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**M. C. Perotto, J. A. Di Rienzo,  
S. Lanati, S. Panonto, R. Macchiavelli,  
E. E. Cafrune & V. C. Conci**

**Australasian Plant Pathology**  
Journal of the Australasian Plant  
Pathology Society

ISSN 0815-3191

Australasian Plant Pathol.  
DOI 10.1007/s13313-014-0312-9



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# Temporal and spatial spread of potyvirus infection and its relationship to aphid populations visiting garlic crops

M. C. Perotto · J. A. Di Rienzo · S. Lanati · S. Panonto ·  
R. Macchiavelli · E. E. Cafrune · V. C. Conci

Received: 27 February 2014 / Accepted: 28 August 2014  
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**Abstract** The potyviruses *Onion yellow dwarf virus* (OYDV) and *Leek yellow stripe virus* (LYSV) are the main causes of serious losses in garlic crops worldwide. Both viruses are transmitted by aphid vectors in a non-persistent manner. The relationships of aphid populations with temporal and spatial patterns of OYDV and LYSV were studied in a commercial main garlic production area from Mendoza, Argentina. The virus incidence in garlic plots during 2 years was quantified by a nitrocellulose-enzyme-linked immunosorbent assay. For temporal analyses performed in 2007 and 2008, disease progress curves were fitted using a logistic model. Epidemics were driven by non-colonising aphid species that spread the viruses primarily from west to east, coinciding with the wind pattern. This directional trend was reflected in the spatial analysis as a left-to-right gradient of virus incidence and cumulative aphid counts. Between 46 and 60 % of plants were infected with

OYDV and LYSV in the first crop cycle exposed to natural infection. A checklist of aphid species visiting the garlic crop was generated, with 34 species detected. We found that total aphid catch is a better predictor of virus spread than catches of any single species or a combination of a few key species.

**Keywords** *Onion yellow dwarf virus* · *Leek yellow stripe virus* · Potyvirus · Vectors

## Introduction

It is widely accepted that all commercial garlic crops are infected with a virus complex. This situation exists because viruses systematically infecting garlic plants are transmitted to offspring by vegetative propagation, the sole method of commercial seed bulb production. The complex mixture of viruses includes those of the genera *Allexivirus*, *Carlavirus* and *Potyvirus* (Van Dijk 1993 b; Conci et al. 1992). While these viruses do not kill the plant, they produce chronic infections that cause severe yield reductions, with recorded losses of up to 88 % in bulb weight (Conci et al. 2003; Cafrune et al. 2006; Perotto et al. 2010). Among the viruses in this complex, the potyviruses *Onion yellow dwarf virus* (OYDV) and *Leek yellow stripe virus* (LYSV) are primarily responsible for serious losses. These viruses have been detected in all garlic production areas worldwide. In the presence of OYDV and LYSV, bulb weight has been found to be reduced by 69 % and 54 %, respectively (Lunello et al. 2007; Canavelli et al. 1998).

Although the use of virus-free plants is currently the only practical control method, the timing of re-infection from neighbouring commercial fields—a key factor in disease management programmes—remains unknown. Due to a long period of hardening and multiple crop-cycle rounds in the soil

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M. C. Perotto · E. E. Cafrune · V. C. Conci  
Instituto de Patología Vegetal (IPAVE-CIAP-INTA),  
Camino 60 cuadras km 5 y ½ (5119), Córdoba, Argentina

M. C. Perotto · V. C. Conci (✉)  
Consejo Nacional de Investigaciones Científicas y Técnicas  
(CONICET), Córdoba, Argentina  
e-mail: concivilma@inta.gob.ar

J. A. Di Rienzo  
Facultad de Ciencias Agropecuarias, Universidad Nacional de  
Córdoba, Av. Valparaíso s/n Ciudad Universitaria, Córdoba,  
Argentina

S. Lanati · S. Panonto  
Estación Experimental Agropecuaria La Consulta-Instituto Nacional  
de Tecnología Agropecuaria (EEA La Consulta-INTA), Córdoba,  
Argentina

R. Macchiavelli  
College of Agricultural Science, University of Puerto Rico,  
Mayagüez, Puerto Rico

are necessary for commercial clove production, multiplication of material must be carried out in isolated areas where re-infections of propagated plants can be avoided (Conci and Nome 1991; Conci et al. 2005). Information regarding reinfection velocity and its relationship to natural vectors is important, because virus reinfection decreases garlic yield and quality. To maintain high production levels, such knowledge is essential for the development of control strategies and suitably scheduled replacement of materials by virus-free plants.

Potyvirus diseases in garlic are transmitted via cloves and by several aphid species in a non-persistent manner. Non-persistent transmission refers to the transfer of viruses whose acquisition, retention and inoculation periods are very short, with their transmission abilities unaffected by starvation. The spread of viruses in a non-persistent manner is mainly caused by non-colonising aphid species that alight on a plant and make superficial brief probes before take-off (Raccah et al. 1985).

The dispersion of viruses is a process dependent on the interactions of host crop, virus source and vector. Under appropriate conditions, potyviruses can spread rapidly, and, if uncontrolled, can cause total infection of some susceptible crops within a few weeks (Shukla et al. 1994). Relationships between various species of winged transient aphid populations and viral spread have been established for several potyviruses: *Lettuce mosaic virus* in lettuce (Nebreda et al. 2004), *Potato virus Y* in potato (Katis et al. 1998), *Cucumber mosaic virus* in pepper (Raccah et al. 1985) and *Soybean mosaic virus* in soybean (Halbert et al. 1981).

Accurate information on the population dynamics of aphid vectors alighting on crops is essential to the development of effective methods to avoid or reduce the spread of garlic viruses. Several aphid species have been reported as vectors or potential vectors of OYDV and LYSV (Drake et al. 1933; Diekmann 1997; Lunello et al. 2002). The most important vectors of both viruses are *Myzus persicae* and various species of the genus *Aphis*. Information about these aphid species and an understanding of the dynamics of aphid crop visitation and its relationship to viral spread can extend present knowledge regarding potential vector species and regional aphid species diversity.

Models can be used to quantify and elucidate vector, virus and host interactions. For viruses, analyses should be conducted on the use of cultural practices and the management of vectors. Efficient epidemic response depends on knowledge of both viral dispersal patterns and vector transmission efficiencies. Limited studies exist regarding the inter-relationship of these factors in the OYDV/LYSV pathosystem. Examination of disease progress curves (DPCs) and the relationships of aphid populations to OYDV and LYSV temporal and spatial patterns is the first step in the design of strategies and tactics to manage plant virus vectors.

In this study, we examined the composition and dynamics of aphid species visiting garlic crops, and also investigated OYDV and LYSV temporal and spatial patterns. Our research, the first investigation of this nature, was made possible by the acquisition of virus-free material for assay development. Experiments were carried out in Mendoza, Argentina, the most important garlic-producing province in the country.

## Materials and methods

### Plant materials

Plant materials used in this study were virus-free garlic (*Allium sativum*) plants obtained by meristem-tip culture and tested by immunosorbent electron microscopy with decoration (ISEM-D) with antisera to potyviruses, carlaviruses and allexiviruses as described by Conci and Nome (1991) and Conci et al. (2005). Plants were multiplied in anti-aphid cages for 3 years. To confirm the absence of both viruses, plants were analysed prior to experiments by a double-antibody sandwich enzyme-linked immunosorbent assay (ELISA) and ISEM-D using antisera against OYDV and LYSV, supplied by IFFIVE-INTA (since 2011 called IPAVE-INTA) as described in Conci et al. (1999) and Lunello et al. (2002), respectively.

### Experimental design

The experiment was repeated in two consecutive years (2007 and 2008) at the INTA La Consulta experimental agricultural station in Mendoza Province, Argentina. The experimental plot was located in the main garlic growing area of Argentina and was surrounded by other garlic fields. For both replicates, garlic was planted in April and harvested in November. Virus-free garlic cloves—9,334 the first year and 4,667 the second year—were planted in 10 rows spaced 60 cm apart with 15 cm between cloves.

In 2007 and 2008, respectively, 90 and 50 plants were randomly chosen for systematic sampling starting in June (sample number was small since the plot size was smaller the second year than the first year). These plants were analysed for viruses every 14 days, with 10 monitoring dates during the first year and eight in the second. A young leaf was collected from each sampled plant on each monitoring date. The presence of OYDV and LYSV was assayed in the collected samples by nitrocellulose-enzyme-linked immunosorbent assay (NC-ELISA) following Lizarraga et al. (1989)'s protocol using specific antisera against OYDV and LYSV provided by IPAVE-INTA.

Fifty garlic plants from neighbouring fields were also randomly sampled and analysed by NC-ELISA with OYDV and LYSV antiserum to ascertain their sanitary condition as inoculum sources for the experiment.

### Disease progress curve

OYDV and LYSV incidence was calculated for each monitoring date as the proportion of diseased plants among sampled individuals. Several common non-linear models, such as logistic, Gompertz and monomolecular, were fitted to the cumulative DPC for each virus disease, with the best-fit model identified using the Akaike information criterion (Akaike 1973).

### Aphid population dynamics

During both years of the experiment, aphid species were monitored weekly from mid-June through mid-November using four yellow water-pan traps (Moericke type) located at the plot corners. The aphid catches were separated, identified and counted; a seasonal curve for each species was also constructed.

A correlation analysis was performed between aphid species and virus incidence. Correlations between aphid population and weather variables were also assessed.

To analyse the relationship between presence of viruses and aphids, we considered the total sum of aphids detected in the plots, with the assumption that all observed aphids were potential vectors of these viruses. This premise is based on the fact that all aphid species previously tested have been able to transmit these viruses.

### Spatial analysis

The disease status of each plant in the monitoring sample ( $n=90$ ) was recorded on each monitoring date, with individuals labelled as virus free, OYDV positive or LYSV positive. For purposes of the statistical analysis, disease status was coded in two indicator variables: pOYDV and pLYSV. If a plant was positive to OYDV, pOYDV was set to 1; otherwise it was set to 0. Similarly, if a plant was positive to LYSV, pLYSV was set to 1, and otherwise 0. A third indicator variable (pOYDV\_LYSV) was used to designate cases in which a plant was positive to both viruses.

For each monitoring date, a logistic regression model was fitted to the above-mentioned indicator variables to test for lack of linearity between a plant within-plot position and its infection chance (in log scale). The explanatory variables were the coordinates of the plants in the plot.

The cumulative number of aphids caught in each trap since the beginning of the experiment up until a given monitoring date was also modelled, in this case by linear regression with the trap coordinates used as the explanatory variables. The purpose of this fit was to estimate the expected cumulative number of aphids to which each monitored plant was exposed until a given monitoring date. Although the number and location of traps imposed restrictions on the variety of models

that could be fitted (in this case, a plane at most) and the power for testing hypotheses on explanatory-variable effects, we were looking for simple trends in aphid dispersion patterns.

A correlation analysis was used to quantify the relationship between the estimated probability of a plant to be declared positive to a given virus (or both viruses) based on its plot position and the estimated cumulative number of aphids to which each plant had been exposed based on its position.

Statistical analyses were performed using InfoStat statistical software (Di Rienzo et al. 2012).

## Results

### Viruses' incidence

In the first year, 5 % of plants were infected with OYDV and 13 % with LYSV on the first monitoring date in June. By the end of the growing cycle, 46 and 60 % of plants were infected with OYDV and LYSV, respectively. In the second year, infection rates of 53 % for OYDV and 31 % for LYSV were recorded on the first monitoring date, with respective levels of 97 and 82 % observed near the end of the cycle.

In this study, infection rates of surrounding garlic plots were in the range of 90–100 %.

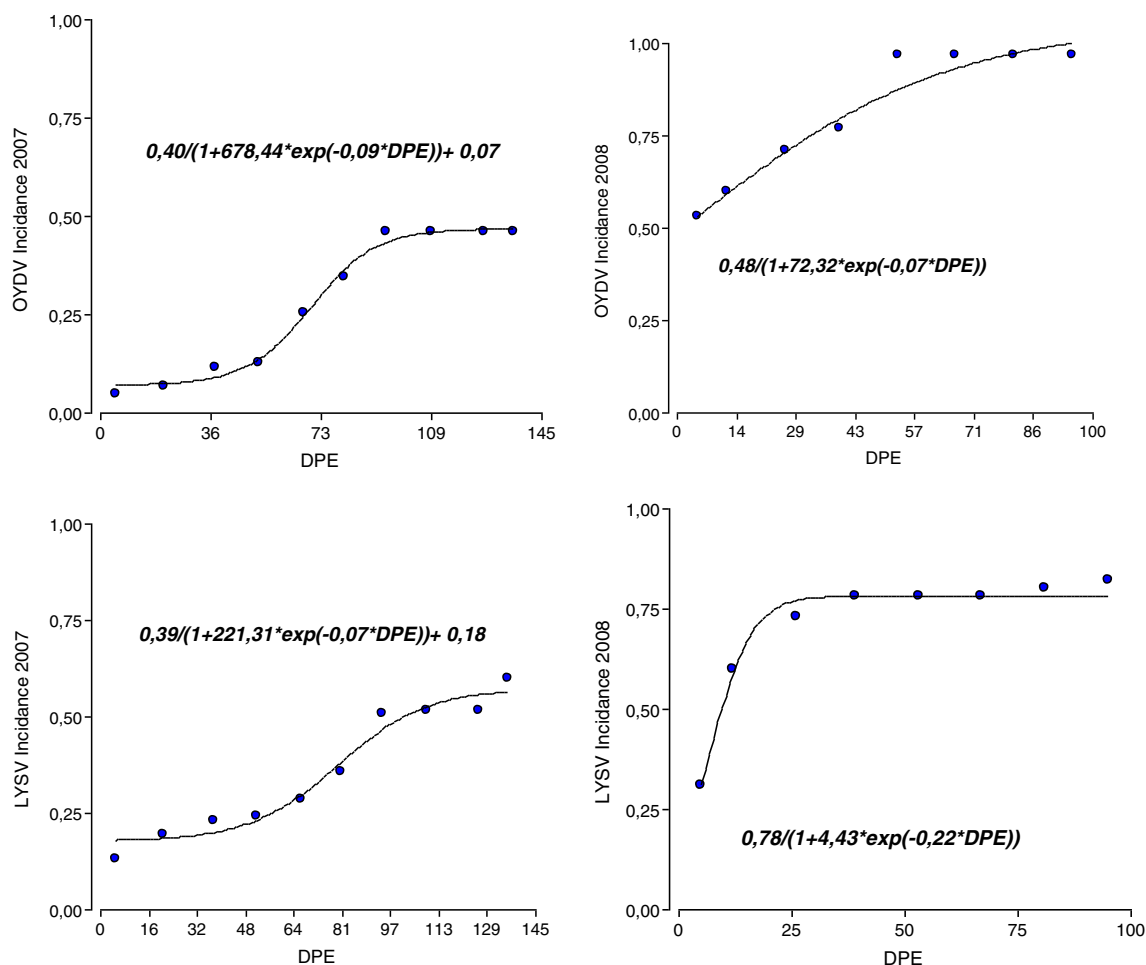
### Disease progress curves

The best DPC fit was a logistic curve for both viruses during each evaluation year. A shift parameter, which allowed the logistic curve to start above zero, was included for the first year of data (Fig. 1).

The entire s-shape of the logistic curve was only evident during the first year, because virus incidence in the second year was already very high (>50 and 25 % for OYDV and LYSV, respectively) at the start of monitoring. The logistic model describing virus incidence was  $\alpha / (1 + \beta * e^{-\gamma * DPE})$ , where DPE refers to days after plant emergence. The logistic model with the incorporated shift parameter was  $\alpha / (1 + \beta * e^{-\gamma * DPE}) + \delta$ .

### Aphid population dynamics and virus incidence

The total number of aphid catches in the first year was 1,056, which were distributed among 19 species. During the second year, the cumulative number of catches was 2,641 aphids belonging to 29 species. During the first year, the highest number of aphids was detected during spring (aphid sampling dates from DPE 71), while counts in the second year were highest in winter (aphid sampling dates between 15 and 36 DPE). *Hyadaphis foeniculi*, *Macrosiphum euphorbiae* and *M. persicae* were the most abundant species in the first year



**Fig. 1** Disease progress curve of onion yellow dwarf virus (OYDV) and leek yellow stripe virus (LYSV) during 2007 and 2008. Day plant emergence (DPE) is the number of days after plants emergence

(Fig. 2). *Brachycaudus helichrysi*, *Capitophorus eleagni*, *M. euphorbiae*, *Myzodium modestum* and *Neotoxoptera oliveri* were the most abundant aphids in the second year (Fig. 3).

#### Spatial analysis

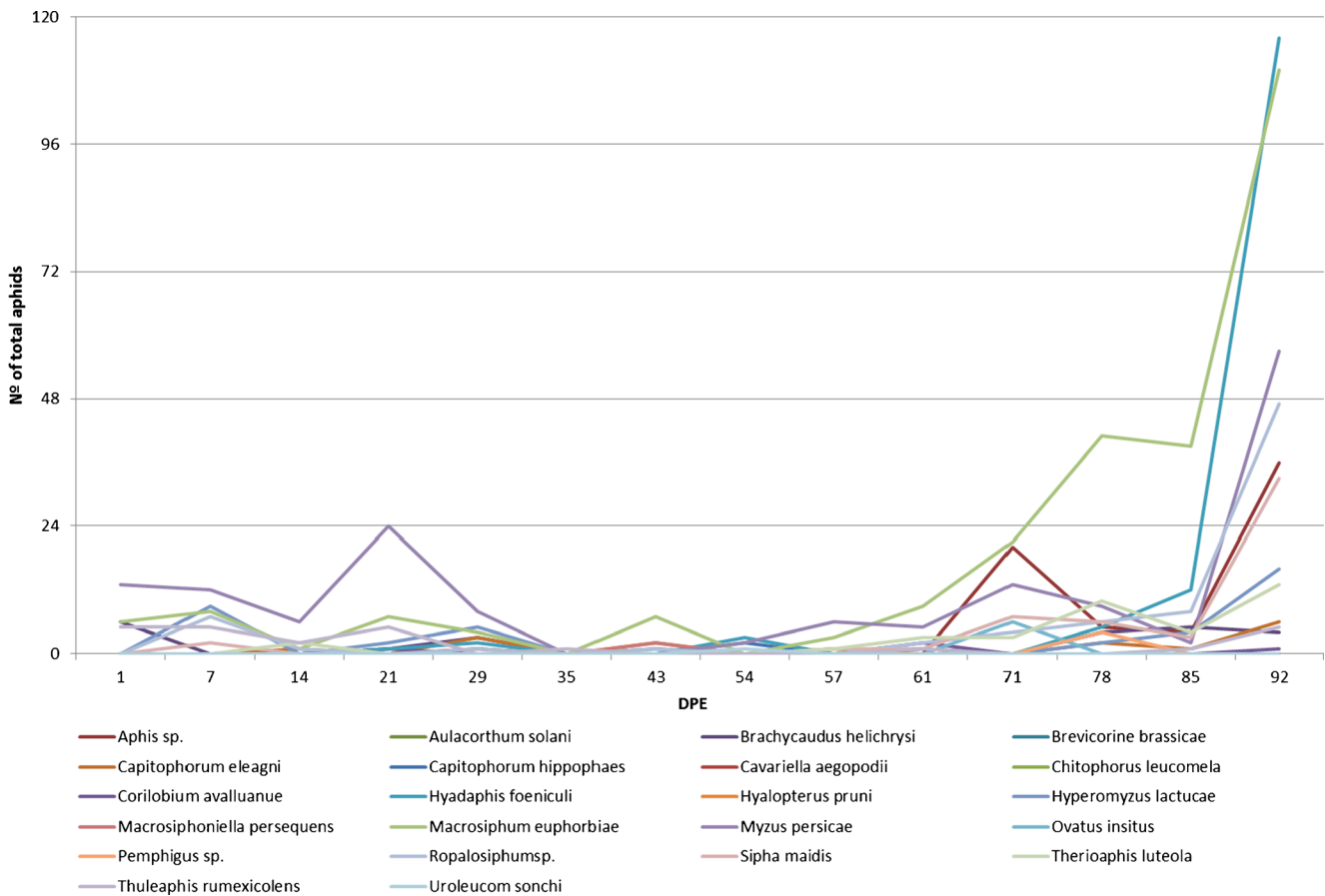
The correlation between estimated incidence of either or both viruses at each plant position (based on logistic regression) and corresponding estimates of cumulative aphid counts was found to increase from the first monitoring date until the fourth, and then reach a plateau (Table 1). All sampling dates showed a significant between-row but not within-row effect, except for the first date where no significant effect of position was observed. A reduced model including only the between-row effect was used to estimate expected incidence at each point within the plot. In Fig. 4, the model-base incidence of both viruses together and model-base cumulative aphid counts for each plant position within the experimental plot on the fourth sampling date are simultaneously represented by black circles and white circles, respectively.

The relative sizes of black and white circles are proportional to predicted incidence and cumulative aphid counts, respectively. For both estimates, the resulting figure shows a gradient from left to right, corresponding to west to east in the experimental plot.

#### Discussion

During 2007 and 2008, 46 and 97 % of plants were respectively infected with OYDV, and 60 % and 82 % were infected with LYSV. More than 46 % of virus-free garlic plants exposed to natural infection in the commercial growing area were infected with potyviruses during the first crop cycle. The detect infection is presumed to have been introduced by aphid transmission as plants were found to be virus free prior to planting.

We analysed the temporal and spatial spread of potyviruses in growing garlic to gain knowledge the biological processes involved, the factors driving epidemics with the aim of finding the best disease management control option.



**Fig. 2** Population dynamics of aphid species caught in four traps during the 2007 garlic crop cycle

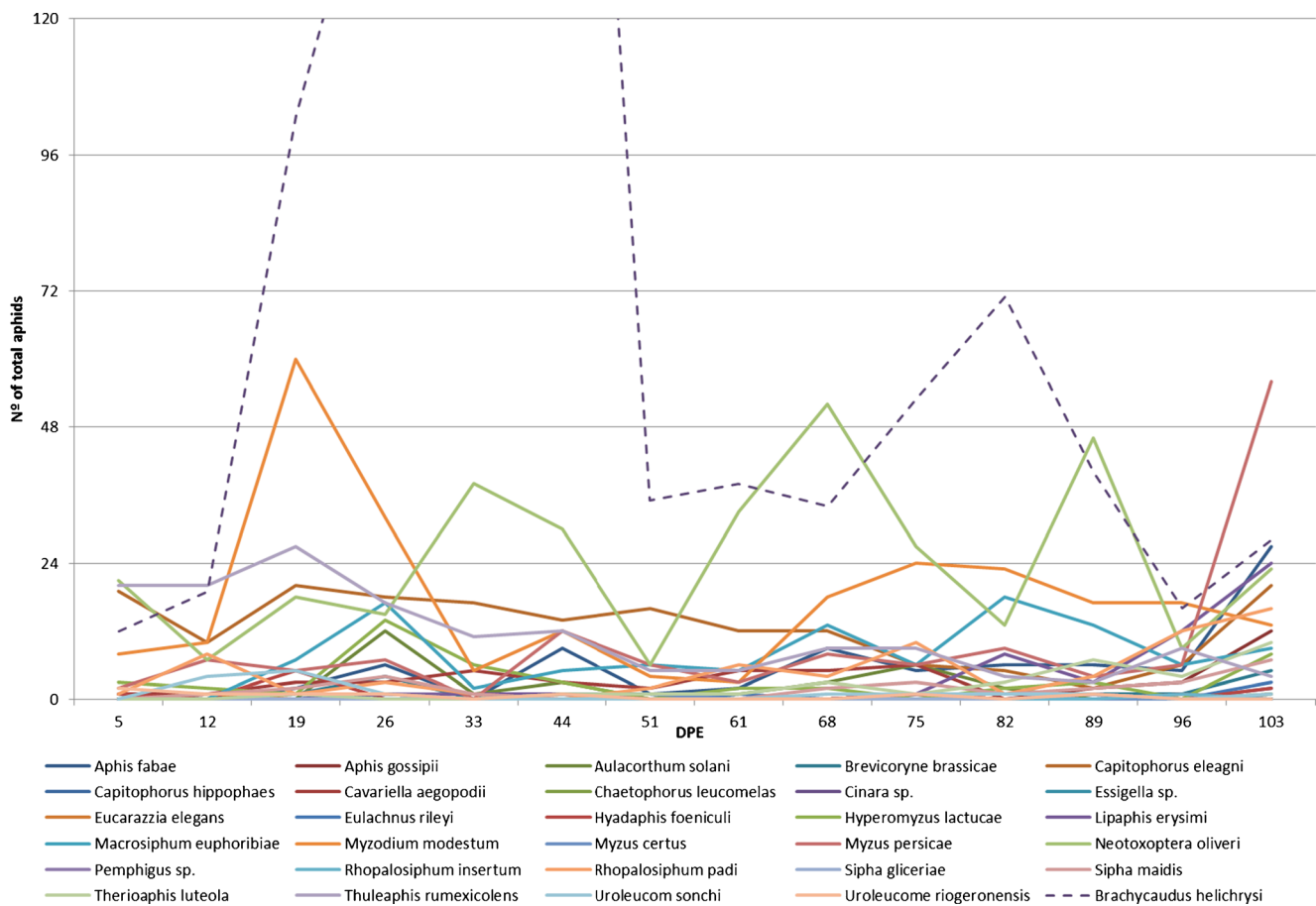
The results of our temporal analysis of viral disease spread suggest that the logistic model best describes DPCs of OYDV and LYSV epidemics in garlic crops in Mendoza, Argentina. This model may be appropriate for most plant disease epidemics where plant-to-plant spread occurs within crops. DPCs from the second year however did not exhibit the typical logistic shape. Their atypical shape may have been due to the rapid infection that took place that year, with more than 50 % of plants infected with OYDV by the second sampling date and more than 25 % infected with LYSV at the beginning of the cycle. These infection levels were in concordance with the abundance of aphids present at the beginning of the crop that year.

OYDV is reportedly spread by over 50 aphid species in a non-persistent manner (Diekmann 1997). Several aphid species have transmitted this virus experimentally (Drake et al. 1933), and may do so in the field when briefly probing in passing (none of them colonise *Allium* crops) (Bos 1976). The efficient spread of these viruses is due to the constant movements of the aphids in the area of cultivation. It is also important to note that garlic is a winter crop, constituting a source of attraction to aphids at a time when other feeding possibilities are reduced. The high numbers of aphids present

at the beginning of the crop cycle may explain the rapid increase in incidences of both viruses in the second year. Similar trends have been observed in potato virus Y (PVY) and other potyviruses that are transmitted by a wide variety of aphids in a non-persistent manner with relatively low vector specificity (Purcell and Almeida 2005).

The garlic crop in this study was visited by many aphid species: 19 in the first experimental year and 29 in the second year. Of the aphids identified in this work, five species, *Aphis gossypii*, *Brevicoryne brassicae*, *M. persicae*, *Rhopalosiphum padi* and *Uroleucon sonchi*, and two genera, *Chaitophorus* and *Macrosiphum*, have been cited as OYDV transmitters (Drake et al. 1933; El-Wahab 2009; Van Dijk 1993b; Ortego 1992). Four species, *A. gossypii*, *M. persicae*, *R. padi* and *U. sonchi*, and the genus *Hyperomyzus* have been reported as transmitters of LYSV (Van Dijk 1993b; Lunello et al. 2002; El-Wahab 2009). The most abundant species observed in both years belonged to the genera *Aphis*, *Myzus* and *Macrosiphum* which are considered the most important because of their polyphagous behaviours.

Random landings, the predominance of the dispersion instinct and the search for a host plant facilitate the transmission of plant viruses, especially to plants not colonised by a vector



**Fig. 3** Population dynamics of aphid species caught in four traps during the 2008 garlic crop cycle

species. In this way, even an inefficient vector can successfully spread a virus if it is common throughout the crop growing season. This success is because of the fact that a vector that colonises a crop immediately on arrival will not spread the virus as quickly as a species that moves from plant to plant

before settling and establishing a colony (Zitter and Simons 1980) or a non-colonising species that moves from plant to plant before leaving the field in search of a host plant. Despite being considered inefficient vectors and only present during the growing season, the species found in this study are capable of spreading viral diseases extremely successfully.

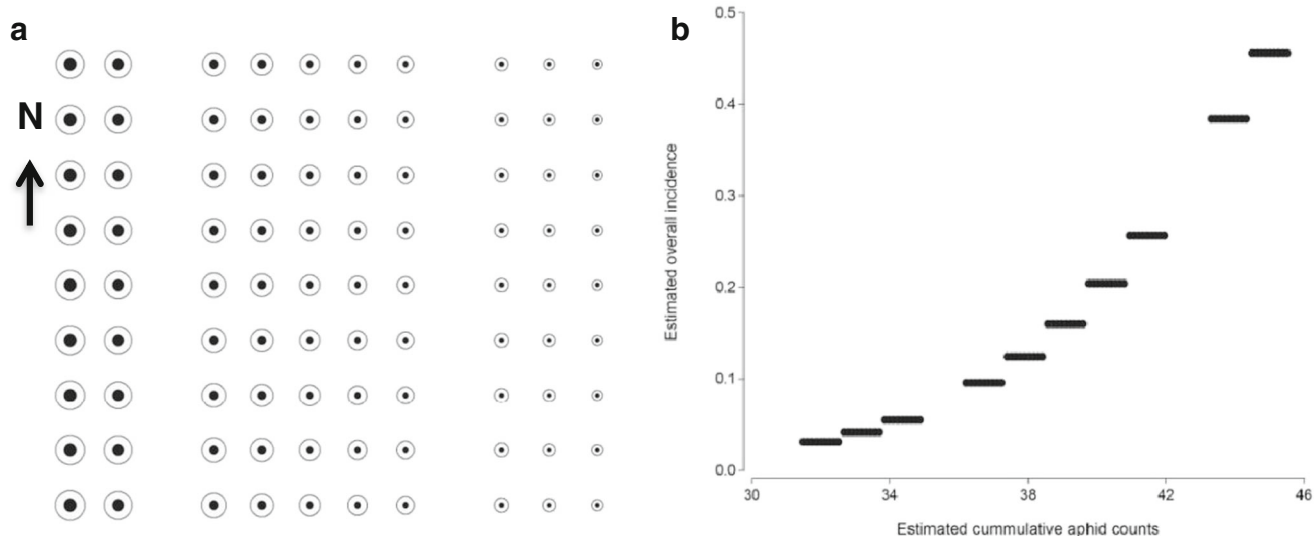
**Table 1** Linear correlation coefficients between estimated virus incidence and cumulative aphid counts in the experimental plot for each sample date

No of monitoring	Total	LYSV	OYDV
1	0.000	0.000	0.000
2	0.693	0.680	0.000
3	0.476	0.472	0.486
4	0.957	0.950	0.974
5	0.977	0.970	0.983
6	0.981	0.975	0.984
7	0.915	0.915	0.915
8	0.806	0.805	0.806
9	0.965	0.964	0.965
10	0.999	0.998	0.999

Notwithstanding the contribution of weather, the most abundant species present during our study—*H. foeniculi*, *M. euphorbiae* and *M. persicae* in the first year and *B. helichrysi*, *C. eleagni*, *Macrosiphum euphorbia*, *M. modestum* and *N. oliveri* in the second year—were not correlated with climatic variables. Their presence was instead related to surrounding crops serving as an aphid reservoir, such as rapeseed, weeds, other horticultural crops (squash, carrots, tomatoes and peppers), aromatics and poplar windbreaks.

Spatial analysis of our data revealed that both viruses and vectors were distributed along a west-to-east gradient. Considering the non-colonising nature of detected aphid species and the fact that the assay began with virus-free material, it is very likely that viruliferous winged aphids introduced the viruses from an external source. In studies of other crops and pathosystems, Moreno et al. (2007) and Robert et al. (2000)





**Fig. 4** Spatial analysis of viral incidence and aphid density for 2007. **(a)** Map representing cumulative viral incidence (*black circles*) and vector density (*white circle*) in the experimental plot. Ten rows with nine sampling points per row are shown. Black and white circle sizes are

proportional to incidence and density levels, respectively. **(b)** Scatter plot of virus incidence and aphid density based on sample position in the field on the fourth sampling date

reached similar conclusions about the role of transient aphid species in the spread of non-persistently transmitted viruses. Considering that many of the collected species were potential potyvirus vectors and that plots surrounding the trial were infected, the infection is likely to have come from these batches. Moreover, the gradients of both vector count and virus incidence within the plot were consistent with the west-to-east direction of the prevailing wind in Mendoza, the “Zonda”, which is a dry wind that comes from the Pacific Ocean and is warmed by its descent from the high crest of the Andes mountain range. In 90 % of cases, the Zonda windstorm occurs between May and November, with more than half of wind events recorded between May and August (autumn and winter). This phenomenon may explain the observed gradient from west to east, which is consistent with the wind direction. In this study, the periods in which the highest numbers of vectors were detected, September in the first year and July–August in the second, corresponded to times of the most intense winds.

The high viral incidence at the beginning of the second assayed year accelerated the progress of the disease, resulting in total infection of the plot. As suggested by Viteri and Gordillo (2009), this rapid infection may have occurred because the disease-free state is always sensitive to small perturbations (unstable), meaning that the introduction of a pathogen, even in small quantities, will start a disease outbreak. In agreement with Robert et al. (2000), who have stated that vegetative propagation has a marked impact on viral disease epidemiology, the initial level of crop infection plays a crucial role in aphid-borne virus spread. Taking into account these observations, the use of virus-free material is very important to

maintain low infection levels in vegetatively propagated species. To reduce yield losses, the use of measures that tend to delay viral disease introduction into plots is particularly important, because the larger the plant at the time of infection, the lower the damage and impact on yield. Our research suggests that OYDV and LYSV epidemics in Mendoza, the most important garlic growing region of Argentina, follow a logistic disease progression and are driven by aphid species spreading the viruses from west to east, the predominant wind direction. Total aphid population catches, rather than those of a single species or a combination of a few key species, may be considered as predictive for virus spread. This observation leads to recommendations of aphid control during highly windy periods and the use of barriers to limit vector spread.

To our knowledge, this study is the first to describe DPCs in garlic crops. Our study was possible only because we had obtained virus-free plants from meristem culture prior to the beginning of the experiment. The use of virus-free stock is critical, as such material is known to be a key yield determinant in crops that are exclusively vegetatively propagated. Our results also represent a valuable contribution for use in certified virus-free garlic seed bulb programmes.

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