

Review

Protecting crops from non-persistently aphid-transmitted viruses: A review on the use of barrier plants as a management tool

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Abstract

Barrier plants are a management tool based on secondary plants used within or bordering a primary crop for the purpose of disease control. Aphid-transmitted viruses account for approximately 50% of the 600 known viruses with an invertebrate vector. Barrier plants may act as real natural sinks for non-persistent aphid-transmitted viruses and have proved in the past to be an effective crop management strategy to protect against virus infection. Increasing the knowledge on aphid host seeking and flying behaviour, and on how barrier plants may affect the behaviour of aphids and their natural enemies will allow further development of this environmentally-friendly habitat manipulation strategy. An ideal plant barrier should be a non-host for the virus and the vector, but appealing to aphid landing and attractive to their natural enemies and should allow sufficient residence time to allow aphid probing before taking-off occurs. In this review, we have addressed why aphids are manageable by barrier cropping, the mechanisms by which barrier plants affect the occurrence of non-persistently aphid-transmitted viruses and the limitations of using barrier plants as a virus control strategy. Finally, we have pointed out future directions of research that should be conducted to integrate barrier cropping with other disease management strategies, and optimise and extend the use of barrier plants as a strategy for managing aphid-transmitted virus diseases.

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1. Introduction

Aphids are among the most serious agricultural insect pests. They cause major economic losses in several crops worldwide, directly because of their feeding and indirectly by inflicting plant impairments (e.g., viruses, phytoalexins). However, their population threshold level as virus vectors is much lower than it is for them as direct pests (Satapathy, 1998). Aphids are the most common vectors of plant viruses, and aphid-borne non-persistently transmitted viral diseases (ABNPV) are of greatest economic importance in several annual cropping systems (Tomlinson, 1987). About 50% of the approximately 600 viruses with invertebrate vectors are transmitted by aphids and most of the roughly 290 known aphid borne viruses are non-persistent (NPV) (Hull, 2002). Non-persistent viruses are transmitted non-specifically by a large number of aphid species after very brief probes (1–2 min), are lost readily after probing on a healthy plant and have a short retention time in the vector (few hours). Conversely, persistent viruses are transmitted specifically by few aphid species that feed and colonise the crop, are retained in the vector for many days and transmitted after long inoculation access periods (optimum 24–48 h). Semipersistent transmission shares some of the properties of non-persistent and persistently transmitted viruses (for more information see reviews by Plumb and Callow, 2002; Ng and Perry, 2004).

Current control strategies for aphids regularly rely upon pesticide applications. However, many aphid species have and continue to become resistant to various classes of chemical compounds (Furk and Hines, 1993; Perring et al., 1999; Nebeshima et al., 2003; Li and Han, 2004). Additionally, insecticides are largely ineffective in managing ABNPVs (Raccach, 1986; Howell, 1993; Perring et al., 1999). Furthermore, insecticides may contribute to the spread of virus transmission by inducing greater vector activity (Budnik et al., 1996). Therefore, the development of non-chemical management strategies for controlling aphid vectors of NPVs is warranted.

It is well known that flora diversification can result in reduced pest population (references in reviews by Andow, 1991; Hooks and Johnson, 2003). It has also been established that the number of alatae and apterae aphids found on primary crops are consistently less in vegetationally diverse than monoculture habitats (Smith, 1969, 1976; Horn, 1981; Costello and Altieri, 1995; Hooks et al., 1998; Showler and Greenberg, 2003). Thus, it is equitable to suppose that if an aphid population is recurrently found at lower numbers on host plants in vegetationally diverse habitats, this will provisionally result in decrease incidences of ABNPV. Still, there are few published studies where secondary crops or plants have been specifically used to reduce the occurrence of ABNPV. Secondary plants used within or bordering a primary crop for the purpose of disease suppression

are often referred to as barrier crops (Deol and Rataul, 1978). This approach belongs to the wide array of habitat manipulation strategies that aims at making crops less favourable for pests and more attractive to beneficial insects. Barrier cropping is a cultural technique that perfectly fits under the philosophy of “Ecological Engineering for Pest Management” recently reviewed by Gurr et al., 2004. Among those studies in which barrier plants were investigated, many showed that barrier cropping lessens the incidence and/or hinders the spread of aphid-borne non-persistent viruses (Fereres, 2000, several references therein). Despite the potential success of using barrier plants for vector management, this tactic has received limited research attention compared with other management strategies. For example, the use of inert material such as reflective mulches and row covers (Perring et al., 1989; Webb and Linda, 1992; Brown et al., 1993; Stapleton and Summers, 2002) and mineral oils (Vanderveken and Semal, 1966; Webb and Linda, 1993; Wang and Pirone, 1996; Asjes, 2000) have been extensively investigated and many growers are familiar with these traditional management practices. Barrier cropping can also become a recognized component of integrated disease management (IDM). Presently, greater dissemination of information on this tactic for viral disease management is needed so that the agricultural community becomes better acquainted with this cultural management tool.

It is not our goal to conduct a thorough review of barrier cropping. We aim by reviewing the literature to: (1) alert readers that plant diversification in the form of barrier plants should receive greater recognition as a tenable management tactic for reducing the occurrence and spread of ABNPV, (2) give a holistic account of the mechanisms most responsible for the rate of spread of NPVs in florally diverse habitats and (3) suggest future direction of barrier cropping research. For the sake of simplicity, any form of plant diversification (e.g., mixed cropping, cover crops, border plants, intercrops, trap crops, flower strips, organic mulch, etc.) used to protect a primary crop from insect transmitted viral diseases will be referred to as barrier cropping regardless of its layout, composition or how it impacts vector behaviour.

2. Limitations of current control strategies

Insecticidal control of aphids that transmit plant viruses in a non-persistent manner may not reliably prevent the spread of disease within the field (Thackray et al., 2000). This is presumably due to the very short acquisition and inoculation times involved (Perring et al., 1999). Aphids are capable of transmitting NPVs prior to obtaining a lethal insecticide dose (Gibson and Rice, 1989). In some instances, insecticides may increase, rather than suppress the spread of virus transmission by destruc-

tion of predators and parasitoids or by causing increased vector activity (Gibson and Rice, 1989; Budnik et al., 1996) due at least in part, to the secretion of aphid alarm pheromones which causes greater vector migration within the field (Rice et al., 1983). Only insecticides that result in reduced vector probing activity, can contribute to management of NPVs (Irwin, 1999). However, continuous invasion of the crop by transient winged forms also means that insecticides need to be persistent or regularly applied, which could lead to the development of insecticide resistance among aphids and other herbivore populations. Additionally, high-priced chemicals may be too expensive for use by resource-poor farmers. Resource challenged farmers require safe, effective, and inexpensive methods for managing aphid borne viruses.

Because of their low toxicity, oil sprays have a general appeal for use against vector transmission of NPVs. Mineral oils have been shown to interfere effectively with NPVs (Kerlan et al., 1987; Webb and Linda, 1993; Powell et al., 1998). These oils are believed to alter the surface structure of aphid stylets and thus interfere with their ability to retain virus particles and hence reduce transmission efficiency (Wang and Pirone, 1996). However, weather related parameters may affect the efficiency and persistency of mineral oil sprays. For instance, ultra violet light causes oil cover on leaves to photodegrade (Hodgkinson et al., 1999). Other limitations involve removal of oil cover by rain or irrigation water. Young plant tissues growing after oil sprays are unprotected to viruses transmitted from landing aphids. Furthermore, mineral oils may reduce crop quality and yield (Webb and Linda, 1993). These and other limitations prevent the widespread commercial use of oil sprays.

The procedure of infecting a plant with a mild strain of a virus to protect it from infection with severe strains is known as cross protection. The protecting virus must be mild in order to minimize losses due to its infection. This technique has been used to protect plants against non-persistent viruses. However, the highly variable nature of plant virus strains (Lisa and Lecoq, 1984) and the fact that aphids can injure plants in several ways (Jackson et al., 2000) may reduce the success of using cross-protection with mild strains. Cross-protection shows at least two other disadvantages: (1) plants must be infected prior to exposure and (2) biological properties of the protective strain must be regularly checked for adverse effects (Gallitelli, 2000). Additionally, several viruses may plague a crop within the same planting period (Purcifull et al., 1988) and infection by one virus may permit the transmission of other viruses (Lecoq et al., 1991). Additionally, some crops are susceptible to several types of NPVs; cross protecting or developing a variety that resists all such viruses could prove unattainable. Further, some crop cultivars that were developed to be physically resistant to hemipteran pests by entrapping them in sticky secretions released on the leaf surface may also have detrimental impact on their associated natural enemies by disrupting their searching behaviour or entrapping them (Gruenhagen and Perring, 1999). The fact that new isolates of existing viruses may emerge also reduces the livelihood of resistant crop varieties. In spite of their difficulties, cross protection and resistant varieties have been successfully employed in several cropping systems.

Biological control of the vector has not been considered as an effective strategy to reduce the spread of non-persistently transmitted plant viruses because only few colonising vector species are involved in the spread of the disease. Although natural enemies are capable of significantly reducing aphid densities, they are believed to be incapable of controlling aphid vectors of NPVs when vectors are within the bounds of the susceptible crop (Irwin, 1999). Because of the brief inoculation period required for disease transmission, they are very unlikely to kill alighting aphids before they infect a healthy plant. Additionally, aphids may emit an alarm pheromone when attacked (Nault, 1973). This pheromone may fail to attract additional predators to the aphid location (Mondor and Roitberg, 2000) but cause nearby aphids to stop feeding, walk, or drop from the plant to avoid predation (Nault and Phelan, 1984). If “escapees” are viruliferous this movement may accelerate virus spread within the field. This is most likely to occur if several aphid vectors are within a crop field. For these reasons, biological control has not been endorsed as a strategy to suppress vectors of NPVs.

Control limitations mentioned above establish the continued need for research directed towards managing ABNPVs. The evaluation of barrier crops as compared with other strategies (i.e., plant resistant, row covers, etc.) has received limited interest. However, there are several aspects of aphid ecology that make them more adequate to the barrier cropping strategy than other management tactics.

3. Why are aphid vectors manageable by barrier cropping?

3.1. Aphid behaviour

There are several aspects of aphid behaviour that conjecturally makes them manageable by barrier cropping; much of which centres around their visual host finding activities while in flight. For example, during flight, aphids respond strongly to visual stimuli (Kring, 1972) and locate host plants by contrasting the soil background with the green colour of plant foliage (Kennedy et al., 1959, 1961). Therefore, the greater the percentage of vegetative cover in a crop field, the lower the probability an aphid will alight in that area (A'Brook, 1968; Halbert and Irwin, 1981). Smith (1976) found that aphid colonization of Brussel sprouts was less when green burlap was placed between host plants than when brown burlap was used. The green burlap was believed to have reduced the contrast between green plants and brown soil making the target crop less recognizable to colonizing aphids. Thus, if the number of vectors entering a field is reduced, the incidence and spread of plant viruses will presumably be abated. Furthermore, the spread of NPV usually start first at the crop edges because viruliferous aphids entering a field tend to land on the margins due to the contrasting colours between the soil background and the plant canopy (Irwin et al., 2000).

Once an aphid lands on a plant, there are additional behaviours that make them tentatively manageable by barrier plants. Aphids cannot distinguish hosts from non-hosts until after alighting on a leaf surface and conducting exploratory tests

Table 1
Effects of barrier plants on aphid transmitted non-persistent plant viruses and crop yield

Crop protected	Virus targeted	Barrier plant	Response	Factors involved	Country	Reference
Family Cucurbitaceae						
Muskmelons	WMV-1, WMV-2	Wheat, swiss chard	Radish and Swiss chard were too competitive. Cantaloupe in wheat protected plots had equal or better quality than check	Delay frequency and reduced virus severity	USA	Toba et al. (1977)
Zucchini	PRSV-W	Buckwheat, weeds, yellow mustard	Increased marketable yields during 1 of 2 years	Delay virus onset no. of alatae reduced	USA, Hawaii	Hooks et al. (1998)
Family Solanaceae						
Chilli	CMV	Sunflower, sorghum sesame, pearl-millet	All barrier crops reduced the disease incidence and increased yield. Fields with pearl-millet gave the highest yields during the spring season	No explanation suggested	India	Deol and Rataul (1978)
Chilli	CVMV	Maize, brinjal	Yields were higher when interplanted with maize or brinjal but maize a better protector	More alatae vectors, disease higher and spread faster in monocrop	Malaysia	Hussein and Samad (1993)
Chilli	CMV	Maize, sorghum, sunflower	All barrier crops reduced disease incidence and increased yield compared to the control. Maize was the most effective barrier plant. Insecticidal sprays applied to the barrier plants further suppressed disease spread	Barrier crops acted as “spread breakers” by preventing direct aphid colonization on the chilli plants	India	Anandam and Doraiswamy (2002)
Pepper	CMV, PVY	Sorghum	A sorghum barrier contributed to a significant reduction of CMV spread and delayed PVY spread	Sorghum plants acted as a sink for both viruses	Spain	Avilla et al. (1996)
Pepper	CMV, PVY	Maize, vetch, sorghum	Reduction in virus spread and yield increase in 2 of the 4 years	Barriers acted as a virus sink, but did not reduce aphid landing in crop	Spain	Fereres (2000)
Pepper	PVY	Sunflowers	Reduced virus spread	Blocked alatae aphid landing rates	USA	Simons (1957)
Potato	PLRV	Wheat, mustard	Potato yield greater in barrier plots, highest yields in wheat	Protector plants acted as a mechanical aphid barrier. Wheat believed to attract less aphids than mustard	Bangladesh	Mannan (2003)
Potato	PVY	Sorghum, potato, soybean, wheat	Aphid landing rates similar in all plots, virus incidence was reduced along the field edge of protected potato	Barriers acted as a sink (e.g., aphid vectors lost virulence prior to landing on seed potato)	USA	Difonzo et al. (1996)
Potato	PVY	Wheat straw mulch	Straw mulch reduced PVY incidence but had no significant impact on yield	Reduced optical contrast between plant and soil	Germany	Saucke and Döring (2004)
Family Fabaceae						
Cowpea	CpMV	Pearl millet	Number of infected plants were significantly reduced in plots screened by pearl millet. Yields were further increased by using a systemic insecticide on the millet	Vector population was greater near the barrier and the insecticide help eliminate the vectors at the barrier	USA	Gay et al. (1973)
Cowpea	CpBMV	Pearl millet, maize	Barriers provide protection to cowpea from virus infection, reduced infection in mixed crop	Infected aphids landed on barrier crop which served as a virus sink and physical barrier limiting movement	India	Sharma and Varma (1984)
French beans	BCMV	Sorghum, maize, okra, sunflower, amaranthus	Maize most effective barrier crop reducing disease incidence and increasing yield followed by sorghum	The taller barrier crops broke aphid flight by intercepting them and then served as a sink	India	Dhanju et al. (1995)
Lupins	BYMV	Oats	13% of plants in protected plots were infected compared with greater than 97% in check	Viruliferous alates probed the oats before reaching lupins	USA	Corbett and Edwardson (1957)

Table 1 (Continued)

Crop protected	Virus targeted	Barrier plant	Response	Factors involved	Country	Reference
Lupins	BYMV	Oats, wheat	Rate and extent of BYMV spread was decreased by 43–65% in the crop edges adjacent to the cereal plots	Greater overall plant density in mixture and borders or admixture with cereals, presence of nonhost plants contributed to virus decrease	Australia	Jones (1993)
Lupins	BYMV	Straw mulch	Straw greatly reduced the rate and amount of virus spread and reduced the number of plants killed by virus	Decrease landing rate of incoming vector alatae	Australia	Jones (1994)
Lupins	BYMV-N	Oats	Decreased incidence of symptomatic plants at crop margin (i.e., slow gradual decline in incidence of symptomatic plants inwards from external virus source)	Incoming migrant aphids cleansed the virus from their mouthparts while probing the oats barrier	Australia	Jones (2005)
Fava bean	BYMV, SCRLV	Barley	Provided short range control of BYMV, minor effect on the spread of SCRLV	Retardation of crawling of infective apterae and interruption of infective alatae movement	Australia	Jayasena and Randles (1985)
Soybean	SMV	Sorghum (dwarf and tall isolines)	Both isolines significantly reduced the % of SMV- induced seed mottling equally	Lower aphid landing rates and/or aphids lost infectivity after landing and probing on sorghum	USA	Bottenberg and Irwin (1992)
Family Poaceae Gamagrass	SCMV- MDMV -B, MDMV	Wildrye, Illinois bunfleflower	Disease less frequent in biculture with bunfleflower and polyculture of wildrye and bunfleflower than in monoculture or biculture with wildrye, highest disease intensity and yields in wildrye	Bunfleflower provided a physical barrier to vector movement	USA	Piper et al. (1996)

(Nault and Styer, 1972). Their initial reaction is to walk over the surface testing it with their antennae and probing epidermal cells with their mouth-parts. During the test phase aphids make brief, shallow exploratory probes with their stylets. While testing the plant for suitability, aphids may initially ingest sap from epidermal cells before withdrawing their stylets (Powell et al., 1995). This behaviour whereby aphids probe and/or feed on non-host plants has important implications in designing disease management strategies. This implies that during host-seeking, aphids may spend a significant amount of time and energy assessing unacceptable host plants in habitats of plant mixtures and would therefore allocate less energy into colonizing and feeding on the host crop. It has also been shown that aphids are attracted to odours emanating from host plants (reviewed by Pickett et al., 1992) and that certain odours from non-host plants disrupt the attraction of aphids to their host plants (Nottingham et al., 1991). However, there is no persuasive ecological evidence that aphids use long-range volatile chemical cues to locate plants from a distance using odour. Still several behavioural aspects of aphids suggest they may be manipulated by using barrier plants.

3.2. Mechanisms whereby barrier plants may affect aphid vectors

In several studies listed in Table 1 the exact mechanisms responsible for lower incidences of virulent plants in diversified plant habitats were not scrupulously examined but in most instances the authors presented some evidence for the involve-

ment of proximate factors in host selection (e.g., host location, host recognition). Finch and Kienneger (1997) suggested that an integral mechanism that determines why fewer herbivores are found on host plants in the company of nonhost plants is ‘appropriate/inappropriate landings’ which suggests that insects flying over plant mixtures will have several inappropriate landings on nonhost plants. The tendency is then to leave the general area completely. Likewise it has been reported that during their host recognition phase, if aphids determine they have alighted on an unsuitable host, their settling response is quickly inhibited and they immediately resume flight (Kloft, 1977). This flight may take an aphid out of the vicinity of a crop field. However, polyphagous aphids may less likely leave a diverse habitat because they may habitually probe many moderate and ‘borderline’ hosts (Kennedy et al., 1961). Further, because their ability to transmit NPVs is lost soon after acquisition, aphids may lose their virulence while seeking suitable host plants.

The virus-sink hypothesis proposes that secondary plants may act as a sink for non-persistent viruses (Fig. 1). With most non-persistent viruses, aphids begin to lose their ability to infect immediately after acquisition and will become non-infective within minutes while feeding (Nault, 1997). Furthermore, when aphids search for a host plant they commonly lose their virus “charge” after making a few brief probes on a healthy or non-susceptible plant (Sylvester, 1954; Bradley, 1959). If aphids then alight and feed on a susceptible host plant there will be no opportunity for virus transmission because they already lost the virus on the barrier plant. The virus sink hypothesis is in agreement with Toba et al. (1977) who suggested that virulifer-

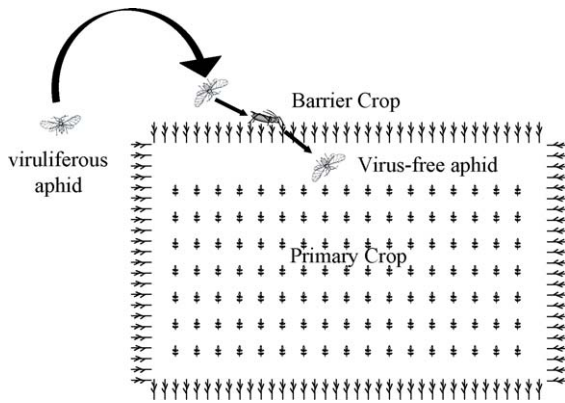


Fig. 1. Demonstration of the virus-sink hypothesis. Viruliferous winged aphid searching for a host plant alights in the barrier crop. After probing a barrier plant, the aphid loses its infectivity. The virus-free aphid now enters the area of the susceptible primary crop where it is no longer capable of transmitting a viral disease.

ous aphids that land on “protector” plants lose their virulence during exploratory probing.

Others contend that barrier plants act as physical impediment and reduce the total number of aphids alighting on the crop (Simons, 1957). In this situation it is suggested that barrier plants reduce the number of potential vectors migrating onto the crop, rather than reducing the number of infective aphids. This suggests that if the barrier strategy is to be effective in reducing aphid colonization, a tall growing barrier plant such as sorghum or a species that is tall relative to the primary crop should be considered. The ability of barrier plants to effectively impede or delay aphid movement into a crop, will among other factors, depend on the kind of virus spread pattern (monocyclic or polycyclic) and the height of the barrier plant at the time of strong virus pressure (Fereres, 2000). In some instances height may be less important than the horizontal profile of the barrier plant in lessening the number of aphid vectors alighting on their host crops. Halbert and Irwin (1981) suggested that the number of aphids entering in a field should be lowest in fields consisting of high vegetative cover. The barrier plants may also protect primary crops from NPVs by camouflaging them from aphid vectors instead of providing a physical barrier.

The concept of trap cropping has not been specifically acknowledged as a potential mechanism by which barrier planting reduces the incidences of non-persistent viruses. Trap crops are plants that are grown to protect primary crops by attracting pest organisms that would normally colonize the primary crop. The principle of trap cropping is based on the fact that all pest organisms show a distinct preference for certain plant species, stage, or cultivar (Hokkanen, 1991). It has been suggested that flying aphids use colour vision primarily to distinguish plants on the soil surface (Moericke, 1955). Kennedy et al. (1961) furthered this notion by showing that alightments by *Myzus persicae* and *B. brassicae* in the field occurred preferentially on leaves reflecting a greater proportion of long-wave energy, independently of host plant status. This was demonstrated in an experiment conducted with alatae *Brevicoryne brassicae* L. (Kennedy et al., 1959). Although cabbage (*Brassica oleracea*)

is a preferred host of *B. brassicae* and sugar beet (*Beta vulgaris*) is not one of its hosts, direct observation of their flights suggested they alighted more often on beets than on cabbage. It is feasible that in florally diverse habitats, aphids landing on a non-host plant is not fortuitous but occurs because aphids are more attracted to the barrier plant. Therefore, barrier plants may also behave as a “decoy” by directing aphids away from the primary crop. Hence, selecting a barrier plant species that is more attractive to aphid landing than the primary crop may result in further protection from the spread of NPV.

Root (1973) proposed that predators and parasitoids are more effective in controlling herbivore populations in vegetationally diverse habitats because the greater assortment of foods (e.g., prey, pollen, nectar) and different microclimates found in these habitats makes them more inhabitable for natural enemies who then exert greater mortality on herbivorous prey (resource concentration hypothesis). Additionally, vegetation within cropping systems may also create environments favorable for epizootics of entomopathogens (Kemp and Barrett, 1989). Although, the activity and density of biological control agents may be greater in mixed plantings, we surmised that natural enemies may have limited impact on the spread of NPVs in crop fields. However, reducing the numbers of colonising aphids in the crop by the action of natural enemies may limit the risk of secondary spread of NPV, especially in cases where the colonising species is an efficient vector of the virus (e.g., *Aphis gossypii* transmitting *Cucumber mosaic virus* (CMV) in melons, Garzo et al., 2004). Therefore, selecting a barrier plant species that is attractive to natural enemies of aphids may give an additional advantage against the spread of NPV diseases.

The following five hypotheses can be proposed to explain how barrier crops can affect aphid vectors and subsequent NPV transmission: (i) appropriate/inappropriate landing, (ii) virus sink, (iii) physical barrier, (iv) trap crop, and (v) biological control. How barrier plants act to protect crops from NPVs are likely not mutually exclusive and all or a mixture of them may operate in tandem. However, it can be acknowledged with certainty that diversification within a crop field interferes with the normal host plant finding capabilities of herbivores (Root, 1973). In the case of aphid vectors, this disruption in searching behaviour and responses to barrier plants should help protect crops from ABNPVs.

4. Mechanisms by which barrier plants affect the occurrence of non-persistently aphid-transmitted viruses

4.1. Virus-sink hypothesis

In several studies investigating the use of barrier plants to manage non-persistently transmitted viruses no attempts were made to determine the underlying causes of experimental findings. An exception involved studies conducted in Spain by Fereres (2000). Fereres used a combination of laboratory and field experiments to test the potential use of sorghum (*Sorghum vulgare*) and maize (*Zea mays*) as barriers to protect pepper (*Capsicum annuum*) plants against *Potato virus Y* (PVY) and

CMV. He concluded that these tall barrier plants did not reduce the number of vectors entering pepper habitats but protected pepper plants by acting as a natural sink for non-persistent viruses. Laboratory tests showed that viruliferous aphids lost their ability to transmit virus to pepper plants after probing maize or sorghum and thus, supported the virus-sink hypothesis. Simons (1957) reported similar results on PVY in peppers but hypothesized sunflower (*Helianthus candatus*) borders lowered aphid landing rates.

Potato (*Solanum tuberosum*) is an important vegetable crop worldwide and because of this much research emphasis has been placed on protecting it from viral infections. *Potato virus Y* is a major disease of potato crops worldwide. Difonzo et al. (1996) investigated the use of soybean (*Glycine max*), wheat (*Triticum aestivum*) and sorghum as crop borders to reduce PVY incidence in seed potato. They found that the number of aphids landing along the border of fallow and barrier treatment plots were equivalent. They also concluded that the crop borders did not block alatae aphid landing. However, PVY incidence was significantly higher in the outer rows of plots with fallow borders. Difonzo et al. (1996) suggested that the border plants were behaving as a virus sink and after probing one or two non-host plants, aphids lost their virus charge and could not transmit PVY again unless feeding on an infected source plant. They further hypothesized that any plant species could be used to reduce potyvirus spread.

Jones (2005) investigated the patterns of spread of *Bean yellow mosaic virus* (necrotic type, BYMV-N) in stands of narrow-leaved lupins (*Lupinus angustifolius*) planted next to an external primary virus source. He found that a 20 or just a 0.25 m-wide perimeter oat barrier decreased the incidence of symptomatic plants along the crop margin. Instead of a sharp gradient in incidence in symptomatic plants inwards from the margin, there was a gradual decline with increasing distance into the planting. Jones (2005) proposed that the oat barrier was not just a physical barrier that separated the virus source from the susceptible narrow-leaved lupins crop but also a 'virus cleansing barrier' that cleanse the virus from the mouthparts of migrant aphids landing on the oat plants.

4.2. Physical barrier

The formation of a physical barrier between the vector and its host plant may be the first line of defense against NPV carriers. Simons (1957) studied the impact of sunflowers as barrier plants on PVY spread in peppers. During his investigation, it was suggested that sunflower decreased virus spread by blocking alatae aphids, which prevented them from landing on neighboring pepper plants. Fostering this assumption was the fact that considerably fewer diseased plants were found in the outer rows than in the central rows. Simons (1957) suggested that this occurred because aphids had difficulties flying through the barrier and thus flew over it. Typically, the barriers are meant to target alatae aphids because they are considered the primary source of NPV spread. However, Jayasena and Randles (1985) concluded that the spread of *Subterranean clover red leaf virus* (SCRLV) was mainly caused by apterae aphids crawling from source plants. Because SCRLV is a luteovirus, colonizing

apterae may be important for plant to plant spread. Secondary spread of BYMV was also believed to be caused by apterae aphid species. Aphid populations in the barley (*Hordeum vulgare*) barrier crop were similar relative to the control. This caused Jayasena and Randles (1985) to believe the barley acted as a physical barrier that retarded infective aphids crawling and interrupted their movement to adjacent rows for a time exceeding the persistence of BYMV.

To this respect, it is important to consider here the composition of aphid species that transit over or colonise the crop. When an efficient vector species is able to colonise the crop, both apterae and alatae may be involved in secondary spread of the virus. However, when the major vector species are unable to reproduce and form colonies on the crop, the virus may only be spread by transient alatae aphids that make brief probes when moving from plant to plant before leaving the field. This situation is well illustrated in the work by Alonso Prados et al. (2003) that studied the temporal and spatial distribution of *Watermelon mosaic virus* (WMV) and CMV infecting melon fields in Spain. They found that CMV was preferentially spread along the rows between adjacent plants following a rectangular pattern, while the spread of WMV rarely occurred between adjacent plants. The observed spatial pattern of CMV suggests the involvement of an aphid species that colonises melon, which tends to disperse within rows in a contagious pattern, in the secondary spread of the virus. In fact, laboratory experiments conducted later showed that the CMV was transmitted with highest efficiency by the colonizer species, *A. gossypii* while WMV was best transmitted by *M. persicae*, which does not colonize melons in Spain (Garzo et al., 2004).

In several instances, plants markedly taller than the primary crop are chosen as barrier plants because of their likelihood to intercept aphids while in flight. Dhanju et al. (1995) investigated and reported that five barrier plants were effective in reducing the occurrence of virus in French beans (*Phaseolus vulgaris*) by breaking the flight of aphids. Because the barrier crops were markedly taller than French bean, the authors suggested that these plants intercepted aphids that then lost their virulence while probing the barrier crops. However, the fact that those barrier plants taller in stature (e.g., sorghum and maize) were marginally better than amaranthus (*Amaranthus candatus*), okra (*Abelmoschus esculentus*), and sunflower in preventing disease spread suggest that barrier crop height may have not been the most critical factor in limiting *Bean common mosaic virus* (BCMV) incidence in French bean.

4.3. Camouflaging or masking the host plant

BYMV is a serious problem in Australia, the USA, southern Africa and Europe (Jones and McLean, 1989). Jones (1993) found that the spread of BYMV among narrow-leaved lupins could be significantly reduced by using borders of oats (*Avena sativa*) or wheat. The decrease in BYMV spread was much greater in plots of lupins mixed with oats than lupins bordered by oats. Jones proposed that the greater overall plant density provided by the mixture contributed to a greater decrease in spread. Additionally, Jones (1993) found that lupin plants grown at low

density had a greater proportion of plants infected than plants at higher densities. However, when weeds were allowed to grow among the lupin plants the proportion of infected plants were similar among low and high densities. Jones (1994) also found that straw mulch placed between rows of lupin plants reduced BYMV ingress to *L. angustifolius* compared to bare-ground plantings. These findings suggest the ratio of plant to soil background is important in determining the severity of non-persistent virus spread in fields of narrow-leafed lupins and further implies that the oats may have served more as a visual than physical impediment to vector spread. These results are not surprising as we already explained that aphids tend to land much more frequently on isolated plants than on a closed canopy (Irwin et al., 2000). In another experiment involving straw mulch, Saucke and Döring (2004), found that straw mulch could be used to reduce the occurrence of PVY in organic potatoes and suggested that the straw helped camouflaged the potato plants from alatae aphids.

Another important virus of lupins in Australia is CMV, a seed-borne virus that decreases grain yields. General recommendation for management of CMV in lupins is sowing less than 0.5% CMV infected seeds, to minimize the infection sources and sowing early at high seeding rates to remove seed infected plants through competition via improved canopy formation of healthy plants (Bwye et al., 1994). Similarly, to BYMV, CMV spread can be significantly suppressed by the application of straw ground-cover in lupin plots (Bwye et al., 1999). These findings with straw mulch suggest that stubble retention or no-till production practices in lupin fields can be used to help manage CMV and BYMV.

Cowpea (*Vigna unguiculata*) is susceptible to several virus species. Sharma and Varma (1984) investigated border (pearl millet, *Pennisetum typhoides*) and mixed cropping (with maize) on the field spread of virus among cowpea plantings. They found that both border and mixed cropping reduced the virus infection compared with pure cowpea stands. In addition, similar to Bwye et al. (1994) they discovered that sowing the primary crop at higher seeding rates per unit area decreased the percentage of infected plants.

4.4. Trap crop

Trap cropping has not been traditionally recommended as a cultural strategy for managing NPVs as this strategy proposes to use a preferred host plant for attracting the pest away from the primary cash crop. Essentially a trap crop is a secondary plant species that is more attractive to the targeted pest than the neighboring primary crop. The pests tend to move and concentrate on the trap crop thus sparing the primary crop from significant pest colonization and associated damages. If pest populations on the trap crop reach high levels some management strategy (e.g., insecticides, biological control) may be directed at the trap crop.

The major concern is that trap crops may serve as a host for vector reproduction and thus increase virus spread in the nearby crop. Toba et al. (1977) investigated the potential use of radish, *Raphanus sativus*, swiss chard, *Beta vulgaris* var. *cicla*, and wheat as protector crops for cantaloupe (*Cucumis melo*) plantings. Cantaloupe planted in the radish and swiss chard plots

showed no or few virus symptoms. Similarly, cantaloupe plants protected by wheat showed a significant delay in the frequency and severity of symptoms associated with *Watermelon mosaic virus* (WMV-1 and -2) currently known as PRSV and WMV, respectively. Toba et al. (1977) believed that the wheat attracted aphid vectors lowering their colonization on cantaloupe plants. This was the only study suggesting that the barrier crop may have been more attracted to aphid vectors than the protected crop itself. In this instance although the wheat was reported to be a better attractant than the primary crop, it was not a host for aphid vectors. However, the species of aphids that commonly infest wheat (*Rhopalosiphum padi* or *Sitobion avenae*) do not reproduce on cantaloupes and are poor vectors of WMV (Castle et al., 1992). Therefore, these aphid species should not be a major threat to the nearby cantaloupe plantings. In another study involving wheat, Mannan (2003) investigated its potential along with mustard to manage *Potato leaf roll* (PLRV) in potato plots and showed a decline in the number of aphids and PLRV. Wheat and mustard reduced disease incidence in potato plots by 50 and 29%, respectively. Mannan (2003), unlike Toba et al. (1977) and Dhanju et al. (1995), suspected that wheat plants with their deep green leaves attracted fewer aphids than light green mustard leaves and this contributed to greater reduction in virus spread in potato habitats mixed with wheat than mustard.

In an earlier study, Gay et al. (1973) used pearl millet (*Pennisetum glaucum*) as a trap crop to protect cowpea (*Vigna sinensis*) from cowpea mosaic diseases. They found that cowpea plants surrounded by the trap crop contain fewer virus-infected plants and significantly greater yield than the control habitats. Further, they found that yield was greatest in plots where they treated the trap plant with a systemic insecticide. However, there was no mention that the pearl millet-trap plant was sampled for aphids or that it was a better attractant. Thus, it is not certain whether the pearl millet behaved as a “true trap crop” in that it was favoured by aphids over cowpea plants or whether it acted more as a physical barrier and blocked aphids from reaching the cowpea.

Field trials were conducted in Malaysia to evaluate the effectiveness of intercropping chilli (*Capsicum annuum*) plants with maize or brinjal (*Solanum melongena*) to suppress *Aphis gossypii* and associated *Chilli vein mottle virus* (CVMV) (Hussein and Samad, 1993). Virus spread of CVMV was faster and trap catches of winged vectors were greater in monoculture compared with diculture chilli habitats. Hussein and Samad (1993) suggested that the brinjal acted as a trap crop by attracting early migrating vectors. However, maize was believed to act as a mechanical barrier and was effective in reducing vector movement within the plot.

5. Limitations of using barrier plants

The findings from several studies indicate that barrier cropping can be successfully used to significantly mitigate the severity of yield lost caused by non-persistently transmitted aphid-borne viruses (Table 1). Still there may be limitations to deploying this strategy under conditions of polycyclic disease spread or when trying to protect a perennial host crop. For example,

eastern gamagrass, *Tripsacum dactyloides* is a perennial grain susceptible to infection by viruses such as *Sugarcane mosaic virus strain maize dwarf mosaic virus B* (SCMV-MDMV-B) and *Maize dwarf mosaic virus* (MDMV). Gamagrass was grown with one or both of two non-host species, wildrye, *Leymus racemosus* and Illinois bundleflower, *Desmanthus illinoensis* at two experimental sites for 5 years (Piper et al., 1996). At one site treatment differences occurred but disappeared by the third year. Here disease occurrence and severity were generally higher within monoculture and gamagrass/wildrye biculture than in treatments containing bundleflower. Perennial crops may have strong inoculum pressure from year to year and this would be somewhat analogous to polycyclic disease spread in an annual system. It has been suggested that barrier cropping is most effective when the disease occurrence is monocyclic and thus there is limited secondary disease spread (Jones, 1993; Fereres, 2000). In situations where secondary spread of the disease commonly occurs selecting a barrier plant species that is attractive to natural enemies of aphids should be a good control strategy, especially when the major vector of the virus is a species that colonises the crop.

Despite these limitations, there may be some benefits to using barrier plants in perennial plant systems. For example, several viruses are known to infect white clover, a commonly used forage legume (McLaughlin and Boykin, 1988). Brink and McLaughlin (1990) examined how tall fescue (*Festuca arundinacea* Schre.) interplanted with white clover would impact clover virus incidences. They found reduced occurrences of *Alfalfa mosaic virus* (AMV) and *White clover mosaic virus* (WCMV) in those plots compared with monoculture stands. Similar results were obtained by Lewis et al. (1985) who found that red clover mixed with ryegrass reduced virus incidence compared with monoculture habitats.

In many cropping systems, viruses may not be the sole cause of yield loss. Under multi-pest circumstances, the positive impact of barrier plants on virus incidence may be negated by other pest organisms unaffected by the presence of barrier plants. For example, Hooks et al. (1998) found that two living mulches buckwheat (*Fagopyrum esculentum*) and yellow mustard (*Sinapis alba*) were effective in delaying the incidence of *Papaya ringspot virus-watermelon strain* (PRSV-W) among zucchini plants. Despite the significant delay in viral diseases among living mulch protected plants, significant fruit damage caused by the melon fly (*Dacus cucurbitae* Coquillett) prevented higher marketable yields in protected plots during the final year of the study.

Another potential challenge in using barrier cropping is choosing an effective barrier plant species. Once the barrier plant is chosen, the next objective is to determine how to best incorporate it into the main crop so that it effectively protects the target crop without negating any positive benefits of disease suppression. Competition between the barrier plant and cash crop may be considered the “Achilles heel” of using the barrier cropping tactic. The potential negative impact of these protector plants on crop growth parameters must be considered (Hooks and Johnson, 2003). If the strategy is to reduce vector numbers entering a crop field by inter-planting, it is important to

pick barrier plants that will achieve complete ground coverage as soon as possible. Determining the acreage to be devoted to the barrier planting, when to plant the barrier crop in relation to the cash crop, and at what density so as to avoid yield loss due to competition may be especially challenging to growers. Bottenberg and Irwin (1992) found that they could significantly reduce SMV-induced seed mottling in soybean by mix cropping it with dwarf and tall sorghum isolines. Despite this reduction, shading by tall and dwarf sorghum reduced soybean yield by an average of 25 and 50%, respectively, compared with monoculture planting. However, competition may be less of a concern if other barrier cropping approaches are used. For example, if the approach is to use the barrier plant as a mechanical barrier against aphid vectors, planting tall cereals such as maize and sorghum as researched by (Alegbejo and Uvah, 1987) along crop perimeters will remove competition or limit it to border row areas.

Deciding which barrier tactic to deploy can be an arduous task because a sufficient amount of information is essential to making a sound judgement. For example, perimeter non-host barrier may not be effective for large acreage plantings, because it may only protect a limited number of rows. In this instance, a row inter-planted barrier may be a more viable choice. Additionally, perimeter non-host barriers may not be practical within an IDM program when the only significant virus source is coming from seed-infected plants (Jones, 2001). Even if the choice of barrier crop and tactic is solved, the logistics of managing two crops concurrently can be taxing in some commercial operations. In some instances using barrier plants may result in production benefits (e.g., reduction in weeds and greater soil quality). Under these circumstances, growers have the arduous task of determining whether these benefits outweigh the inconveniences associated with planting barrier crops.

Another critical issue associated with the adoption of ecological-based methods includes the cost differences to farmers (Mausolff and Farber, 1995). There may be increased production costs associated with adding barrier plants to the primary crop field, especially if the barrier plant is row intercropped. Therefore, from an economic viewpoint, any increase in marketable yield due to barrier cropping must compensate for additional expenditures associated with the barrier crop. Use of control measures that involves major disruption to normal production practices is costly and rarely feasible unless there is a high return on the protected crop (Jones, 2004).

6. Incorporating barrier cropping with other disease management strategies

In this review, we focus our attention on one tool (i.e., barrier cropping) for mitigating yield constraints menaced by aphid carriers of NPVs. However, it has been suggested that understanding environmental influences on insect-borne viruses requires more than knowledge on the effects of individual tactics (Irwin et al., 2000). Indeed it is critical that multiple pest management tactics be examined concomitantly, so that the opportunity for successful vector suppression rises. In many instances, barrier cropping may not significantly lessen the severity of disease

incidences inflicted by aphids when used as a single treatment. However, when integrated with other management strategies (e.g., cross protection, mineral oils, insecticides, resistant cultivars, and cultural management) these alliances may repress disease significantly more than any single tactic alone. For example, Anandam and Doraiswamy (2002) found that maize, sorghum, and sunflower used as barrier plants significantly reduced CMV in chilli over control habitats. However, spraying the barrier plants with insecticides further increased their effectiveness resulting in greater disease suppression. Saucke and Döring (2004) combined wheat mulching and pre-sprouting to manage PVY and found that this mixture had a synergistic, complementary impact on PVY reduction. They further suggested that combined mulching/pre-sprouting could decrease the dependency of either treatment alone. In a more rigorous experiment involving straw mulch, Kendall et al. (1991) determined that straw disposal and tillage methods can be manipulated to lower the incidence of BYDV in winter barley.

Alegbejo and Abo (2002) indicated that an integrated pest management strategy that involves using resistant cultivars, close spacing, barrier crops, and sanitation (e.g., removing weed hosts of the virus) is being effectively used to keep *Pepper veinal mottle virus* (PVMV) below economic injury levels in Northern Africa. Harrewijn and Minks (1987) suggested a similar integrated strategy to protect arable crops from direct and indirect damage imposed by aphids. From 1986 to 2001, a 15-year research program was conducted to develop effective and affordable IDM strategies against CMV and BYMV in narrow-leafed lupin (Jones, 2001). Upon completion of the program, Jones (2001) concluded that IDM strategies whereby host resistance and cultural practices are combined together in a complementary manner offer the best chance of success. Although, we suppose that barrier cropping should be coupled with other management tactics, before increasing the complexity of vector management by uniting control tactics, it is important that aphid vectors reactions to individual tactics be meticulously investigated and documented.

7. Future use of barrier cropping

Several field experiments (Table 1) have shown that barrier cropping can be successfully used to lessen the occurrence of insect transmitted diseases resulting in increased crop yields. In addition to their potential to reduce the severity of ABNPVs, barrier plants may help lower the occurrences of other insect transmitted plant pathogens. For example, Heathcote (1968) found that rows of mustard (*Brassica juncea*) or barley intercropped with sugar beet (*Beta vulgaris*) could reduce the occurrence of *Beet mild yellowing virus* (BMV), a virus transmitted in a persistent manner. In addition to aphids, barrier crops may protect crops from viruses transmitted by other insects. Ahohuendo and Sarkar (1995) showed that intercropping cassava (*Manihot esculenta*) with maize, cowpea, and peanut (*Arachis hypogaea*) reduced the population size of the whitefly, *Bemisia tabaci* Genadius and the associated *African cassava mosaic virus* disease (ACMV). Page et al. (1999) found that intercrops of beans and millets reduced the occurrence of *Maize streak virus* disease

(MSVD) transmitted by leafhoppers, *Cicadulina* spp., in maize. More recently, Coutts et al. (2004) found that a 15 m-wide barrier of cabbage could delay infection and reduce clustering of *Tomato spotted wilt virus* (TSWV) in lettuce (*Lactuca sativa* L.) plantings. Van Rheenen et al. (1981) found that growing beans with maize resulted in less incidence of several diseases and pests including halo blight, *Bean common mosaic*, anthracnose, common blight, scab and mildew respectively compared with monoculture stands. In another study involving a maize-bean diculture, Power (1987) showed that growing maize with beans or weeds reduced leafhopper abundance and decreased *Spiroplasma kunkelii* disease in maize. Across-row movement of *Dalbulus maidis*, which transmits the bacterium to maize, was significantly inhibited in maize polycultures. This was especially apparent in maize/bean habitats, where leafhopper emigration rates were also highest. These protector plants may also be used to mitigate non-insect caused plant diseases. For example, cover crops were found to reduce the splash dispersal of *Colletotrichum acutatum* conidia (Ntahimperera et al., 1998) and suppress plant parasitic nematodes (Wang et al., 2001). Thus, barrier plants may be used to suppress a diverse array of pest organisms within pathosystems.

In addition to its direct impact on crop yield, barrier cropping may help alleviate social and environmental fears regarding current production practices. Vegetables are indispensable for healthy nutrition and consumers are becoming more concerned about health risks associated with chemical use. The criteria that establish vegetable quality are changing and consumers are considering the overall production method, making reduced chemical use a significant selling point (Theunissen, 1997). The scope of using biological control for vector and their associated pathogen suppression is limited. In many instances, it is believed that biological control may contribute modestly if any to preventing carriers of NPVs from inflicting damage to susceptible cropping systems. Thus, cultural management practices such as barrier cropping offer one of the few advisable options. Replacing chemicals with barrier crops (e.g., intercrop, cover crop) creates more environmentally sound management practices that will ultimately help increase consumer confidence in the quality of agricultural products.

Furthering the need for cultural based viral management practices is the fact that organic farm establishments preclude the use of synthetic chemicals and genetically modified crop plants. According to the most recent survey of the Research Institute of Organic Agriculture (FiBL) more than 5.7 million hectares are under organic management in the European Union, representing ca. 3.5% of the total agricultural land. At the present time, there are more than 6.3 million hectares throughout Europe (Anonymous, 2005). Moreover, certified organic farmland in the United States alone increased by 1 million acres between 1997 and 2001 (Anonymous, 2002). Managing farms according to restrictions attached with organic produce is a serious challenge and forces scientists and growers to seek alternative pest management strategies. As consumers and farmers become more concerned over the health of the environment and the trend towards sustainable agriculture and organic farming continues to grow, use of barrier crops alone or in combination with other

disease management strategies may become a more demanded preference.

8. Future research

8.1. Vector behaviour

One aim of the review was to bring to surface the techniques responsible for virus occurrences in barrier cropped habitats. The findings revealed may not unequivocally explain all mechanisms contributable to reduced virus spread in flora diverse habitats, but it provides some clarification on the crucial factors accountable for disease suppression. Still, most of the reasons cited for disease occurrences in Table 1 were based on the original authors' opinion and in most instances the experimental protocols were not designed to determine the method(s) accountable for experimental outcomes. It is important that future studies evaluating the effect of barrier cropping on levels of NPVs take an unyielding look at factors liable for experimental findings.

An edifying approach would be to investigate behavioural aspects of host seeking aphids to plant mixtures. Visual detection of plants by herbivorous insects has been reviewed by Prokopy and Owens (1983). Several works have shown that insect herbivores locate host plants initially through indiscriminate visual attractions to (yellow) green (Finch and Collier, 2000). It has also been determined that most aphids are attracted preferentially to certain yellow and green colours (Moericke, 1955). It is well known that landing alatae aphids are repelled by shorter wavelengths and attracted by yellow (Hardie, 1989) and by green targets on contrasting backgrounds (Döring et al., 2004). Various plant species differ in their reflected colours, largely due to differences in leaf chlorophyll content. Therefore, vector responses to habitats with barrier plants may be largely influenced by optical parameters. Antignus (2000) and Raviv and Antignus (2004) reviewed how visual cues affecting the phototactic responses of insects were compromised, and used to develop cultural practices for protecting crops from insect transmitted viruses. Thus, researchers investigating the reasons for virus occurrence in barrier crop habitats may gain valuable insight by conducting quantitative spectral measurements and behavioural tests to identify how alatae vectors react to differing wavelengths generated by barrier plants.

Once a viruliferous aphid lands on a potential barrier plant and starts probing, a NPV may be released from its stylet during the probing act. It has been suggested that once an aphid has landed on a plant target it will react in a different way than when landing on the background near the target (soil). Smooth surfaces such as leaves will induce probing activity, whereas rough surfaces such as the soil may be easily distinguished from leaves and no probing is done (Döring et al., 2004). Therefore, an effective barrier plant should induce aphid probing soon after landing.

Residence time, which may be influenced by barrier cropping, is also an important parameter in predicting the spread of insect-borne plant viruses, but is rarely examined by methods that could be used to determine its influence on disease spread (Power, 1990). Bottenberg and Irwin (1991) researched

the impact of bean-maize diculture on the residence time of winged *Uroleucon ambrosiae* (Thomas) aphids. They found that *U. ambrosiae* took flight more readily in bean-maize diculture than alatae in bean monoculture and suggested that this occurred because wind speed was lower in these habitats than in monoculture. Wind speed is known to influence aphid takeoff (Dixon and Mercer, 1983). Bottenberg and Irwin (1991) acknowledged that more controlled experiments were needed to confirm the effect of crop mixture on aphid residence time and subsequent virus spread. Aphid behavioral studies can help clarify how the presence of barrier plants affects aphid movement and host-plant searching, and ultimately provide some definitive insight on the cause for vector dynamics and virus dissemination. From the perspective of applied research, understanding the movement and management of viral diseases necessitate an appreciation of the vector and its behaviour (Ng and Perry, 2004).

8.2. Trap cropping

Trap cropping has been successfully used in several systems to reduce the damage imposed by herbivorous insects (see review by Hokkanen, 1991). Still, trap cropping has not been well explored as a method for preventing non-persistent virus spread. Researchers may be reluctant to use this technique out of fear that the trap crop may harbour aphids that could potentially spread virus to the protected crop. This may be avoided by using trap plants that are visually attractive to vectors without providing a suitable nutrient source. Trap crops may function to reduce virus spread by several methods: (1) these plants may lure vectors away from the protected crop, (2) they may reduce the ratio of soil to plant background thus camouflaging the target crop, (3) trap plants may serve as hosts for some aphid vectors that remain on the trap, (4) aphid vectors may lose their ability to transmit the virus after probing the trap plant (i.e., virus sink hypothesis) and finally, (5) these plants may attract biological control agents that impose significant mortality upon aphids. In choosing a trap crop, it is important that the plant of choice is incapable of hosting large populations of aphids or any viruses that may affect the primary crop. Unless an investigator is familiar with the arthropod fauna associated with a potential trap crop, it should be initially screened for its suitability to serve as a barrier plant.

8.3. Genetic diversity

Similarly to trap cropping, little is known about the influence of genetic diversity among crop plants on the occurrence of plant viruses. During the preparation of this review, no studies designed to explore the influence of plant genetic diversity on the dissemination of non-persistent viruses were encountered. However, this approach could work similarly to trap cropping. Irwin and Kampmeier (1989) compared the attractiveness of two soybean cultivars to vectors of *Soybean mosaic virus* (SMV). They found that more vector specimens were attracted to Clark 63 (a normal dark green) than to Clark Y₁₁Y₁₁ (a light yellow) line. However, these authors did not determine experimentally how the two lines affect SMV epidemics. Power (1991) exam-

ined the influence of genetically diverse oats (*Avena sativa*) on the spread of *Barley yellow dwarf virus* (BYDV), a virus transmitted in a persistent manner. Despite the fact that aphid abundance was similar in the different oat habitats, the incidence of virus was consistently lower in genetically diverse oat plantings. It was suggested this disease reduction was due mainly to reduced tenure times and increased travel times among plants in genetically diverse oat habitats which led to a reduction in virus transmission. However, BYDV requires several hours of aphid feeding for effective transmission therefore the constant movement of aphids probably reduced the chance for successful transmission. Power suggested that the effect of increased vector movement depends crucially on the relationship between vector tenure time and the probability of transmission of a particular pathogen. Aphid vectors may transmit NPVs in a matter of seconds; therefore, this constant movement could potentially result in increased pathogen transmission. However, it is important to note that during the study no truly resistant oat variety was used in the genetically mixed oat population and as recognized by Power (1991), if one of the varieties was truly resistant to infection, virus incidence may have been even lower than observed.

Irwin et al. (2000) suggested that the breeding and adoption of desirable mixtures of crop varieties with resistance to pests and pathogens should be encouraged. The notion is that if virus-susceptible plants are scattered among resistant plants within a field, vectors are less likely to encounter susceptible plants than if they were in pure stands. Irwin et al. (2000) also proposed that if a viruliferous aphid probes a resistant plant this would reduce its infectivity. Furthermore, models of pathogens have suggested that the durability of resistance is enhanced in genetic plant mixtures and as a rule the evolution to prevail over resistance is slower in mixtures than in pure stands of resistant varieties (Barrett, 1981). However, others feel this strategy may promote the propagation of viruses. For example, Harrewijn (1983) advised that the breeding of partly resistant or unacceptable cultivars may be unfavourable with regard to NPVs, as he believed frequent probing may be stimulated, which is unfavourable in regards to NPV spread. Thus, research devoted to clarifying how genetically diverse cropping systems impact the spread of NPV and vector dynamics is warranted.

8.4. Biological control

Biological control is an important component of Integrated Pest Management (IPM) but has not been evaluated as a strategy for slowing the spread or reducing the severity of NPVs. The general perception is that biological control organisms act too gradually on vectors to prevent their dissemination of non-persistent viruses when vectors are within the crop bounds (Irwin, 1999). Moreover, it is believed that when being attacked by natural enemies, aphids emit alarm pheromones (Nault, 1973) and this presumably triggers increased vector movement and brings about greater virus spread. However, Roy et al. (1999) found that aphids infected with an entomopathogenic fungus were less sensitive to the aphid alarm pheromone than uninfected aphids.

The results of a field study conducted by Webber et al. (1996) supported the supposition that biological control agents could favour virus spread. They found that when sugar beet plants were infested with parasitized and non-parasitized viruliferous bean aphid, *Aphis fabae* Scopoli, *Beet yellows virus* (BYV) incidence was greater on plants neighboring the virus source in parasitized than in non-parasitized treatment, respectively. Webber et al. suggested that the parasitized aphids were more mobile than non-parasitized aphids. Still, these results must be viewed with caution. BYV is transmitted in a semi-persistent manner with acquisition access and test feeding times of 12 and 6 h, respectively. Therefore, disease spread of BYV may differ from a typically NPV disease. Also, their study was conducted in small monoculture plots and may not truly represent virus spread in a mixed flora ecosystem. Mixed plant habitats tend to have a greater diversity of natural enemies, thus after leaving the plant these vectors may succumb to additional mortality factors not found in monoculture systems. Vector “escapees” may also inappropriately colonize non-host barrier plants and while on these plants lose their infectivity while probing or feeding. Another factor to consider is that aphid wing development is commonly inhibited by parasitization (Christiansen-Weniger and Hardie, 2000). Thus, if aphid vectors are parasitized this will limit their movement to walking which will further reduce their likelihood to successfully encounter another susceptible host plant. On the other hand, wingless female aphids are more fecund than their winged sisters as energy is directed to reproduction rather than flight muscle (Dixon, 1998). Thus, some may argue that this will increase the number of offsprings that can potentially become virus carriers.

The potential of biological control agents to limit the spread of non-persistent virus is not well known but we suspect this strategy may complement cultural management practices such as barrier cropping. Biological control may be administered with less reservation if used to prevent secondary virus spread by suppressing aphid vectors that could migrate to susceptible plantings. Reducing aphid numbers will have a major impact on situations where polycyclic disease patterns prevail and where the main virus vector is able to colonise the crop and spread the disease to nearby plants (e.g., *Aphis gossypii* spreading CMV to melons in Spain; Alonso Prados et al., 2003). Also, not all aphids within a crop setting are viruliferous and if biological control organisms can impose significant mortality among healthy aphids this may reduce the population of aphids that could potentially become viruliferous. Further, the effect of biological control organisms on the movement dynamics of viruliferous aphids are likely imperceptible, especially when compared with environmental influences. Still whether biological control agents will enhance or suppress NPV spread is difficult to predict, as this area has received only limited attention.

8.5. Combining management factors

Finally, more research should be conducted to exploit the potential synergistic benefits of combining barrier cropping with other management strategies. The benefits of combining management tactics such as cultural, chemical, and biological that act

in different ways may cause significantly greater repression of virus diseases than any single tactic administered alone (Jones, 2001, 2004). For example, Irwin et al. (2000) used a computer model to study various environmental parameters associated with SMV. Irwin et al. found that date of planting affected vectors alighting behaviour and that intercropping affected their landing and virus transmission. They predicted that if soybeans were sowed considerable time before or a short time after major vector flights, incidence of virus would lessen and that intercropping would further reduce disease spread. However, Irwin et al. (2000) dutifully suggested that the reliability of their findings should be experimentally tested.

Jones et al. (2005) conducted a spatial analysis of *Carrot virus Y* (CarVY) epidemics in carrots plantings. The study revealed the need for several control measures (i.e., intervening fallow, planting upwind, safe planting distance and etc.) to successfully manage CarVY. Jones et al. (2005) further suggested that the safe planting distance needed to help reduce CarVY spread from infection sources to newly sown carrot crops is likely to diminish if non-host barriers are used instead of fallow. This recommendation made by Jones et al. is likely feasible for several NPVs. However, to help confirm these beliefs, studies examining how non-host barrier influence the spread pattern of NPVs in concurrence with other management practices warrant future attention. Unless this information is obtained through research only tentative recommendations can be advised regarding the mixing of barrier crops with other control measures.

9. Concluding remarks

This review has identified several studies showing that barrier cropping is a promising tactic for mitigating yield losses caused by ABNPVs. Despite the number of published “triumphs” on barrier cropping, most studies fail to scrutinize the underlying reasons for reduced virus spread. In many instances, readers have to make tentative assumptions or entrust suggestions made by the original authors on the causes of virus suppression. This review has recognized several possible mechanisms, which we consider important contributors to virus delay and/or reduction in the presence of barrier plants. These include the (1) virus-sink, (2) physical barrier, (3) host plant masking and (4) trap cropping. An investigation of these or other responsible mechanisms should be included in future studies exploring the potential benefits of barrier plants. If the precise means for vector and virus responses to barrier plants are identified, barrier cropping tactics can be better designed to increase their assurances of successful application.

Although economic losses in world agriculture due to non-persistently aphid transmitted viruses impact a copious number of crop species, literature obtained during the preparation of this review suggest that barrier cropping research has been largely dominated by a few crop types. As evident by Table 1, crops in the family Solanaceae (i.e., pepper and potato) and Fabaceae (i.e., lupins) have been well researched compared to other crops vulnerable to non-persistent viruses. More studies are needed to demonstrate how barrier plants impact the spread of NPVs in other cropping systems. During this review, we also alluded to the verity that barrier cropping might be one of the most unrec-

ognizable management tactics for disease suppression. The fact that barrier cropping research is more partial to a few cropping systems may heedlessly contribute to the overall lack of recognition among consultants, farmers, and other agricultural personnel. If barrier plant research is extended to more cropping systems, it may become a more widely identifiable and acceptable disease management tactic.

Finally, in recent years, there has been a steady increase in research devoted to molecular virology in detriment to ecological studies and applied field research. As this trend continues, the ability to react decisively when virus epidemics threaten world food crops is becoming increasingly lost (Jones, 2001). We hope this review bequeath the agricultural community with information that will spurn greater interest in researching barrier cropping and other cultural management tactics as tools for disease management. Still, the widespread adoption of barrier plants into future disease management programs will ultimately depend on a well-devised plan to ensure that the benefits of barrier cropping are properly disseminated throughout the agricultural communities.

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