Reed, R.C. Wilson, O. Gutbrod, and T.C. Allen. 1988. Prevention of potato virus Y transmission in potato seed stock with direct covers. Plasticulture 79:31-36.

Herrbach, E. 1992. Alarm pheromones and allelochemics as a means of aphid control. Neth J Plant Pathol 98, suppl 2:63-71.

Hiddema, J. 1972. Inspection and quality grading of seed potatoes. *In*: de Bokx, J.A. (ed), Viruses of Potatoes and Seed-potato Production. Pudoc, Wageningen. pp. 206-215.

Hille Ris Lambers, D. 1972. Aphids: their life cycles and their role as virus vectors. *In*: de Bokx, J.A (ed), Viruses of Potatoes and Seed-Potato Production. Pudoc, Wageningen. pp. 36-56.

Hille Ris Lambers, D., and M.E. MacGillivray. 1959. Scientific names of potato-infesting aphids. Can Entomol 91:321-328.

Hinz, von B. 1966. Beiträge zur Analyse der Vektoreignung einiger wirtschaftlich wichtiger Blattlausarten und -rassen I. Versuche zur Ermittlung der Vektoreigenshaften für das Blattrollvirus der Kartoffel bei Rassen yon *Myzus persicae* (Sulz.). Phytopathol Z 56:54-77.

Hodgson, C. 1991. Dispersal of apterous aphids (Homoptera: Aphididae) from their host plant and its significance. Bull Entomol Res 81:417-427.

Hogenhout S.A., F. van der Wilk, M. Verbeek, R.W. Goldbach, and J.F.J.M. van den Heuvel. 1998. Potato leafroll virus binds to the equatorial domain of the aphid endosymbiotic GroEL homolog. J Virol 72:358-365.

Hogenhout S.A., M. Verbeek, F. Hans, P.M. Houterman, M. Fortas, F. van der Wilk, H. Huttinga, and J.F.J.M. van den Heuvel. 1996. Molecular basis of the interaction between luteoviruses and aphids. Agronomie 16:167-173.

Holbrook, F.R. 1977. Aldicarb and thiofanox: effect on the feeding activity of green peach aphids. J Econ Entomol 70:742-744.

Hollings, M. 1955. Aphid movement and virus spread in seed potato areas of England and Wales, 1950-53. Plant Pathol 4:73-82.

Howell, P.J. 1974. Field studies of potato leaf roll virus spread in south-eastern Scotland, 1992-1969, in relation to aphid populations and other factors. Ann Appl Biol 76:187-197.

Ioannou, N. 1989. The infection pressure of potato leafroll virus and potato virus Y in relation to aphid populations in Cyprus. Potato Res 32:33-47.

IRAC (Insecticide Resistance Action Committee). 2000. Guidelines for preventing and managing insecticide resistance in the peach-potato aphid, *Myzus persicae*. http://www.pesticides.gov.uk/committees/Resistance/IRAG/myzper01.pdf.

Irwin, M.E. 1980. Sampling aphids in soybean fields. *In*: Kogan, M., and D. Herzog (eds), Sampling Methods in Soybean Entomology. Springer-Verlag, New York. pp. 239-259.

Irwin, M.E., and W.G. Ruesink. 1986. Vector intensity: a product of propensity and activity. *In*: McLean, G.D., R.G. Garrett, and W.G. Ruesink (eds), Plant Virus Epidemics: Monitoring, Modelling and Predicting Outbreaks. Academic Press, Sydney. pp. 13-33.

Johnson, B. 1957. Studies on the degeneration of the flight muscles of alate aphids. I. A comparative study of the occurrence of muscle breakdown in relation to reproduction in several species. J Insect Physiol 1:248-256.

Johnson, B. 1959. Studies on the degeneration of the flight muscles of alate aphids. II. Histology and control of muscle breakdown. J Insect Physiol 3:367-377.

Johnson, C.G. 1969. Migration and Dispersal of Insects by Flight. Methuen, London. 763 pp.

Johnson, C.G., and L.R. Taylor. 1955. The development of large suction traps for airborne insects. Ann Appl Biol 43:51-62.

Kawada, K. 1987. Polymorphism and morph determination. *In*: Minks, A.K., and P. Harrewijn (eds), Aphids: Their Biology, Natural Enemies and Control, 2A, World Crop Pests. Elsevier, Amsterdam. pp. 255-268.

Kennedy, J.S., and C.O. Booth. 1951. Host alternation in *Aphis fabae* Scop. I. Feeding preferences and fecundity in relation to age and kind of leaves. Ann Appl Biol 38:25-64.

Kennedy, J.S., and C.O. Booth. 1963a. Free flight of aphids in the laboratory. J Exp Biol 40:67-85.

Kennedy, J.S., and C.O. Booth. 1963b. Co-ordination of successive activities in an aphid. The effect of flight on the settling responses. J Exp Biol 40:351-369.

Kennedy, J.S., M.F. Day, and V.F.A. Eastop. 1962. A Conspectus of Aphids as Vectors of Plant Viruses. Commonw Inst Entomol, London. 114 pp.

Kerns, D.L., J.C. Palumbo, and D.N. Byrne. 1998. Relative susceptibility of red and green color forms of green peach aphid to insecticides. Southwest Entomol 23:17-24.

Killick, R.J. 1979. The effect of infection with potato leaf roll virus (PLRV) on yield and some of its components in a variety of potato (*Solanum tuberosum*). Ann Appl Biol 91:67-74.

Kindlmann, P., and A.F.G. Dixon. 1989. Developmental constraints in the evolution of reproductive strategies: telescoping of generations in parthenogenetic aphids. Functional Ecol 3:531-537.

Kindlmann, P., and A.F.G. Dixon. 1992. Optimum body size: effects of food quality and temperature, when reproductive growth rate is restricted, with examples from aphids. J Evol Biol 5:677-690.

Kindlmann P., A.F.G. Dixon, and L.J. Gross. 1992. The relationship between individual and population growth rates in multicellular organisms. J Theor Biol 157:535-542.

King, R.R., Y. Pelletier, R.P. Singh, and L.A. Calhoun. 1986. 3,4-di-O-isobutyryl-6-O-caprylsucrose: the major component of a novel sucrose ester complex from the type B glandular trichomes of *Solanum berthaultii* Hawkes (PI 473340). J Chem Soc, Chem Commun 14:1078-1079.

Kish, L.P., I. Majchrowicz, and K.D. Biever. 1994. Prevalence of natural fungal mortality of green peach aphid (Homoptera: Aphididae) on potatoes and nonsolanaceous hosts in Washington and Idaho. Environ Entomol 23:1326-1330.

Klingauf, F.A. 1975. Die Frühphase in der Wirtswahl von Blattläusen. Mededelingen Faculteit Landbouwwetenschappen Gent 40:351-364.

Klingauf, F.A. 1987a. Host plant finding and acceptance. *In*: Minks, A.K., and P. Harrewijn (eds), Aphids: Their Biology, Natural Enemies and Control, 2A, World Crop Pests. Elsevier, Amsterdam. pp 209-224.

Klingauf, F.A. 1987b. Feeding, adaptation and excretion. *In*: Minks, A.K., and P. Harrewijn (eds), Aphids: Their Biology, Natural Enemies and Control, 2A, World Crop Pests. Elsevier, Amsterdam. pp 225-253.

Klostermeyer, E.C. 1959. The relationship between insecticide-altered aphid populations and the spread of potato leaf roll. J Econ Entomol 52:727-730.

Kolbe, W. 1970. Influence of direct feeding damage on yields of heavily aphid-infested potato crops. Pfanzenschutz-Nachr 23:273-282.

Kostiw, M. 1979. Transmission of potato virus Y by *Rhopalosiphum padi* L. Potato Res 22:237-238.

Kring, J.B. 1970. Determining the number of aphids over reflective surfaces. J Econ Entomol 63:1350-1353.

Kuno, E. 1969. A new method of sequential sampling to obtain the population estimates with a fixed level of precision. Res Popul Ecol 11:127-136.

Kurppa, S., and P. Rajala. 1986. Occurrence of winged aphids on potato plants and pressure for potato virus Y transmission in Finland. Ann Agr Fenniae 25:199-214.

Labonne, G., G. Fauvel, F. Leclant, and J.-B. Quiot. 1983. Intérêt des pièges à fils dans l'étude des populations de pucerons ailés. Agronomie 4:315-325.

Lagnaoui, A., and E.B. Radcliffe. 1998. Potato fungicides interfere with entomopathogenic fungi impacting population dynamics of green peach aphid. Am J Potato Res 75:19-25.

Latgé, J.-P., P. Silvie, B. Papierok, G. Remaudière, C.A. Dedryver, and J.M. Rabasse. 1983. Advantages and disadvantages of *Conidiobolus obscurus* and of *Erynia neoaphidis* in the biological control of aphids. *In*: Cavalloro, R. (ed), Aphid Antagonists. Balkema, Rotterdam. pp. 20-32.

Leclercq-Le Quillec, F., S. Tanguy, and C.A. Dedryver. 1995. Aerial flow of barley yellow dwarf viruses and of their vectors in western France. Ann Appl Biol 126:75-90.

Lees, A.D. 1959. The role of photoperiod and temperature on the determination of parthenogenetic and sexual forms in the aphid *Megoura viciae* Buckton. I. The influence of these factors on apterous virginoparae and their progeny. J Insect Physiol 3:92-117.

Lees, A.D. 1966. The control of polymorphism in aphids. Advances Insect Physiol 3:207-277.

Lees, A.D. 1979. The maternal environment and the control of morphogenesis in insects. *In*: Newth, D.R., and M. Balls (eds), Maternal Effects in Development. British Soc Develop Biol Symp 4. pp. 221-239.

Lefko, S.A., L.P. Pedigo, W.D. Batchelor, and M.E. Rice. 1998. Spatial modeling of preferred wireworm (Coleoptera: Elateridae) habitat. Environ Entomol 27:184-190.

Leonard, M.D., H.G. Walker, and L. Enari. 1970. Host plants of *Myzus persicae* at the Los Angeles State and County Arbouretum, Arcadia, California. Proc Entomol Soc Wash 72:294-312.

Leonard, S.H., and F.R. Holbrook. 1978. Minimum acquisition and transmission times for potato leaf roll virus by the green peach aphid. Ann Entomol Soc Am 71:493-495.

Loebenstein, G., M. Alper, and M. Deutsch. 1964. Preventing aphid-spread cucumber mosaic virus with oils. Phytopathology 54:960-962.

Lopez-Abella, D., R.H.E. Bradley, and K.F. Harris. 1988. Correlation between stylet paths made during superficial probing and the ability of aphids to transmit nonpersistent viruses. Adv Dis Vect Res 5:251-285.

Loughnane, J.B. 1943. *Aphis rhamni* Boyer; its occurrence in Ireland and its efficiency as a vector of potato viruses. J Dep Agric Eire 40:291-298.

Lowery, D.T., and G. Boiteau. 1988. Effects of five insecticides on the probing, walking, and settling behavior of the green peach aphid and the buckthorn aphid (Homoptera: Aphididae) on potato. J Econ Entomol 81:208-214.

Lowery, D.T., and M.K. Sears. 1986a. Effect of exposure to the insecticide azinphosmethyl on reproduction of green peach aphid (Homoptera: Aphididae). J Econ Entomol 79:1534-1538.

Lowery, D.T., and M.K. Sears. 1986b. Stimulation of reproduction of the green peach aphid (Homoptera: Aphididae) by azinphosmethyl applied to potatoes. J Econ Entomol 79:1530-1533.

Loxdale, H.D., J. Hardie, S.E. Halbert, R.G. Foottit, N.A.C. Kidd, and C.I. Carter. 1993. The relative importance of short- and long-range movement of flying aphids. Biol Rev 68:291-311.

MacGillivray, M.E. 1972. The sexuality of *Myzus persicae* (Sulzer), the green peach aphid, in New Brunswick (Homoptera: Aphididae). Can J Zool 50:469-471.

MacGillivray, M.E. 1981. Aphids. *In*: Hooker, W.J. (ed), Compendium of Potato Diseases. American Phytopathogical Society, St. Paul. pp. 101-103.

Mackauer, M., and M.J. Way. 1976. *Myzus persicae* Sulz, an aphid of world importance. *In*: Delucchi, V.L. (ed), Int. Biol Programme 9, Studies in Biological Control. Cambridge University Press, London. pp. 51-119.

MacKinnon, J.P. 1969. Transmission of leaf roll virus from potato to potato by a green clone of *Macrosiphum euphorbiae*. Am Potato J 46:23-24.

MacRae, I.V. 1998. Site specific IPM. *In*: Radcliffe, E.B and W.D. Hutchison (eds), Radcliffe's IPM World Textbook, http://ipmworld.umn.edu/chapters/ipmgis.htm.

Manzer, F.E., D.C. Merriam, R.H. Storch, and G.W. Simpson. 1982. Effect of time of inoculation with potato leafroll virus on development of net necrosis and stem-end browning in potato tubers. Am. Potato J. 59:337-349.

Marco, S. 1986. Incidence of aphid-transmitted virus infections reduced by whitewash sprays on plants. Phytopathology 76:1344-1348.

Marco, S. 1993. Incidence of nonpersistently transmitted viruses in pepper sprayed with whitewash, oil and insecticide, alone or combined. Plant Dis 77:1119-1122.

Martín, B., J.L. Collar, W.F. Tjallingii, and A. Fereres. 1997. Intracellular ingestion and salivation by aphids may cause the acquisition and inoculation of non-persistently transmitted plant viruses. J Gen Virol 78:2701-2705.

Martínez-Torres, D., R. Carrió, A. Latorre, J.C. Simon, A. Hermoso, and A. Moya. 1997a. Assessing the nucleotide diversity of three aphid species by RAPD. J Evol Biol 10:459-477.

Martínez-Torres, D., A.L. Devonshire, and M.S. Williamson. 1997b. Molecular studies of knockdown resistance to pyrethroids: cloning of domain II sodium channel gene sequences from insects. Pestic Sci 51:265-270.

McAllister, M.K., and B.D. Roitberg. 1987. Adaptive suicidal behaviour in aphids. Nature 328:797-799.

Minks, A.K., and P. Harrewijn. 1987. Preface. *In:* Minks, A.K., and P. Harrewijn (eds), Aphids: Their Biology, Natural Enemies and Control, 2A, World Crop Pests. Elsevier, Amsterdam. pp. v-vi.

Missonnier, J., Y. Robert, and G. Thoizon. 1970. Circonstances épidémiologiques semblant favoriser le développement des mycoses à Entomophthorales chex trois aphides, *Aphis fabae* Scop., *Capitophorus horni* Borner et *Myzus persicae* (Sulz.). Entomophaga 15:169-190.

Mittler, T.E. 1970. Uptake rates of plant sap and synthetic diet by the aphid *Myzus persicae.* Ann Entomol Soc Am 63:1701-1705.

Mittler, T.E., and R.H. Dadd. 1965. Differences in the probing responses of *Myzus persicae* (Sulzer) elicited by different feeding solutions behind a parafilm membrane. Entomol Exp Appl 8:107-122.

Mittler, T.E., and M. Matsuka. 1985a. Male production by apterous viviparae of the aphid *Myzus persicae* temporarily exposed to different scotoperiods. J Insect Physiol 31:171-177.

Mittler, T.E., and M. Matsuka. 1985b. The production of different morphs by alate viviparae of the aphid *Myzus persicae* temporarily exposed to long scotophases. Entomol Exp Appl 37:175-182.

Miyamoto, S., and Y. Miyamoto. 1966. Notes on aphid-transmission of potato leafroll virus. Sci Rep Hyogo Univ Agric 7:51-66.

Miyamoto, S., and Y. Miyamoto. 1971. Notes on aphid-transmission of potato leafroll virus. 1. Transference of the virus to nymphs from viruliferous adults of *Myzus persicae* Sulz. Sci Rpt Fac Agric Kobe Univ 9:59-70.

Miyazaki, M. 1987. Forms and morphs of aphids. *In:* Minks, A.K., and P. Harrewijn (eds), Aphids: Their Biology, Natural Enemies and Control, 2A, World Crop Pests. Elsevier, Amsterdam. pp. 27-50.

Moericke, V. 1951. Eine Farbfalle zur Kontrolle des Fluges von Blättlausen insbesondere der Pfirsichblattlaus, *Myzodes persicae* (Sulz.). NachrBl dtsch PflSchutz Dienst (Braunschweig) 3:23-24.

Moericke, V. 1955. Über die Lebensgewohnheiten der geflügelten Blättlause (*Aphidina*) unter besonderer Berücksichtigung des Verhaltens beim Landen. Z Angew Entomol 37:29-91.

Montgomery, M.E., and L.R. Nault. 1977. Aphid alarm pheromones: dispersion of *Hyadaphis erysimi* and *Myzus persicae.* Ann Ent Soc Am 70:669-672.

Montllor, C.B. 1991. The influence of plant chemistry on aphid feeding behavior. *In:* Bernays, E. (ed), Insect-Plant Interactions. CRC Press, Boca Raton. pp. 125-173.

Moores, G.D., G.J. Devine, and A.L. Devonshire. 1994. Insecticide-insensitive acetylcholinesterase can enhance esterase-based resistance in *Myzus persicae* and *Myzus nicotianae.* Pestic Biochem Physiol 49:114-120.

Moran, N.A. 1988. The evolution of host-plant alternation in aphids: evidence for specialization as a dead end. Am Nat 132:681-706.

Moran, N.A. 1990. Aphid life cycles: two evolutionary steps. Am Nat 136:135-138.

Moran, N.A. 1992. The evolution of aphid life cycles. Annu Rev Entomol 37:321-348.

Mordvilko, A. 1928. The evolution of cycles and the origin of heteroecy (migrations) in plant-lice. Ann Mag Nat 10:570-582.

Mowry, T.M. 1994. Potato leafroll virus management in the Pacific Northwest (USA). *In:* Zehnder, G.W., M.L. Powelson, R.K. Jansson, and K.V. Raman (eds), Advances in Potato Pest Biology and Management. APS Press, Saint Paul. pp. 111-123.

Mowry, T.M. 2001. Green peach aphid (Homoptera: Aphididae) action thresholds for controlling the spread of potato leafroll virus in Idaho. J Econ Entomol 94:1332-1339.

Muggleton, J., S. Hockland, B.B. Thind, A. Lane, and A.L. Devonshire. 1996. Long-term stability in the frequency of insecticide resistance in the peach-potato aphid, *Myzus persicae,* in England. Proc Brighton Crop Protect Conf — Pests Dis 739-744.

Nakamuta, K. 1991. Aphid alarm pheromone component, (*E*)-β-farnasene, and local search by a predatory lady beetle, *Coccinella septempunctata bruckii* Mulsant (Coleoptera: Coccinellidae). Appl Ent Zool 26:1-7.

Nanne, H.W., and E.B. Radcliffe. 1971. Green peach aphid populations on potatoes enhanced by fungicides. J Econ Entomol 64:1569-1570.

Naranjo, S.E., and W.D. Hutchison. 1997. Validation of arthropod sampling plans using a resampling approach: software and analysis. Am Entomol 43:48-57.

NASS (U.S. National Agricultural Statistics Service). 2000. Agricultural Chemical Usage, 1999 Field Crops Summary, http://usda.mannlib.cornell.edu/reports/nassr/other/pcu-bb/agch0500.pdf.

Nault, L.R. 1997. Arthropod transmission of plant viruses: a new synthesis. Ann Entomol Soc Am 90:521-541.

Nemecek, T., J.O. Derron, A. Fischlin, and O. Roth. 1995. Use of a crop-growth model coupled to an epidemic model to forecast yield and virus infection in seed potatoes. *In:* Haverkort, A.J., D.K.L. MacKerron (eds), Potato Ecology and Modelling of Crops Under Conditions Limiting Growth. Kluwer Academic Publ, Dordrecht. pp. 281-291.

Nemecek, T., J.O. Derron, O. Roth, and A. Fischlin. 1996. Adaptation of a crop-growth model and its extension by a tuber size function for use in a seed potato forecasting system. Agric Systems 52:419-437.

Newton, C., and A.F.G. Dixon. 1988. The cost of switching from asexual to sexual reproduction in an aphid. Entomol Exp Appl 47:283-287.

Nie, X., and R.P. Singh. 2001. A novel usage of random primers for multiplex RT-PCR detection of virus and viroid in aphids, leaves, and tubers. J Virol Methods 91:37-49.

Nie, X., and R.P. Singh. 2002. A new approach for the simultaneous differentiation of biological and geographical strains of *Potato virus Y* by uniplex and multiplex RT-PCR. J Virol Methods (in press).

Nisbet, A.J., J.A.T. Woodford, and R.H.C. Strang. 1996. The effects of azadirachtin on the acquisition and inoculation of potato leafroll virus by *Myzus persicae.* Crop Protect 15:9-14.

Nixon R. 1972. Message from the President of the United States transmitting a program on environmental protection. Washington, DC: House of Representatives, 92nd Congr, 2nd Sess Doc 92-247. 16 pp.

Novy, R.G., and J.P. Helgeson. 1994a. Somatic hybrids between *Solanum etuberosum* and diploid tuber-bearing Solanum clones. Theor Appl Genet 89:775-782.

Novy, R.G., and J.P. Helgeson. 1994b. Resistance to potato virus Y in somatic hybrids between *Solanum etubersosum* and *S. tuberosum* x *S. berthaultii* hybrid. Theor Appl Genet 89:783-786.

Novy, R.G., A. Nasruddin, D.W. Ragsdale, and E.B. Radcliffe. 2002. Genetic resistances to potato leafroll virus, potato virus Y, and green peach aphid in progeny of *Solanum etuberosum.* Am J Potato Res 79:9-18.

Nyrop, J.P., and M. Binns. 1991. Quantitative methods for designing and analyzing sampling programs for use in pest management. *In:* Pimentel, D. (ed), Handbook of Pest Management in Agriculture, vol 2. CRC Press, Boco Raton. pp. 67-132.

Ohshima, K., K. Sako, and C. Hiraishi. 2000. Potato tuber necrotic diseases occurring in Japan: its association with *Potato Virus Y* necrotic strain. Plant Dis 84:1109-1115.

Parry, R.H. 1987. Aphid and virus management in potatoes in eastern Canada. *In*: Boiteau, G., R.P. Singh, and R.H. Parry (eds), Potato Pest Management in Canada. Proc Symp Improv Potato Pest Protect, Fredericton, NB. pp. 9-22.

Pelletier, Y., and R.R. King. 1987. Semiochemicals and potato pests: review and perspective for crop protection. *In*: Boiteau, G., R.P. Singh, and R.H. Parry (eds), Potato Pest Management in Canada. Proc Symp Improv Potato Pest Protect, Fredericton, NB. pp. 146-172.

Perrin, R.M., and R.W. Gibson. 1985. Control of some insect-borne plant viruses with the pyrethroid PP321 (Karate). Int Pest Control 27:142-145.

Perring, T.M., N.M. Gruenhagen, and C.A. Farrar. 1999. Management of plant viral diseases through chemical control of insect vectors. Annu Rev Entomol 44:457-481.

Peters, R.D., H. Förster, H.W. Platt, and M.D. Coffey. 2001. Novel genotypes of *Phytophora infestans* in Canada during 1994 and 1995. Am J Potato Res 78:39-45.

Pickett, J.A., L.J. Wadhams, C.M. Woodcock, and J. Hardie. 1992. The chemical ecology of aphids. Annu Rev Entomol 37:67-90.

Pickup, J., and A.M. Brewer. 1994. The use of aphid suction-trap data in forecasting the incidence of potato leafroll virus in Scottish seed potatoes. Proc Brighton Crop Protect Conf — Pests Dis 351-358.

Piron, P.G.M. 1986. New aphid vectors of potato virus Y^N. Neth J Plant Pathol 92:223-229.

Pirone, T.P., and K.F. Harris. 1977. Nonpersistent transmission of plant viruses by aphids. Annu Rev Phytopathol 15:55-73.

Pirone, T.P., and D.W. Thornbury. 1988. Quantity of virus required for aphid transmission of a potyvirus. Phytopathology 78:104-107.

Plaisted, R.L. W.M. Tingey, and J.C. Steffens. 1992. The germplasm release of NYL 235-4, a clone with resistance to the Colorado potato beetle. Am Potato J 69:843-846.

Pollard, D.G. 1973. Plant penetration by feeding aphids (Hemiptera: Aphidoidea): a review. Bull Entomol Res 62:631-714.

Pollard, D.G. 1977. Aphid penetration of plant tissues. *In*: Harris, K.F., and K. Maramorosch (eds), Aphids as Virus Vectors. Academic Press, New York. pp. 105-118.

Powell, G. 1992. The effect of mineral oil on stylet activities and potato virus Y transmission by aphids. Entomol Exp Appl 63:237-242.

Powell, G., J. Hardie, and J.A. Pickett. 1996. Effects of the repellent polygodial on stylet penetration behaviour and non-persistent transmission of plant viruses by aphids. J Appl Entomol 120:241-243.

Powell, G., J. Hardie, and J.A. Pickett. 1998. The effects of antifeedant compounds and mineral oil on stylet penetration and transmission of potato virus Y by *Myzus persicae* (Sulz.) (Hom., Aphididae). J Appl Entomol 122:331-333.

Proeseler, G., and H. Weidling. 1975. Die Retentionszeit von Stämmen des Kartoffel-Y-Virus in verschiedenen Aphidenarten und Einfluβ der Temperatur. Archiv Phytopathol PflSchutz, Berlin 11:335-345.

Raccah, B., A. Gal-on, and V.F. Eastop. 1985. The role of flying aphid vectors in the transmission of cucumber mosaic virus and potato virus Y to peppers in Israel. Ann Appl Biol 106:451-460.

Radcliffe, E.B. 1982. Insect pests of potato. Annu Rev Entomol 27:173-204.

Radcliffe, E.B., K.L. Flanders, D.W. Ragsdale, and D.M. Noetzel. 1991. Pest management systems for potato insects. *In*: Pimentel, D. (ed), CRC Handbook of Pest Management in Agriculture, 2nd edition, Vol III. CRC Press, Boca Raton. pp. 587-621.

Radcliffe, E.B., D.W. Ragsdale, and R.A. Suranyi. 2002. IPM case studies — potato, *In*: van Emden, H.F., and R. Harrington (eds), Aphids as Crop Pests. CABI Publ, Wallingford (submitted).

Ragsdale, D.W., E.B. Radcliffe, and C.D. DiFonzo. 2001. Epidemiology and field control of PVY and PLRV. *In*: Loebenstein, G., P.H. Berger, A.A. Brunt, and R.H. Lawson (eds), Virus and Virus-like Diseases of Potatoes and Production of Seed-potatoes. Kluwer Academic Publishers, Dordrecht. pp. 237-270.

Ragsdale, D.W., E.B. Radcliffe, C.D. DiFonzo, and M.S. Connelly. 1994. Action thresholds for an aphid vector of potato leafroll virus. *In*: Zehnder, G.W., M.L. Powelson, R.K. Jansson, and K.V. Raman (eds). Advances in Potato Pest Biology and Management. Am Phytopathol Soc. pp. 99-110.

Raman, K.V., and E.B. Radcliffe. 1992. Pest aspects of potato production. Part 2, Insect pests. *In*: Harris, P.M. (ed), The Potato Crop, The Scientific Basis for Improvement, 2nd edition. Chapman & Hall, London. pp. 476-506.

Reestman, A.J. 1970. Importance of the degree of virus infection for the production of ware potatoes. Potato Res 13:248-68.

Remaudière, G., and M. Remaudière. 1997. Catalogue des Aphididae du Monde Homoptera — Aphidoidea. Institut National de la Recherche Agronomique, Versailles. 478 pp.

Remaudière, G., J.-P. Latgé, and M.-F. Michel. 1981. Écologie comparée des Entomophthoracées pathogènes des pucerons en France littorale et continentale. Entomophaga 26:157-178.

Ribbands, C.R. 1963. The spread of apterae of *Myzus persicae* (Sulz.) and of yellows viruses within a sugar-beet crop. Bull Ent Res 54:267-283.

Robert, Y. 1971. Épidémiologie de l'enroulement de la pomme de terre: capacité vectrice de stades et de formes des pucerons *Aulacorthum solani* Kltb. *Macrosiphum euphorbiae* Thomas et *Myzus persciae* Sulz. Potato Res 14:130-139.

Robert, Y. 1979. Recherches écologiques sur les pucerons *Aulacorthum solani* Kltb., *Macrosiphum euphorbiae* Thomas et *Myzus persicae* Sulz. dans l'Ouest de la France. II. Evolution spatio-temporelle de leurs populations sur la pomme de terre. Ann Zool Ecol Anim 11:67-83.

Robert, Y. 1987. Dispersion and migration. *In*: Minks, A.K., and P. Harrewijn (eds), Aphids: Their Biology, Natural Enemies and Control, 2A, World Crop Pests. Elsevier, Amsterdam. pp. 299-313.

Robert, Y., and D. Bourdin. 2001. Aphid transmission of potato viruses, *In*: Loebenstein, G., P.H. Berger, A.A. Brunt, and R.H. Lawson (eds), Virus and Virus-like Diseases of Potatoes and Production of Seed-potatoes. Kluwer Academic Publishers, Dordrecht. pp. 195-225.

Robert, Y., and Y. Maury. 1970. Capacités vectrices comparées de plusieurs souches de *Myzus persicae* Sulz., *Aulacorthum solani* Kltb. et *Macrosiphum euphorbiae* Thomas dans l'étude de la transmission de l'enroulement de la pomme de terre. Potato Res 13:199-209.

Robert, Y., and J. Rouzé-Jouan. 1971. Premières observations sur le rôle de la température au moment de la transmission de l'Enroulement par *Aulacorthum solani* Kltb., *Macrosiphum euphorbiae* Thomas et *Myzus persicae* Sulz. Potato Res 14:154-157.

Robert, Y., C.A. Dedryver, and J.S. Pierre. 1988. Sampling techniques. *In*: Minks, A.K., and P. Harrewijn (eds), Aphids: Their Biology, Natural Enemies and Control, 2B, World Crop Pests. Elsevier, Amsterdam. pp. 1-17.

Robert, Y., J.A.T. Woodford, D. Griblot Ducray-Bourdin. 2000. Some epidemiological approaches to the control of aphid-borne diseases in seed potato crops in northern Europe. Virus Res 71:33-47.

Roosen, J., R.G. Huffaker, R.J. Folwell, T.L. Marsh, and R.C. Mittelhammer. 1997. The relation of potato leaf roll virus net necrosis in potato tubers to the interval between planting and inoculation. Crop Protect 16:533-539.

Ruano-Rossil, J.M., E.B. Radcliffe, and D.W. Ragsdale. 2002. Disruption of entomopathogenic fungi of green peach aphid, *Myzus persicae* (Sulzer), by fungicides used to control potato late blight. Aphids in a New Millenium, INRA, Rennes:137 (submitted).

Rydén, K., S. Brishammar, and R. Sigvald. 1983. The infection pressure of potato virus Y^{o} and the occurrence of winged aphids in potato fields in Sweden. Potato Res 26:229-235.

Salazar, L.F. 1996. Potato Viruses and Their Control. CIP, Lima. 214 pp.

Sawicki, R.M., A.D. Rice, and R.W. Gibson. 1983. Insecticide-resistance in the peach-potato aphid *Myzus persicae* and the prevention of virus spread. Aspects Appl Biol 2:29-33.

Sawicki, R.M., A.L. Devonshire, A.D. Rice, G.D. Moores, S.M. Petzing, and A. Cameron. 1978. The detection and distribution of organophosphorous and carbamate insecticide-resistant *Myzus persicae* (Sulz.) in Britain in 1976. Pestic Sci 9:189-201.

Schoonhoven, L.M., and I. Derksen-Koppers. 1976. Effects of some allelochemics on food uptake and survival of a phytophagous aphid, *Myzus persicae*. Entomol Exp Appl 19:52-56.

Schreiber, A. 1995. The value of aldicarb (Temik) use on potatoes. Washington State Univ, Agrichem Environ News 110:12-14.

Setiawan, D.P., and D.W. Ragsdale. 1987. Use of aluminum-foil and oat-straw mulches for controlling aster leafhopper, *Macrosteles fascifrons* (Homoptera: Cicadellidae), and aster yellows in carrots. Great Lakes Entomol 20:103-109.

Shah, P.A., M. Aebi, and U. Tuor. 1999. Production factors involved in the formulation of *Erynia neoaphidis* as alginate granules. Biocontrol Sci Technol 9:19-28.

Shands, W.A. 1977. Control of aphid-borne potato virus Y in potatoes with oil emulsions. Am Potato J 54:179-187.

Shands, W.A., G.W. Simpson, and I.M. Hall. 1963. Importance of entomogenous fungi in controlling aphids on potatoes in northeastern Maine. Maine Agric Exp Stn, Tech Bull 6.

Shands, W.A., G.W. Simpson, and L.B. Reed. 1954. Subunits of sample for estimating aphid abundance on potatoes. J Econ. Entomol 47:1024-1027.

Shands, W.A., G.W. Simpson, and H.E. Wave. 1969. Canada plum, *Prunus nigra* Aiton, as a primary host of the green peach aphid, *Myzus persicae* (Sulzer), in northeastern Maine. Univ Maine, Tech Bull 39.

Shands, W.A., G.W. Simpson, I.M. Hall, and C.C. Gordon. 1972a. Further evaluation of entomogenous fungi as a biological agent of aphid control in northeastern Maine. Life Sci Agric Exp Stn, Univ Maine Tech Bull 58. 33 pp.

Shands, W.A., G.W. Simpson, C.F.W. Muesebeck, and H.E. Wave. 1965. Parasites of potato-infesting aphids in northeastern Maine. Univ Maine Agric Exp Stn and Agric Res Ser, US Dep Agric, Bull T 19, Tech Series. 77 pp.

Shands, W.A., G.W. Simpson, H.E. Wave, and C.C. Gordon. 1972b. Importance of arthropod predators in controlling aphids on potatoes in northeastern Maine. Univ Maine, Tech Bull 54. 49 pp.

Shands, W.A., G.W. Simpson, B.A. Seaman, F.S. Roberts, and C.M. Flynn. 1972a. Effects of differing abundance levels of aphids and of certain virus diseases upon yield and virus disease spread in potatoes. Life Sci Agric Exp Stn, Univ Maine, Tech Bull 56. 40 pp.

Shanks Jr., C.H., and R.K. Chapman. 1965. The effects of insecticides on the behavior of the green peach aphid and its transmission of potato virus Y. J Econ Entomol 58:79-83.

Shaposhnikov, G.C. 1987. Evolution of aphids in relation to evolution of plants. *In*: Minks, A.K., and P. Harrewijn (eds), Aphids: Their Biology, Natural Enemies and Control, 2A, World Crop Pests. Amsterdam: Elsevier. pp. 409-414.

Shields, E.J., J.R. Hygnstrom, D. Curwen, W.R. Stevenson, J.A. Wyman, and L.K. Binning. 1984. Pest management for potatoes in Wisconsin — a pilot program. Am Potato J 61:508-516.

Sigvald, R. 1984. The relative efficiency of some aphid species as vectors of potato virus Y^{o} ($\mathrm{PVY}^{\mathrm{o}}$). Potato Res 27:285-290.

Sigvald, R. 1985. Mature plant resistance of potato plants against potato virus Y^{o} ($\mathrm{PVY}^{\mathrm{o}}$). Potato Res 28:135-143.

Sigvald, R. 1986. Forecasting the incidence of potato virus Y^{o}. *In*: McLean, G.D., R.G. Garrett, and W.G. Ruesink (eds). Plant Virus Epidemics: Monitoring, Modelling and Predicting Outbreaks. Academic Press, Sydney. pp. 419-441.

Sigvald, R. 1987. Aphid migration and the importance of some aphid species as vectors of potato virus Y^{o} ($\mathrm{PVY}^{\mathrm{o}}$) in Sweden. Potato Res 30:267-283.

Sigvald, R. 1989. Relationship between aphid occurrence and spread of potato virus Y^{o} ($\mathrm{PVY}^{\mathrm{o}}$) in field experiments in southern Sweden. J Appl Entomol 108:35-43.

Sigvald, R. 1992. Progress in aphid forecasting systems. Neth J Plant Pathol 98:55-62.

Simons, J.N., and T.A. Zitter. 1980. Use of oils to control aphid-borne viruses. Plant Dis 64:542-546.

Singh, M.N., S.M.P. Khurana, B.B. Nagaich, and H.O. Agrawal. 1988. Environmental factors influencing aphid transmission of potato virus Y and potato leafroll virus. Potato Res 31:501-509.

Singh, R.P. 1987. Role of weeds in potato virus spread. *In*: Boiteau, G., R.P. Singh, and R.H. Parry (eds), Potato Pest Management in Canada. Proc Symp Improv Potato Pest Protect, Fredericton, NB. pp. 355-362.

Singh, R.P. 1999. A solvent-free, rapid and simple virus RNA-release method for potato leafroll virus detection in aphids and plants by reverse transcription polymerase chain reaction. J Virol Methods 83:27-33.

Singh, R.P., and G. Boiteau. 1986. Reevaluation of the potato aphid, *Macrosiphum euphorbiae* (Thomas), as vector of potato virus Y. Am Potato J 63:335-340.

Singh, R.P., and G. Boiteau. 1987. Control of aphid borne diseases: non-persistent viruses. *In*: Boiteau, G., R.P. Singh, and R.H. Parry (eds), Potato Pest Management in Canada. Proc Symp Improv Potato Pest Protect, Fredericton, NB. pp. 30-53.

Singh, R.P., M. Singh, and J.G. McDonald. 1998. Screening by a 3-primer PCR of North American $\mathrm{PVY}^{\mathrm{n}}$ isolates for European-type members of the tuber necrosis-inducing $\mathrm{PVY}^{\mathrm{ntn}}$ subgroup. Can J Plant Pathol 20:227-233.

Singh, R.P., J. Kurz, G. Boiteau, and G. Bernard. 1995. Detection of potato leafroll virus in single aphids by the reverse transcription polymerase chain reaction and its potential epidemiological application. J Virol Methods 55:133-143.

Singh, R.P., J. Kurz, G. Boiteau, and L.M. Moore. 1997. Potato leafroll virus detection by RT-PCR in field-collected aphids. Am Potato J 74:305-313.

Slack, S.A. 1993. Seed certification and seed improvement programs. *In*: Rowe, R.C. (ed), Potato Health Management. APS Press, St. Paul. pp. 61-65.

Soper, R.S. 1981. Role of entomophthoran fungi in aphid control for potato integrated pest management. *In*: Lashomb, J.H., and R. Casagrande (eds), Advances in Potato Pest Management. Hutchison Ross, Stroudsburg. pp. 153-177.

Soper, R.S., and D.M. MacLeod. 1981. Descriptive epizootiology of an aphid mycosis. US Dep Agric, Tech Bull 1632. 17 pp.

Souza-Dias, J.A.C., and S.A. Slack. 1987. Relation of potato leafroll virus concentration in potatoes to virus concentration in aphids. Am Potato J 64:459 (abstr).

Starý, P. 1988a. Natural enemies. Parasites. Aphidiidae. *In*: Minks, A.K., and P. Harrewijn (eds), Aphids: Their Biology, Natural Enemies and Control, 2B, World Crop Pests. Elsevier, Amsterdam. pp. 171-184.

Starý, P. 1988b. Natural enemies. Parasites. Aphelinidae. *In*: Minks, A.K., and P. Harrewijn (eds), Aphids: Their Biology, Natural Enemies and Control, 2B, World Crop Pests. Elsevier, Amsterdam. pp. 185-188.

Stegwee, G. 1960. Further investigations on the relation between *Myzus persicae* and the potato leaf-roll virus. Proc 4th Potato Viruses, Braunschweig:106-110.

Storch, R.H., and F.E. Manzer. 1985. Effect of time and date of inoculation, plant age and temperature on translocation of potato leafroll virus into potato tubers. Am Potato J 62:137-143.

Stufkens, M.A.W., D.A.J. Teulon, D. Nicol, and J.D. Fletcher. 2000. Implications of aphid flight patterns for pest management of potatoes. NZ Plant Protect 53:78-82.

Sullivan, D.J., S.J. 1988. Hyperparasitoids. *In*: Minks, A.K., and P. Harrewijn (eds), Aphids: Their Biology, Natural Enemies and Control, 2B, World Crop Pests. Elsevier, Amsterdam. pp. 189-203.

Sullivan, D.J., S.J., and R. van den Bosch. 1971. Field ecology of the primary parasites and hyperparasites of the potato aphid, *Macrosiphum euphorbiae*, in the East San Francisco Bay Area (Homoptera: Aphididae). Ann Entomol Soc Am 64:389-394.

Suranyi, R.A., C.A. Longtine, D.W. Ragsdale, and E.B. Radcliffe. 1999. Controlling leafhoppers with below-label rates. Valley Potato Grower 64(113):11-13, 16, 31.

Suranyi, R.A., I.V. MacRae, D.W. Ragsdale, and E.B. Radcliffe. 2002. Site specific management of green peach aphid, *Myzus persicae* (Homoptera: Aphididae), in seed potatoes — a case study. Am J Potato Res (submitted).

Sutherland, O.R.W., and T.E. Mittler. 1971. Influence of diet composition and crowding on wing production by the aphid *Myzus persicae*. J Insect Physiol 17:321-328.

Syller, J. 1994. The effects of temperature on the availability and acquisition of potato leafroll luteovirus by *Myzus persicae*. Ann Appl Biol 125:141-145.

Sylvester, E.S. 1958. Aphid transmission of plant viruses. Proc 10th Int Congr Entomol, 1956, Montreal, 3:195-200.

Sylvester, E.S. 1980. Circulative and propagative virus transmission by aphids. Annu Rev Entomol 25:257-286.

Tamada, T., B.D. Harrison, and I.M. Roberts. 1984. Variation among British isolates of potato leafroll virus. Ann Appl Biol 104:107-116.

Tamaki, G. 1981. Exploiting the ecological interaction of the green peach aphid on peach trees. US Dep Agric, Tech Bull 1640. 6 pp.

Tamaki, G., and J.E. Halfhill. 1968. Bands on peach trees as shelters for predators of the green peach aphid. J Econ Entomol 61:707-711.

Tamaki, G., and D. Olsen. 1979. Evaluation of orchard weed hosts of green peach aphid and the production of winged migrants. Environ Entomol 8:314-317.

Tamaki, G., and D.M. Powell. 1968. Egg distribution as a factor in suppressing the green peach aphid by pruning. J Econ Entomol 61:1437-1439.

Tamaki, G., and D.M. Powell. 1972. An insecticide and a defoliant evaluated for use in a program of integrated control designed to suppress the green peach aphid on peach trees. J Econ Entomol 65:271-275.

Tamaki, G., and R.E. Weeks. 1968. Use of chemical defoliants on peach trees in integrated program to suppress populations of green peach aphids. J Econ Entomol 61:431-435.

Tamaki, G., L. Fox, and R.L. Chauvin. 1980. Green peach aphid: orchard weeds are host to fundatrix. Environ Entomol 9:62-66.

Tamaki, G., B.J. Landis, and R.E. Weeks. 1967. Autumn populations of green peach aphid on peach trees and the role of syrphid flies in their control. J Econ Entomol 60:433-436.

Tamaki, G., J.U. McGuire, and J.A. Onsager. 1973. Spatial distribution of the green peach aphid used in estimating the populations of gynoparae. Res Pop Ecol 15:64-75.

Tanaka, S., and H. Shiota. 1970. Latent period of potato leaf roll virus in the green peach aphid (*Myzus persicae* Sulzer). Ann Phytopathol Soc Japan 36:106-111.

Taylor, C.E. 1955. Growth of the potato plant and aphid colonization. Ann Appl Biol 43:151-156.

Taylor, C.E. 1962. The population dynamics of aphids infesting the potato plant with particular reference to the susceptibility of certain varieties to infestation. Eur Potato J 5:204-219.

Taylor, L.R. 1957. Temperature relations of teneral development and behaviour in *Aphis fabae* Scop. J Exp Biol 34:189-208.

Taylor, L.R. 1961. Aggregation, variance and the mean. Nature 189:732-735.

Taylor, L.R. 1965. Flight behavior and aphid migration. Proc N Centr Branch Entomol Soc Am 20:9-19.

Taylor, L.R. 1974. Insect migration, flight periodicity and the boundary layer. J Anim Ecol 43:225-238.

Taylor, L.R., and R.A.J. Taylor. 1983. Insect migration as a paradigm for survival by movement. *In*: Swingland, I.R., and P.J. Greenwood (eds), The Ecology of Animal Movement. Clarendon Press, Oxford. pp. 181-214.

Taylor, L.R., I.P. Woiwod, and R.A.J. Taylor. 1979. The migratory ambit of the hop aphid and its significance in aphid population dynamics. J Anim Ecol 48:955-972.

Thieme, T., U. Heimbach, R. Thieme, and H.-L. Weidemann. 1998. Introduction of a method for preventing transmission of potato virus Y (PVY) in Northern Germany. Aspects Appl Biol 52:25-29.

Thomas, A.A.G., A.R. Ludlow, and J.S. Kennedy. 1977. Sinking speeds of falling and flying *Aphis fabae* Scopoli. Ecol Entomol 2:315-326.

Thomas, P.E. 1983. Sources and dissemination of potato viruses in the Columbia Basin of the Northwestern United States. Plant Dis 67:744-747.

Thomas, P.E., W.K. Kaniewski, and E.C. Lawson. 1997a. Reduced field spread of potato leafroll virus in potatoes transformed with the potato leafroll virus coat protein gene. Plant Dis 81:1447-1453.

Thomas, P.E., E.C. Lawson, J.C. Zalewski, G.L. Reed, W.K. Kaniewski. 2000. Extreme resistance to *Potato leafroll virus* in potato cv. Russet Burbank mediated by viral replicase gene. Virus Res. 71:49-62.

Thomas, P.E., K.S. Pike, and G.L. Reed. 1997b. Role of green peach aphid flights in the epidemiology of potato leaf roll disease in the Columbia Basin. Plant Dis 81:1311-1316.

Thresh, J.M. 1988. Eradication as a virus control measure. *In*: Clifford, B.C., and E. Lester (eds), Control of Plant Diseases: Costs and Benefits. Blackwell Scientific, Oxford. pp. 155-194.

Tingey, W.M. 1991. Potato glandular trichomes defensive activity against insect attack. *In*: Hedin, P.A. (ed), Naturally Occurring Pest Bioregulators. ACS Symposium Series 449. ACS, Washington. pp. 126-135.

Tingey, W.M., and J.E. Laubengayer. 1981. Defense against the green peach aphid and potato leafhopper by glandular trichomes of *Solanum berthaultii*. J Econ Entomol 74:721-725.

Tingey, W.M., R.L. Plaisted, J.E. Laubengayer, and S.A. Mehlenbacher. 1982. Green peach aphid resistance by glandular trichomes in *Solanum tuberosum* x *S. berthaultii*. Am Potato J 59:241-251.

Turchin, P. 1990. Rarity of density dependence or population regulation with lags? Nature 344:660-663.

Unruh, T., A. Knight, and M.R. Bush. 1996. Green peach aphid (Homoptera: Aphididae) resistance to endosulfan in peach and nectarine orchards in Washington State. J Econ Entomol 89:1067-1073.

Valkonen, J.P.T., G. Brigneti, L.F. Salazar, E. Pehu, and R.W. Gibson. 1992. Interactions of the *Solanum* spp. of the *Etuberosa* group and nine potato-infecting viruses and a viroid. Ann Appl Biol 120:301-313.

van den Heuvel, M. Verbeek and F. van der Wilk. 1994. Endosymbiotic bacteria associated with circulative transmission of potato leafroll virus by *Myzus persicae*. J Gen Virol 75:2559-2565.

van den Heuvel, J.F.J.M., C.M. de Blank, D. Peters, and J.W.M. van Lent. 1995. Localization of potato leafroll virus in leaves of secondarily-infected potato plants. Eur J Plant Pathol 101:567-571.

van den Heuvel, J.F.J.M., J.A.A.M. Dirven, G.J van Os, and D. Peters. 1993. Acquisition of potato leafroll virus by *Myzus persicae* from secondarily-infected potato plants of different genotypes. Potato Res 36: 89-96.

van den Heuvel, J.F.J.M., S.A. Hogenhout, M. Verbeek, and F. van der Wilk. 1998. *Azadirachta indica* metabolites interfere with the host-endosymbiont relationship and inhibit the transmission of potato leafroll virus by *Myzus persicae*. Entomol Exp Appl 86:253-260.

van den Heuvel, J.F.J.M., A. Bruyère, S.A. Hogenhout, V. Ziegler-Graff, V. Brault, M. Verbeek, F. van der Wilk, and K. Richards. 1997. The N-terminal region of the Luteovirus readthrough domain determines virus binding to *Buchnera* GroEL and is essential for virus persistence in the aphid. J VirologyJ Virol 71:7258-7265.

van der Zaag, D.E. 1987. Yield reduction in relation to virus infection. *In*: de Bokx, J.A. (ed), Viruses of Potatoes and Seed-potato Production. Pudoc, Wageningen. pp. 146-150.

van Emden, H.F. 1972. Aphids as phytochemists. *In*: Harbourne, J.B. (ed), Phytochemical Ecology. Academic Press, London. pp. 25-43.

van Emden, H.F., and M.A. Bashford. 1969. A comparison of the reproduction of *Brevicoryne brassicae* and *Myzus persicae* in relation to soluble nitrogen concentration and leaf age (leaf position) in the Brussels sprout plant. Entomol Exp Appl 12:351-364.

van Emden, H.F., and M.A. Bashford. 1971. The performance of *Brevicoryne brassicae* and *Myzus persicae* in relation to plant age and leaf amino acids. Entomol Exp Appl 14:349-360.

van Emden, H.F., V.F. Eastop, R.D. Hughes, and M.J. Way. 1969. The ecology of *Myzus persicae*. Annu Rev Entomol 14:197-270.

van Harten, A. 1983. The relation between aphid flights and the spread of potato virus Y^N (PVY^N) in the Netherlands. Potato Res 26:1-15.

van Hoof, H.A. 1980. Aphid vectors of potato virus Y^N. Neth J Plant Pathol 86:159-162.

van Hoof, H.A. 1977. Determination of the infection pressure of potato virus Y^N. Neth J Plant Pathol 83:123-127.

van Regenmortal, M.H.V., C.M. Fauquet, D.H.L. Bishop (eds). 2000. Virus Taxonomy: The Classification and Nomenclature of Viruses. The Seventh Report of the International Committee on Taxonomy of Viruses. Academic Press, San Diego. 1167 pp.

Vancanneyt, G., C. Sanz, T. Farmaki, M. Paneque, F. Ortego, P. Castañera, and J.J. Sánchez-Serrano. 2001. Hydroperoxide lyase depletion in transgenic potato plants leads to an increase in aphid performance. PNAS 98:8139-8144.

Villacarlos, L.T. 1987. Effect of systemic insecticides on the feeding behavior and mortality of green peach aphid and its transmission of potato leaf roll virus. Philipp Entomol 7:121-128.

Wallis, R.L., and J.E. Turner. 1969. Burning weeds in drainage ditches to suppress populations of green peach aphids and the incidence of beet western yellows disease in sugarbeets. J Econ Entomol 62:307-309.

Ward, S.A. 1987a. Cyclical parthenogenesis and the evolution of host range in aphids. *In*: Holman, J., J. Pelikan, A.F.G. Dixon, and L. Weismann (eds), Population Structure, Genetics and Taxonomy of Aphids and Thysanoptera. SPB Academic Publishing, The Hague. pp. 39-44.

Ward, S.A. 1987b. Optimal habitat selection in time-limited dispersers. Am Nat 129:568-579.

Ward, S.A. 1991. Reproduction and host selection by aphids: the importance of 'rendezvous' hosts. *In*: Bailey, W.J., and J. Ridsdill-Smith (eds), Reproductive Behaviour in Insects. Chapman & Hall, London. pp. 202-226.

Ward, S.A. 1992a. Assessing functional explanations of host-specificity. Am Nat 139:883-891.

Ward, S.A. 1992b. Environmental uncertainty and polyphagy in herbivorous insects. Oikos 63:506-512.

Ward, S.A., S.R. Leather, J. Pickup, and R. Harrington. 1998. Mortality during dispersal and the cost of host-specificity in parasites: how many aphids find hosts? J Anim Ecol 67:763-773.

Watson, M.A. 1966. The relation of annual incidence of beet yellowing viruses in sugar beet to variations in weather. Plant Pathol 15:145-149.

Watson, M.A., and G.D. Heathcote. 1966. The use of sticky traps and the relation of their catches of aphids to the spread of viruses in crops. Rpt, Rothamsted Exp Stn, 1965. pp. 292-300.

Watson, M.A., G.D. Heathcote, F.B. Lauckner, and P.A. Sowray. 1975. The use of weather data and counts of aphids in the field to predict the incidence of yellowing viruses of sugar-beet crops in England in relation to the use of insecticides. Ann Appl Biol 81:181-198.

Watt, A. D., and A.F.G. Dixon. 1981. The role of cereal growth stages and crowding in the induction of alatae in *Sitobion avenae* and its consequences for population growth. Ecol Entomol 6:441-447.

Weidemann, H.-L. 1988. Importance and control of potato virus Y^N (PVY^N) in seed potato production. Potato Res 31:85-94.

Weisz, R., S. Fleischer, and Z. Smilowitz. 1995. Map generation in high-value horticultural integrated pest management: appropriate interpolation methods for site-specific pest management of Colorado potato beetle (Coleoptera: Chrysomelidae). J Econ Entomol 88:1650-1657.

Weisz, R., S. Fleischer, and Z. Smilowitz. 1996. Site-specific integrated pest management for high-value crops: impact on potato pest management. J Econ Entomol 89:501-509.

Werker, A.R., A.M. Dewar, and R. Harrington. 1998. Modelling the incidence of virus yellows in sugar beet in the UK in relation to numbers of migrating *Myzus persicae*. J Appl Ecol 35:811-818.

Whalon, M.E., and Z. Smilowitz. 1979a. Temperature-dependent model for predicting field populations of green peach aphid, *Myzus persicae* (Homoptera: Aphididae). Can Entomol 111:1025-1032.

Whalon, M.E., and Z. Smilowitz. 1979b. GPA-CAST, a computer forecasting system for predicting populations and implementing control of the green peach aphid on potatoes. Environ Entomol 8:908-913.

Whitworth, J.L., A.R. Mosley, and G.L. Reed. 2000. Monitoring current season potato leafroll virus movement with an immunosorbent direct tissue blotting assay. Am J Potato Res 77:1-9.

Wilson, C.R., and R.A.C. Jones. 1993. Resistance to potato leafroll virus infection and accumulation in potato cultivars, and the effects of previous infection with other viruses on expression of resistance. Aust J Agric Res 44:1891-1904.

Woiwod, I.P., and I. Hanski. 1992. Patterns of density dependence in moths and aphids. J Anim Ecol 61:619-629.

Woiwod, I.P., G.M. Tatchell, and A.M. Barrett. 1984. A system for the rapid collection, analysis and dissemination of aphid-monitoring data from suction traps. Crop Protect 3:273-288.

Woodford, J.A.T. 1968. Difference in flight capacity between naturally occurring spring and summer forms of *Myzus persicae* (Sulz.) (Hemiptera: Aphididae). Nature 217:583-584.

Woodford, J.A.T. 1969. Behavioural and developmental components of the teneral stage in *Myzus persicae*. Entomol Exp Appl 12:337-350.

Woodford, J.A.T. 1988. The impact of cropping policy on methods to control potato leafroll virus. Aspects Appl Biol 17:163-171.

Woodford, J.A.T. 1992. Effects of systemic applications of imidacloprid on the feeding behaviour and survival of *Myzus persicae* on potatoes and on transmission of potato leafroll virus. Pflanzenschutz-Nachr Bayer 45:527-546.

Woodford, J.A.T., and H. Barker. 1986. Problems of detecting potato leafroll virus following late infection. Aspects Appl Biol 13:325-331.

Woodford, J.A.T., and S.C. Gordon. 1990. New approaches for restricting spread of potato leafroll virus by different methods of eradicating infected plants from potato crops. Ann Appl Biol 116:477-487.

Woodford, J.A.T., S.C. Gordon, and G.N. Foster. 1988. Side-band application of systemic granular pesticides for the control of aphids and potato leafroll virus. Crop Protect 7:96-105.

Woodford, J.A.T., C.A. Jolly, and C.S. Aveyard. 1995. Biological factors influencing the transmission of potato leafroll virus by different aphid species. Potato Res 38:133-141.

Woodford, J.A.T., B.D. Harrison, C.S. Aveyard, and S.C. Gordon. 1983. Insecticidal control of aphids and the spread of potato leafroll virus in potato crops in eastern Scotland. Ann Appl Biol 103:117-130.

Woodford, J.A.T., M.W. Shaw, R.G. McKinlay, and G.N. Foster. 1977. The potato aphid spray warning scheme in Scotland, 1975-1977. Proc 1977 British Crop Protect Conf — Pests Dis. pp. 247-254.

Wurr, D.C.E. 1978. 'Seed' tuber production and management. *In*: Harris, P.M. (ed), The Potato Crop, The Scientific Basis for Improvement. Chapman & Hall, London. pp. 327-354.

Wyman, J.A., N.C. Toscano, K. Kido, H. Johnson, and K.S. Mayberry. 1979. Effects of mulching on the spread of aphid-transmitted watermelon mosaic virus to summer squash. J Econ Entomol 72:139-143.

Yeo, H., J.K. Pell, B.J. Pye, and P.G. Alderson. 1998. A biorational approach to selecting mycoinsecticides for aphid management. Proc Brighton Crop Protect Conf — Pests Dis 307-308.

Zimmerman-Gries, S. 1979. Reducing the spread of potato leaf roll virus in seed potatoes by sticky yellow polyethylene sheets. Phytoparasitica 7:41.