

Modeling Temporal Trends in Aphid Vector Dispersal and Cucumber Mosaic Virus Epidemics in Snap Bean

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ABSTRACT Cucumber mosaic virus (CMV) has become a major limiting factor in snap bean production in the Great Lakes region of North America, and epidemics have occurred more frequently since the soybean aphid, *Aphis glycines* Matsumura, was introduced. Major aphid vectors of CMV epidemics were identified by statistically relating their temporal dispersal trends to the incidence of CMV. Alates were monitored weekly using water pan traps in 74 snap bean fields in New York and Pennsylvania from 2002 to 2006. Plants were tested for CMV by ELISA one time during late bloom in 2002 and 2003 and weekly over the season from 2004 to 2006. Principal vectors of CMV included *Acyrtosiphon pisum* (Harris), *A. glycines*, *Aphis gossypii* Glover, and *Therioaphis trifolii* (Monell). Among these, *A. glycines* and *T. trifolii* were likely responsible for severe CMV epidemics because they were among the most abundant species captured, they efficiently transmit CMV, and their dispersal activity was positively correlated with periods when CMV incidence was highest. Moreover, because high numbers of *A. glycines* and *T. trifolii* disperse during July and August, snap bean fields planted beyond late June are at risk for infection during early vegetative stages and are subsequently more at risk for yield loss. In contrast, plantings up to late June are less likely to become infected during early developmental stages and should escape yield loss because major vectors are dispersing infrequently. CMV-resistant or tolerant snap bean varieties should be planted after late June to reduce the risk of yield loss.

KEY WORDS *Acyrtosiphon pisum*, *Aphis glycines*, *Aphis gossypii*, *Therioaphis trifolii*, *Phaseolus vulgaris*

Snap bean, *Phaseolus vulgaris* L., is a major crop in the Great Lakes region of North America. Up to 70% of the processing snap bean acreage in the United States is concentrated in this area, with an estimated annual value of \$76 million since 2001 (NASS 2008). Snap bean fields are grown close to vegetable processing facilities and are harvested over a 2-mo period, typically beginning in mid-July. Processing demands that beans are delivered continuously to facilities during this period. Therefore, fields are sequentially planted from mid May through the end of July and harvested 55–65 d later.

Viruses have become a major limiting factor in snap bean production in the Great Lakes region. Since 2000, alfalfa mosaic virus, bean common mosaic virus, bean pod mottle virus, bean yellow mosaic virus, clover yellow mosaic virus, clover yellow vein virus (CLYVV), cucumber mosaic virus (CMV), tobacco streak virus, and white clover mosaic virus have been detected in snap bean fields (Grau et al. 2002, Larsen et al. 2002, Shah et al. 2006). Among these viruses, CLYVV and CMV significantly reduce yield and quality of snap bean (Taylor and Shail 2006, Larsen et al. 2008). CLYVV causes a disease called “chocolate pod,” in which pods become necrotic both internally and externally (Larsen et al. 2008), whereas CMV not only reduces the number of pods produced but can also distort their shape (Hall 1994). In both cases, pods are not suitable for processing.

CMV is the most prevalent virus detected in snap bean fields in the Great Lakes region (Larsen et al. 2002, Shah et al. 2006). In New York in 2005, up to 100% of plants in some snap bean fields were infected with CMV (Nault et al. 2006). The impact of CMV on snap

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bean yield can be severe, but depends substantially on variety (Taylor and Shail 2006), environmental conditions, and timing of infection relative to plant growth stage. Typically, infection during early vegetative stages will cause greater yield losses than infection initiated during reproductive stages (Walkey 1991, Jones et al. 2008). CMV is transmitted by aphids in a nonpersistent, stylet-borne manner (Nault 1997), and aggregated patterns of CMV-infected plants in New York snap bean fields have been consistent with aphid-initiated virus epidemics (Shah et al. 2005).

The most common species migrating into snap bean fields in New York were the pea aphid, *Acyrtosiphon pisum* (Harris), soybean aphid, *Aphis glycines* Matsumura, corn leaf aphid, *Rhopalosiphum maidis* (Fitch), and yellow clover aphid, *Therioaphis trifolii* (Monell) (Nault et al. 2004). *A. glycines* was first detected in Wisconsin in 2000, New York in 2001, and many other states and provinces in the Great Lakes region around this time (Losey et al. 2002, Ragsdale et al. 2004). Severe epidemics of CMV in Wisconsin and New York snap bean fields occurred concomitantly with the detection of *A. glycines* (Larsen et al. 2002). Consequently, *A. glycines* was surmised to be the principal vector of CMV epidemics. However, in New York, *A. glycines* was not detected in a season-long survey of snap bean fields in 2002, but on average, 41% of plants in these fields were infected with CMV (Nault et al. 2004, Shah et al. 2006). Also, >30 yr ago, a severe CMV epidemic in New York snap bean fields was attributed to a migration of viruliferous aphids, but the species responsible were not identified (Providenti 1976). Both observations indicate that aphid species other than *A. glycines* are also important vectors of CMV in snap bean fields.

Gildow et al. (2008) showed that *A. pisum*, *A. glycines*, *A. gossypii*, and *T. trifolii* could efficiently transmit legume strains of CMV from infected to noninfected snap bean plants. Other species such as the cowpea aphid, *Aphis craccivora* (Koch), bean aphid, *Aphis fabae* Scopoli, spirea aphid, *Aphis spiraeicola* (Patch), potato aphid, *Macrosiphum euphorbiae* (Thomas), green peach aphid, *Myzus persicae* (Sulzer), clover aphid, *Nearctaphis bakeri* (Cowen), and *R. maidis* were considered moderate to poor transmitters of CMV to snap bean.

Clearly, more research was needed to identify the major vectors of CMV, as well as their within-season dispersal patterns in snap bean fields in the Great Lakes area. This information is crucial for predicting future epidemics and developing management strategies. The primary objective of this study was to identify major aphid vectors associated with CMV epidemics in processing snap bean fields. Dispersal trends of potential vectors were examined to determine possible within-season periods of higher than average risk of CMV transmission to snap bean. Finally, the within-season temporal aspects of CMV incidence in snap bean were studied. Based on the findings, the period during the season when snap bean plantings are most at risk for yield loss from CMV infection was esti-

mated. The implications of CMV mitigation in snap bean are discussed.

Materials and Methods

Description of Fields. The study included 56 fields in western New York (12, 12, 8, 12, and 12 fields in each year from 2002 to 2006, respectively) and 18 fields in central Pennsylvania (6 in each year from 2004 to 2006). In New York, sampled fields were planted from 19 May through 29 July, whereas fields in Pennsylvania were planted between 14 June and 11 July. Sampling included 11 cultivars in New York, but nearly one half of the fields sampled were the cultivar 'Hystyle'. In Pennsylvania, 10 cultivars were represented across the sampled fields. The cultivars 'Soleil' and 'Masai' were the only ones common to both states among the sampled fields. Mean field size was \approx 14 ha (range, 3.8–38.5 ha), and fields typically bordered woods, sweet or field corn, wheat, other vegetable crops, and orchards.

Aphid Sampling and Identification. Alates were passively captured from the early trifoliate stages up to 7–10 d before harvest (\sim 6-wk period) using water-pan traps (described in the next paragraph). In New York in 2002 and 2003, nine water-pan traps were placed in a field such that three traps were positioned along each of two parallel field edges and three in the center of the field. In 2002 and 2003, aphid abundance and diversity were identical when estimated from traps located either in the center of the field or along field edges (Nault et al. 2004), indicating that traps did not need to be placed in both areas of the field. Subsequently, from 2004 to 2006, five traps were placed within the first 2 m of one edge of each field in New York and Pennsylvania. Traps were spaced a minimum of 7 m apart. Traps were distributed in a 2:1:2 (edge:middle:edge) pattern designed to sample most of the field.

Traps consisted of a 1.8-liter clear plastic container (Rubbermaid Commercial Products, Winchester, VA) fastened to a wire-framed supporter (Woodstock Gardens, Woodstock, IL). The supporter was anchored 20 cm deep into the ground. The top of the container was positioned 22 cm above the soil surface when plants were small and elevated to 44 cm shortly before the bloom stage. Containers were filled with 0.5-liter solution of water and propylene glycol (80:20); glycol broke the surface tension of the water, causing alates to sink to the bottom of the container. A snap bean plant was mimicked using a ceramic tile with a mottled green surface, which was placed in the bottom of the plastic container. The tile was 10.8 by 10.8 cm from the tile series Provence and the color was moss green (Jasba, Ötzingen, Germany). Solution in the container was changed weekly, and all alatae were extracted at that time, counted, and transferred to glass vials containing 70% ethyl alcohol. R. Eckel (RVWE Consulting, Frenchtown, NJ) identified all aphids captured in New York using keys by Smith et al. (1992) and Blackman and Eastop (1984); W. Sackett and A. Bachmann identified species collected in Pennsylvania using the same keys. Voucher specimens are located at the New

Table 1. Common aphid species captured in water pan traps in snap bean fields in New York from 2002 to 2006 and in Pennsylvania from 2004 to 2006

Species	New York ^a		Pennsylvania	
	Total	Percent of Total	Total	Percent of Total
<i>Therioaphis trifolii</i> (Monell)	2,274	30.4	535	40.0
<i>Aphis glycines</i> Matsumura	1,475	19.7	131	9.8
<i>Acyrtosiphon pisum</i> (Harris)	1,106	14.8	28	2.1
<i>Rhopalosiphum maidis</i> (Fitch)	685	9.2	75	5.6
<i>Pemphigus populicaulis</i> Fitch	239	3.2	0	0.0
<i>Aphis craccivora</i> Koch	179	2.4	123	9.2
<i>Aphis gossypii</i> Glover	130	1.7	201	15.0
<i>Hayhurstia atriplicis</i> (Linnaeus)	128	1.7	1	0.1
<i>Lipaphis erysimi</i> (Kaltenbach)	128	1.7	0	0.0
<i>Myzus persicae</i> (Sulzer)	97	1.3	26	1.9
<i>Capitophorus eleagni</i> (Del Guercia)	79	1.1	7	0.5
<i>Aphis</i> sp.	77	1.0	0	0.0
<i>Rhopalosiphum padi</i> (Linnaeus)	77	1.0	45	3.4
<i>Aphis fabae</i> Scopoli	15	0.2	14	1.0
<i>Anoecia</i> sp.	1	<0.1	14	1.0
<i>Brachycaudus persicae</i> (Passerini)	2	<0.1	15	1.1
Unknown	216	2.9	38	3.0
Others (74 species in NY; 33 species in PA) ^b	576	7.7	84	6.3
Total (90 species in NY; 46 species in PA) ^c	7,484	100	1,337	100

^a This list includes and expands on data published in Nault et al. (2004), which presented species captured in 2002 and 2003 only.

^b Other species include those representing <1% of total no. of aphids captured in snap bean crop.

^c Total no. of species from New York and Pennsylvania was 102.

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Estimation of CMV Incidence. Plants were sampled for CMV weekly from the early trifoliolate stages up to 7–10 d before harvest in 2004–2006. In 2002 and 2003, sampling was done only one time at the late-bloom stage. Plants within fields were sampled for CMV using a quadrat-based sampling approach (five plants per quadrat) as previously described (Shah et al. 2006). In 2002 and 2003, 16 quadrats were sampled per field (Shah et al. 2006), and 25 quadrats were sampled per field from 2004 to 2006. Foliar symptoms in snap bean are a poor indicator of CMV infection (Taylor and Shail 2006), so plants were tested using ELISA for the presence of CMV (Shah et al. 2006). Plants were tested either individually or in a group in which all five plants in a quadrat were pooled into one composite sample. When individual plants were tested, CMV incidence (proportion of sampled plants positive for CMV) was estimated by x/n , where x is the number of plants positive for CMV out of n tested by ELISA. When a group was tested, CMV incidence was estimated by

$$p = 1 - (1 - p_q)^{1/v} \quad [1]$$

where p is the estimate of CMV incidence, p_q is the proportion of quadrats positive for CMV, and $v = 3.903$ to account for the aggregation of infected plants within quadrats (Shah et al. 2005). In general, group testing was used from 2004 onward during periods when CMV incidence was expected to be low.

Association Between CMV Incidence and Principal Vector Species. Expanding on the approach taken by Raccach et al. (1988), a mixed model approach was

used to fit a basic equation linking CMV incidence to cumulative aphid counts per trap:

$$\text{logit}(y) = \beta_0 + \beta_1 X_1 + \dots + \beta_n X_n \quad [2]$$

In equation 2, y is the incidence of plants with CMV at some time t , and X_a is the natural logarithm of the cumulative number of aphids per trap + 1 for aphid species a , up to and including time t . Raccach et al. (1988) modeled y as a function of X_a at $t - 7$ because their aphid trap counts were assessed daily, and virus incidence was monitored three times per week. The resolution of these data was coarse in comparison (weekly virus assays and aphid counts), and therefore, a latent period was not explicitly included in the model. In beans, CMV is serologically detectable within 7 d of inoculation (Davis and Hampton 1986). Note also that the proportion of viruliferous alates was unknown and was incorporated into the parameter estimates. A two-step approach was taken to fitting equation 2. In the first step, equation 2 was fit using a generalized linear mixed model, coded in SAS PROC GLIMMIX (SAS 2003, Littell et al. 2006), in which field, cultivar, and year were random effects and in which a binomial distribution was specified for CMV incidence. A RANDOM_RESIDUAL_statement was also used to address overdispersion. Only aphid species that constituted $\geq 5\%$ of the total aphid count in either New York or Pennsylvania (Table 1) were considered. Thus, equation 2 was fit to a maximum of six species. This first step identified possible associations between CMV incidence and aphid species, based on a t statistic for the significance ($P < 0.05$) of the estimated β parameters not being zero. Using this approach, the species identified as significant contrib-

utors to CMV incidence were *A. pisum*, *A. glycines*, *A. gossypii*, and *T. trifolii*.

Aphis glycines alates were not trapped in all snap bean fields that tested positive for CMV (Nault et al. 2004, Shah et al. 2006). This observation motivated a second modeling step, in which equation 2 was fit to the data as described above but limited to the four aphid species identified in step 1. An indicator variable i was used to obtain separate parameter estimates representing the situations in which (a) *A. glycines* was present and (b) *A. glycines* was absent. This scenario mimicked conditions before and after the establishment of *A. glycines* in the United States.

Temporal Trends in Principal Vector Dispersal.

The next step was to elucidate possible trends in the dispersal activity of the four main vectors. The main problem with this analysis was the large variability in trap counts both within season and across years, including a large number of occasions in which no alatae of a given species were trapped. Data were analyzed with generalized additive models (Hastie and Tibshirani 1990). For each species, counts per trap were standardized to a Gaussian distribution (0, 1) within each year-state combination (e.g., Pennsylvania in 2005). A semiparametric generalized additive model was fit to the standardized counts per trap (y_i^N) as a function of calendar day (d_i), where the subscript i indexes the data point and the superscript N is used to indicate these are standardized data. The model was specified using PROC GAM in SAS. Year and state were included as categorical parametric explanatory variables, and a smoothing spline was used to non-parametrically model y_i^N as a function of d_i . The process was repeated with degrees of freedom (df) ranging from 3 to 6, representing different levels of smoothing.

The smoothed curves can be represented by

$$y_i^N = s(d_i, \lambda) + e_i \quad [3]$$

where $s(\cdot)$ is the smoothing function representing the trend, and e_i is the residual caused by short-term variation. Here λ is the amount of smoothing, represented by df. Equation 3 was fit by a smoothing spline with $df = 4$. The residuals e_i were subtracted from the raw y_i^N values to give the deseasonalized data [i.e., $s(d_i, \lambda = 4) = y_i^N - e_i$]. The value $s(d_i, \lambda)$, which represented the trends, was fit parametrically to a cubic polynomial

$$s(d_i, \lambda) = \beta_0 + \beta_1 d_i + \beta_2 d_i^2 + \beta_3 d_i^3 + \varepsilon_i \quad [4]$$

Equation 4 was fit to each of the four aphid species using PROC GLIMMIX in SAS, with field, cultivar, and year included as random effects.

Note that $s(d_i, \lambda)$ fluctuates about $s(d_i, \lambda) = 0$. The times when $s(d_i, \lambda) < 0$ are indicative of lower than average dispersal activity for the given species. The converse situation $s(d_i, \lambda) > 0$ is indicative of dispersal activity higher than average and thereby identify periods at higher risk to CMV infection. The parameterized version of equation 4 was used to calculate the points (d_0) along the calendar day-axis at which $s(d_i, \lambda) = 0$.

CMV Incidence and Variability Among Plantings.

The maximum observed CMV incidence among early-season (19 May to 7 June; $n_1 = 20$), mid-season (8 June to 18 July; $n_2 = 39$), and late-season (19–29 July; $n_3 = 15$) fields was used as the basis of comparisons of the different planting periods. Preliminary plots made it obvious that the analysis should account for the heterogeneity in CMV across the three defined seasonal periods. A generalized mixed modeling approach was taken analogous to the environmental variance model for means (equation 6 in Piepho 1999). The model formulation specified a conditional binomial distribution for CMV incidence. Planting period (early, mid- or late season; analogous to genotype in Piepho 1999) was specified as a fixed effect, and field ($n = \sum_{i=1}^3 n_i = 74$) was considered a random effect (analogous to environment in Piepho 1999). This model fits separate variances for each of the three planting periods. A lower variance indicates less variability in CMV incidence within the planting period. The environmental variance model was expanded by specifying snap bean cultivar as an additional random effect.

Another approach was to dichotomize the maximum percent CMV per field. Let x_t be some threshold percent CMV. A new binary variable CMV_b was created according to the following rule. If maximum CMV (%) $> x_t$, then $CMV_b = 1$; otherwise $CMV_b = 0$. This new binary variable CMV_b was analyzed by a random intercepts logistic regression, in which field was the random effect and planting period was the fixed effect. Odds ratios were estimated using the odds ($CMV_b > x_t$) in the early season as the baseline. The above models were fit using PROC GLIMMIX in SAS.

Temporal Increase of CMV Incidence Within Plantings.

A Gompertz model was used to study the temporal trends in CMV incidence, using data from fields in which CMV was detected and in which virus assays had been done multiple times (i.e., fields from 2004 onward). The Gompertz model was chosen over the logistic because it offers more flexibility in shape (Madden et al. 2007). The data were fit to a nonlinear mixed model extension (Vonesh and Chinchilli 2006) of the Gompertz using PROC NL MIXED in SAS:

$$y_{ij} = \exp\{-B \exp[-(r + \mu_i)t_{ij}]\} + e_{ij} \quad [5]$$

In equation 5, y_{ij} is the incidence of CMV in the i th field at the j th assay time, and t_{ij} is the number of days from planting. The parameter $B = -\ln(y_0)$, where y_0 is the initial incidence of CMV at $t = 0$. The $r = [r_e, r_m, r_l]$ are fixed-effect rate parameters corresponding to the three different planting periods (early, mid, and late), respectively. The μ_i are random effect parameters, which are assumed to be independent, identically distributed (iid) Normal(0, σ^2_μ). The e_{ij} are residual errors, which are assumed to be iid Normal(0, σ^2_e) and independent of the μ_i . The conditional distribution of the y_{ij} was binomial(n, p), and the random effects μ_i were set to vary with each field by specifying field as a subject in the RANDOM statement of the NL MIXED procedure. Fitting equation 5 requires an estimate for y_0 . In principle, $y_0 = 0$, assuming initial

Table 2. Fitted fixed-effect parameter estimates describing the association between cucumber mosaic virus incidence and cumulative aphid counts in snap bean fields

Scenario ^a	Aphid species	Estimate	SE	df ^b	P value ^c
<i>A. glycines</i> absent	β_0	-9.2699	1.6469	6.9	0.0008
	<i>A. gossypii</i>	8.4302	2.5458	292.4	0.0010
	<i>A. pisum</i>	1.3043	0.5892	225	0.0279
	<i>T. trifolii</i>	1.0067	0.6827	55.4	0.1460
<i>A. glycines</i> present	β_0	-10.2803	1.5940	6.2	0.0006
	<i>A. glycines</i>	3.7092	0.3952	338	<0.0001
	<i>A. pisum</i>	0.1580	0.3874	273.2	0.6837
	<i>T. trifolii</i>	3.1943	0.5162	270.9	<0.0001

^a See equation 2. Separate parameters were estimated for the situation where (1) *A. glycines* was present and (2) *A. glycines* was absent in the cumulative no. per trap up to time *t*.

^b The denominator df estimated by the Kenward-Roger option, i.e., $ddf_{kr} = kr$.

^c The two-tailed *P* value for the *t* statistic with the associated degrees of freedom. The *t* statistic is the estimate divided by its SE.

CMV infection is caused solely by the influx of viruliferous alates. As a practical estimate, $y_0 = 0.0001$ was used.

Results

Aphid Species Identified. Nearly 9,000 alatae and 102 species were captured in snap bean fields in New York (90 species) and Pennsylvania (46 species) during this 5-yr study. Species representing 1% or more of the total are listed in Table 1. *T. trifolii* was the dominant species captured in both states, whereas *A. glycines* was the second most common species collected in New York and the third most common in Pennsylvania.

Association Between CMV Incidence and Principal Vector Species. Fitting of equation 2 was restricted to counts of aphid species constituting $\geq 5\%$ of the total aphid count in either New York or Pennsylvania, under the assumption that CMV epidemics have been highly associated with species that were most numerous. The association between CMV incidence and aphid counts also possibly depends on CMV transmission efficiency (Gildow et al. 2008) and the proportion of viruliferous aphids (Madden et al. 2000), but these two factors were not explicitly included in fitting equation 2. Aphid species were kept or discarded from the model based on the log-likelihood, tests of significance, and sign of the estimated parameters, leading to a final model with four aphid species. The fixed-effect fitted parameters are shown in Table 2. The best linear unbiased predictors of CMV incidences were close to actual CMV values (Fig. 1). In the absence of *A. glycines*, the species most associated with CMV incidence were *A. gossypii* and *A. pisum*. Although the estimated β parameter for *T. trifolii* was slightly >1 , it was not statistically >0 . When *A. glycines* was present, both *A. glycines* and *T. trifolii* were positively associated with CMV incidence. Most of the highest levels of CMV (e.g., $>80\%$) were observed in snap bean fields where *A. glycines* was present (Fig. 1).

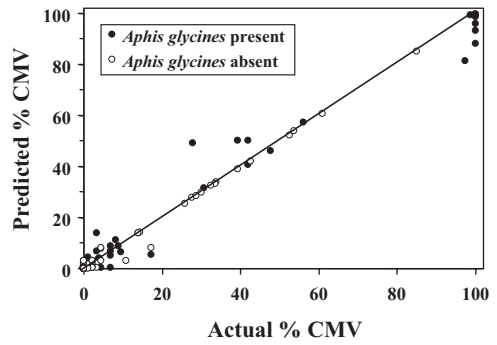


Fig. 1. Actual and predicted incidence of plants with CMV where predicted CMV incidence was estimated from the parameterized version of equation 2 and the cumulative counts per trap of *A. pisum*, *A. glycines*, *A. gossypii*, and *T. trifolii*.

Temporal Trends in Principal Vector Dispersal. Dispersal activity of the principal vectors was greatest during the second half of the season for all species, except *A. pisum* (Figs. 2A and B and 3A-F). The generalized additive models indicated that year and state were not statistically significant contributors ($P > 0.5$), and therefore, these two variables were removed from the models. Smoothing splines with $df = 4$ plus the associated smoothing component plots indicated significant nonlinear trends ($P < 0.05$ for all four aphid species) in y^N_t over time. Smoothing component plots produced when higher *df* were specified for the smoothing spline began to show the within- and across-season variations, making it more difficult

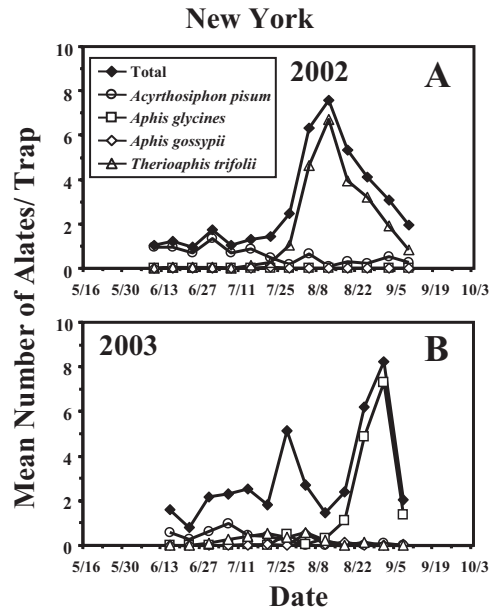


Fig. 2. Mean number of *A. pisum*, *A. glycines*, *A. gossypii*, and *T. trifolii* alates captured per trap in snap bean fields in New York in (A) 2002 and (B) 2003. Means of each sampling date represents four to six fields.

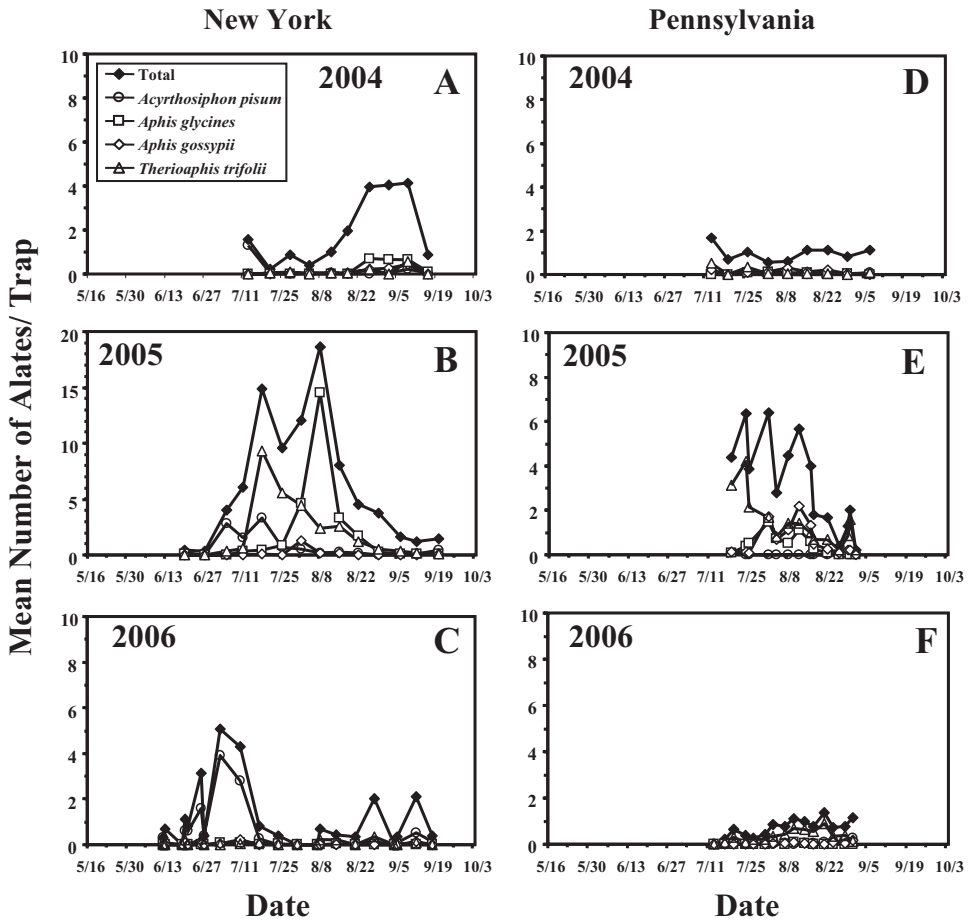


Fig. 3. Mean number of *A. pisum*, *A. glycines*, *A. gossypii*, and *T. trifolii* alates per trap captured in snap bean fields in New York and Pennsylvania in 2004 (A and D), 2005 (B and E), and 2006 (C and F). Means on each sampling date represents four to six fields. Note: the scale of the y -axis in B is twice that shown in the other figures.

to identify trends. The polynomials resulting from fitting equation 4 to the deseasonalized data $s(d_i, \lambda)$, depicting the trends in dispersal activity for each species are shown in Fig. 4A.

Periods of higher than average dispersal activity, based on the fitted polynomials, are represented in Fig. 4B. Dispersal activity of *A. pisum* was higher than average during 28 May to 6 August; a secondary period of higher than average activity also occurred after 9 September. The other three aphid species exhibited higher than average dispersal during mid- to late season: *T. trifolii* from 3 July to 11 September; *A. glycines* from 1 August to 5 September; *A. gossypii* from 23 July to 19 September. Estimated peaks in dispersal activity for *A. pisum*, *T. trifolii*, *A. glycines*, and *A. gossypii* were 25 June, 2 August, 20 August, and 24 August, respectively. Relatively low dispersal activity of the principal CMV vectors early in the season (i.e., May through late June) suggests that snap bean is less at risk for CMV infection (Fig. 4B) unless *A. pisum* dispersal activity is high. In contrast, the increased dispersal activity of vector species during the latter part of the season

highlighted a greater risk of CMV infection during the mid- and late-season plantings (Fig. 4B).

CMV Incidence and Variability Among Plantings. The maximum observed percent CMV varied considerably across years and among planting periods within years (Table 3), ranging from 0 to 100% of sampled plants per field testing positive for CMV (Fig. 5). Statistically significant differences among planting periods were observed in 2002 and 2004 (Table 3). The general trend was an increase in variability in percent CMV per field as mean percent CMV increased. The overall trend (2002–2006) was toward higher mean levels of CMV per field as one progressed from early- to late-season plantings. However, the variance in percent CMV per field also increased as well (Table 3; Fig. 5), and it was not possible to discern a significant trend in mean CMV across planting periods.

There was a tendency for CMV incidence to be higher in fields planted mid- or late season than early season (Fig. 6). Consider first when a threshold $x_t = 0$ was used to dichotomize percent CMV per field. Notice that in Fig. 6 at $x_t = 0$, the odds ratios are <1 .

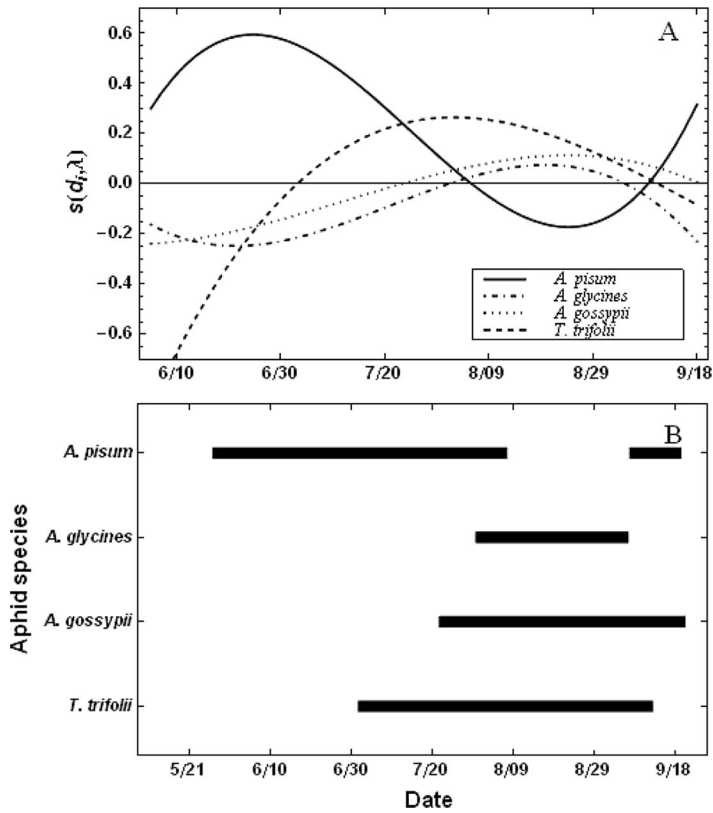


Fig. 4. (A) Long-term trends in aphid dispersal activity in New York and Pennsylvania snap bean fields during the growing season. Aphid counts per trap were standardized within year-state and deseasonalized (equation 3) to give the $s(d_i, \lambda)$ values. The curves for each species were generated by fitting equation 4 to $s(d_i, \lambda)$. Fitted parameter estimates [species, β_0 , β_1 , β_2 , β_3] were [*A. pisum*, -55.2635, 0.8500, -0.00424, 6.896×10^{-6}], [*T. trifolii*, -27.0131, 0.3326, -0.00132, 1.689×10^{-6}], [*A. glycines*, 23.0051, -0.3607, 0.001834, -3.04×10^{-6}], and [*A. gossypii*, 7.0406, -0.1231, 0.000671, -1.16×10^{-6}]. (B) The horizontal bars represent periods during the growing season when dispersal activity for the aphid species is higher than average [by solving for d when $s(d_i, \lambda) = 0$ in equation 4], indicating periods of elevated risk for CMV infection.

This means that the odds of a field having some level of CMV were higher in early-planted fields than mid- or late-planted fields. However, between $x_t = 25$ or 30 and $x_t = 40$, the odds ratios became >1 , indicating that the odds of mid- and late-planted fields having $>x_t$ percent plants infected by CMV were higher than the

same odds for early-planted fields. Thus, mid- and late-planted fields were more likely to have more severe (>25 – 30% plants infected) epidemics of CMV than early-planted fields. For example, late-planted fields were six times more likely to have CMV in excess of 40% than early-planted fields (Fig. 6).

Table 3. Mean percent of snap bean plants positive for cucumber mosaic virus in fields in New York and Pennsylvania, in relation to planting period, and restricted max likelihood (REML) estimates for the variance-covariance structure^a

Year	Cultivar	Planting period						P value ^c
		Variance estimate			CMV (%) ^b			
		Early	Middle	Late	Early	Middle	Late	
2002	0.18 (0.13)	0.55 (0.55)	12.03 (8.62)	NA	27.3 (6)	54.3 (5)	53.6 (1)	0.0117
2003	0 (0.20)	21.73 (12.50)	4.97 (2.83)	NA	15.7 (6)	4.6 (6)	NA	0.0742
2004	3.13 (2.44)	NA	0.49 (0.41)	21.05 (13.21)	NA	0.9 (8)	9.3 (6)	0.0222
2005	73.49 (.)	31.86 (.)	0 (.)	0 (.)	12.2 (4)	40.0 (10)	100 (4)	0.0823
2006	5.08 (3.28)	2.49 (2.17)	0.67 (0.42)	1.04 (0.73)	5.1 (4)	1.2 (10)	0.3 (4)	0.3152
All years	0.46 (0.44)	17.42 (5.98)	55.01 (13.61)	92.43 (33.70)	16.3 (20)	18.4 (39)	34.0 (15)	0.2303

^a An environmental variance model for means was fit (Piepho 1999) in which planting period was a fixed effect and field was a random (environmental) effect. Cultivar was added as an additional random effect. SEs of the variance estimates are shown in parentheses.

^b Mean percent of CMV-infected plants per field. The no. of fields is shown in brackets.

^c P value is for a test of differences among the planting periods in terms of mean CMV.

NA, not applicable.

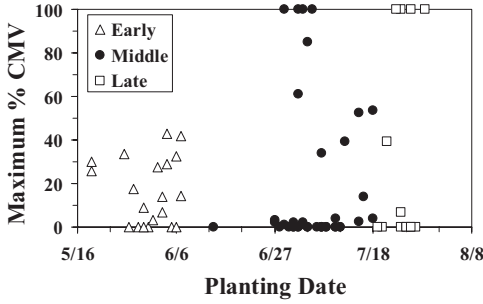


Fig. 5. Maximum incidence of CMV relative to planting date in 74 snap bean fields sampled during 2002–2006.

Temporal Increase of CMV Incidence Within Plantings. Timing of CMV infection within a planting period also varied considerably within year (Fig. 7A–C). In 2004 and 2006, CMV was not detected in fields until the crop was producing pods, and infection levels never exceeded 5, 3, and 14% in early-, middle-, and late-planted fields, respectively (Fig. 7A–C).

In early-planted fields in 2005, CMV was not detected until late in the crop’s development and only reached 12% infected plants (Fig. 7A). In contrast, all fields planted in the middle and late part of the 2005 season had 100% of the plants infected with CMV (Fig. 7B and C). Percent infection levels as high as 80 and 100% were reached during early trifoliolate stages in middle and late plantings, respectively (Fig. 7B and C).

Equation 5 was fit to the temporal data for 20 fields representing each of the three planting periods. The random effects μ_i were included for r_m and r_l but were set to 0 for r_e because preliminary model fitting indicated that the variance of the random effects for r_e approached zero. This approach also allowed model convergence. The estimates for r plus the associated

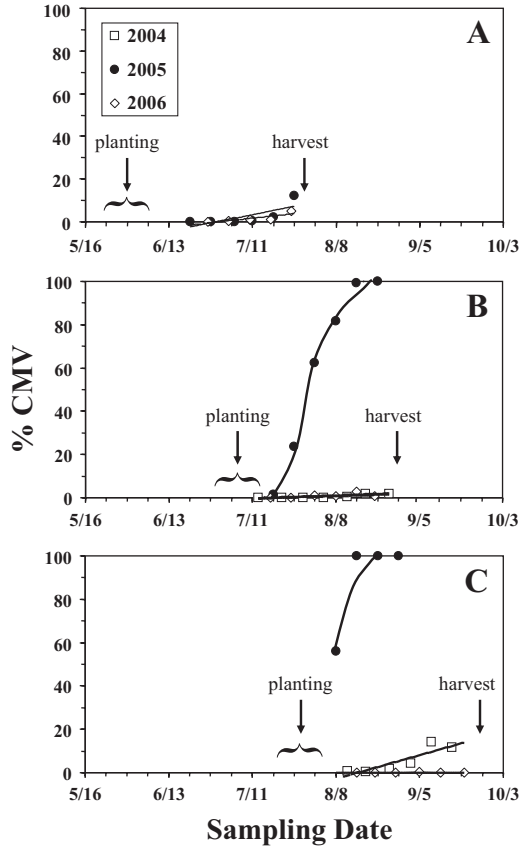


Fig. 7. Mean percent of snap bean plants with CMV in (A) early-planted, (B) middle-planted, and (C) late-planted snap bean fields in New York ($n = 4$ fields/yr).

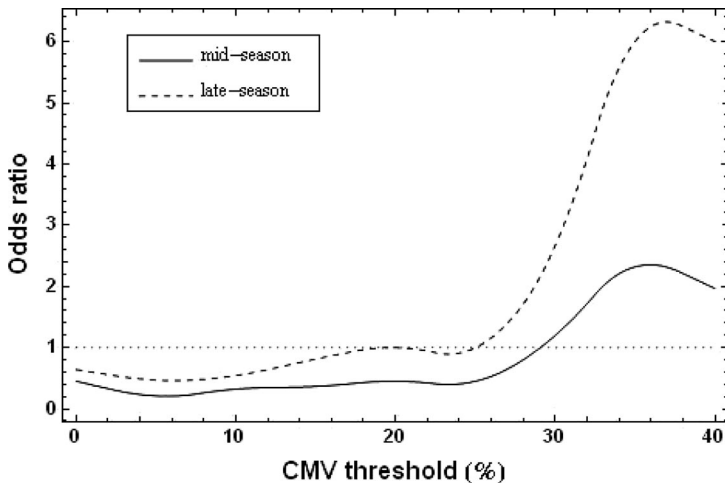


Fig. 6. Smoothed plots of the odds ratio for the odds of CMV exceeding a given threshold percent in mid- and late-season fields compared with the same odds in early-season fields. The odds ratios were estimated from a random intercepts logistic regression of a binary variable CMV_b representing whether percent CMV was above ($CMV_b = 1$) a specified threshold level or not ($CMV_b = 0$).

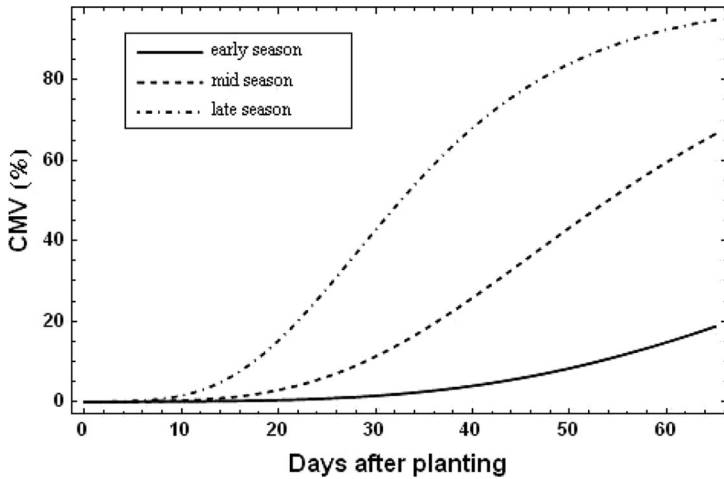


Fig. 8. Mean percent of plants positive for CMV in early-, mid-, and late-season fields, based on the fit of the data to a nonlinear mixed model Gompertz equation (equation 5).

SEs (in parentheses) were $r_e = 0.026$ (0.008), $r_m = 0.048$ (0.017), and $r_l = 0.079$ (0.024). The estimate for σ^2_μ was 0.002 (SE = 0.001). The fitted mean temporal progress of CMV incidence for each of the planting periods is shown in Fig. 8. Epidemics of CMV increased at higher rates and reached higher final mean incidences as the season progressed from early through mid- to late plantings. Assuming the end of the vegetative period (beginning of bloom) occurs roughly at 30 d after planting, the model-fitted results at 30 d indicated mean incidences (plus 95% confidence intervals) of plants infected by CMV of 1.5 (0–4.7), 11.3 (0–37.3), and 42.7% (0–96.7%) in early-, mid-, and late-planted fields, respectively.

Virus infection early in plant development is more likely to cause yield loss than when infection occurs during reproductive stages (Walkey 1991, Jones et al. 2008). Thus, our results suggest that snap bean fields planted beyond 27 June (approximate planting date in which high levels of CMV incidence occurred during middle-planting period) are at greater risk for becoming infected with high levels of CMV during early plant growth, which can cause significant yield loss. In contrast, fields planted up to 27 June were not likely to become infected with CMV, at least not until late in their development. A risk model for likelihood of yield loss from CMV was developed from this information (Fig. 9).

Discussion

Since the arrival of *A. glycines* in 2000–2001 (Losey et al. 2002, Ragsdale et al. 2004), CMV epidemics have become more frequent and severe in the Great Lakes region. *A. glycines* was identified as a significant vector of CMV in snap bean fields along with *A. gossypii*, *A. pisum*, and *T. trifolii*. Among these four species, *A. glycines* and *T. trifolii* were likely responsible for the most severe CMV epidemics. These two species were among the most commonly captured aphids in snap

bean fields, they efficiently transmit CMV to snap bean, and their dispersal activity was positively correlated with periods when CMV prevalence was the greatest, often during early phenological stages.

Aphis glycines uses soybean, *Glycine max* L., as its summer host, whereas *T. trifolii* reproduces on various legume hosts such as alfalfa, *Medicago sativa* L., red clover, *Trifolium pratense* L., and white clover, *Trifolium repens* L. Soybean and alfalfa are two of the most widely grown crops in western New York and Pennsylvania. Despite the relatedness of snap bean, soybean, and alfalfa, the major CMV vectors do not survive well on snap bean. Therefore, the major vectors can be considered as noncolonizing species, which are often responsible for virus epidemics (Halbert et al. 1981, Raccach et al. 1985, Irwin 1994).

Acyrtosiphon pisum and *A. gossypii* were primarily responsible for spreading CMV in snap bean fields when *A. glycines* was absent. When early-planted fields were infected with CMV, *A. pisum* was likely the principal vector because it tended to disperse earlier in the season than *A. gossypii*. CMV levels in these fields were predicted to be generally low, with infec-

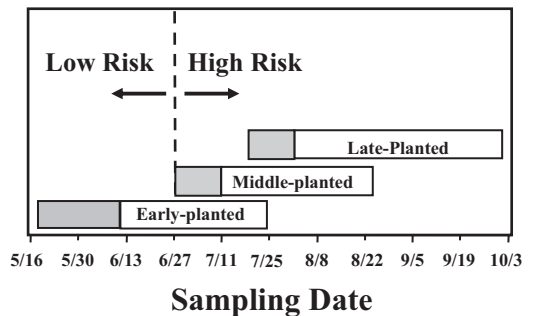


Fig. 9. Planting periods in which the potential risk of yield loss from CMV in snap bean fields is estimated to be either low or high.

tion not occurring until later in the crop's development. Perhaps, CMV incidence observed in early-planted snap bean fields in New York in 2002, when *A. glycines* was absent, was caused largely by *A. pisum*. In mid-season and late-planted snap bean fields, *A. gossypii* likely would be responsible for low levels of CMV infection in fields because it dispersed more frequently than *A. pisum* in July and August.

In snap bean fields where *A. glycines* was present, CMV was detected at high levels and spread by both *A. glycines* and *T. trifolii*. In 2005, all eight fields planted from mid- to late season had 100% of the plants in the field infected with CMV. *A. glycines* and *T. trifolii* alates were dispersing in high numbers during early vegetative stages in those fields. Because dispersal of these two vectors occur in July and August, snap bean fields planted beyond late June are at risk for infection during early trifoliolate stages and are subsequently at risk for yield loss. In contrast, plantings up to late June are less likely to become infected during early developmental stages and should escape yield loss because these vectors are dispersing infrequently.

Despite the common relative abundance of *T. trifolii* and *A. glycines* in Pennsylvania snap bean fields, trap-catch densities were consistently lower and CMV was not detected in the surveys. Perhaps, a difference exists between agroecosystems in New York and Pennsylvania. For example, the size of the CMV reservoir in the landscape may differ between the two. Alfalfa is a host for CMV and it dominates the landscape in western New York more so than in central Pennsylvania. Shah et al. (2006) reported that 57% of alfalfa fields in western New York were infected with CMV at levels averaging 28% plants infected (range, 5–72.5%). Another possibility to explain the difference could be intensity of major vector dispersal. In New York snap bean fields in 2005, peak numbers of *A. glycines* and *T. trifolii* alates captured in traps were 14.6 and 9.3 per week, respectively; 100% of plants in these fields were infected with CMV. In Pennsylvania snap bean fields in 2005, peak numbers of *A. glycines* and *T. trifolii* were only 1.5 and 4.2 per trap per week. More research is needed in snap bean producing states to identify the factor or factors responsible for CMV epidemics in some regions and not in others.

Management Implications. Based on the CMV risk model shown in Fig. 9, snap bean fields planted before late June (27 June) are at low risk for yield loss from CMV. In contrast, plantings beyond 27 June are at risk for substantial loss from CMV in some years. Management of CMV, the major vectors, or both, should focus on these later plantings.

Control of the Vector. Developing strategies to control vectors of viruses transmitted in a nonpersistent, stylet-borne manner is difficult and often more complicated than controlling the virus using virus-resistant cultivars. In many cases, however, virus-resistant cultivars are not available, and vegetable growers are left with trying to manage the vector. This is the case for snap bean; no CMV-resistant cultivars are commercially available.

Using insecticides to control major vectors of CMV to reduce virus spread in snap bean has been unsuccessful. In New York, systemic insecticides applied to kill vectors in an attempt to reduce CMV in snap bean plantings failed (Nault and Taylor 2003). The percentage of snap bean plants infected with CMV that were grown from seed treated with either imidacloprid (Gaucho 480) or thiamethoxam (Cruiser 5FS) was 55 and 48, respectively, whereas 51% of the plants in the untreated control were infected with CMV. Foliar sprays of insecticides also did not reduce CMV levels in snap bean field trials in Wisconsin (Wyman and Chapman 2004).

Escaping the major vectors in space or time to reduce CMV levels in snap bean is not feasible in our production system. Snap bean fields planted at least 1 km away from CMV-infected alfalfa fields did not reduce the number of major vectors migrating into the fields or levels of CMV in these fields (Nault et al. 2004, Shah et al. 2006). Separation in space between snap bean fields and sources of CMV like alfalfa at distances much further than 1 km could reduce CMV infection. However, such an approach would be difficult in western New York and other snap bean-producing areas in the Great Lakes because alfalfa is a dominant crop in the landscape. Moreover, other sources of CMV undoubtedly exist, and their role in CMV epidemics in snap bean is not known. CMV epidemics in snap bean could be avoided in time if all fields were planted early in the season, when *A. glycines* and *T. trifolii* are not dispersing into snap bean fields. Unfortunately, this approach is not logistically feasible because processing facilities must receive beans throughout the entire growing season.

Placing barrier crops around or within the main crop has been successful in managing nonpersistently aphid-transmitted viruses (Hooks and Fereres 2006). Arranging barrier crops along the periphery of snap bean fields to either impede vector colonization or intercept major vectors before they spread CMV into snap bean fields is unlikely to work in our system. For this strategy to be effective, major vectors must initially colonize snap bean fields from the field edge. A nonhost for CMV could be planted along the field edge where viruliferous aphids would probe the leaf surface and purge their stylets of the virus, thereby minimizing the risk of infection to snap bean. In New York snap bean fields in 2002 and 2003, *A. glycines* and *T. trifolii* alates were captured equally within field centers and field edges (Nault et al. 2004). Thus, the absence of an edge effect in this colonization pattern precludes pursuing this management strategy.

Positioning a barrier crop within legume fields has reduced levels of nonpersistently aphid-transmitted viruses such as bean yellow mosaic virus (BYMV) and CMV (Jones 1993, 1994; Bwye et al. 1999). In these examples, the main crop, lupins, had lower levels of virus infection in treatments that had either a higher plant density or straw mulch between rows. The mechanism responsible for the success of these strategies was camouflaging the crop from the vector. Aphids rely on a visual contrast between plant foliage

and the soil background to locate their host (Kennedy et al. 1961), so an increase in vegetative cover in the field will reduce numbers of aphids that will alight (Halbert and Irwin 1981). In our snap bean system, growers are averse to increasing plant density within fields because this decreases air movement within the snap bean canopy and creates conditions conducive for outbreaks of white mold and gray mold (Steadman 1983). Placing straw mulch in between rows is neither practical nor economical given the cost of straw mulch and the relatively large field sizes (mean size around 14 ha). No-till snap bean could be effective in reducing CMV as long as the cover crop remained alive until several weeks after the snap bean crop was established, thereby maintaining a high vegetative density to soil background ratio.

Biological control of vectors within snap bean fields is unlikely to impact virus levels because biological control organisms cannot kill the vector before it transmits the virus, which only takes seconds. However, areawide control or suppression of *A. glycines* in soybean fields at the agroecosystem scale could reduce the threat of CMV epidemics in snap bean. For example, soybean cultivars containing the *Rag-1* gene (Hill et al. 2006), which confers resistance to *A. glycines*, could be adopted throughout the Great Lakes region and beyond. Lower population levels of *A. glycines* in soybean would likely result, leading to smaller subsequent summer emigrations into snap bean fields. Because aphids are notorious for developing resistance to crops in which resistance is mediated by a single gene (Smith 2005), soybean lines with either multigenic resistance, cultivars with resistance mediated by different single genes, or both would be important for long-term suppression of soybean aphid. Management of *T. trifolii* in alfalfa at the agroecosystem scale is not likely because *T. trifolii* is not considered a pest of alfalfa. Thus, deployment of aphid-resistant alfalfa is unlikely. Moreover, most alfalfa growers do not grow snap bean and therefore have no incentive to protect neighboring snap bean fields from viruses.

Interfering with the vectors' ability to find snap bean or transmit CMV after alighting on snap bean is neither logistically nor economically feasible. Strategies such as reflective mulches, row covers, and foliar applications of mineral oils have been used successfully in some vegetable cropping systems to control or repel aphid vectors to reduce or delay infection by viruses (Loebenstein et al. 1975, Simons and Zitter 1980, Basky 1984, Perring et al. 1989). The relatively low value of the processing snap bean crop precludes these strategies from becoming adopted because of the high cost of materials and labor.

Control of the Virus. The most effective solution to manage CMV in snap bean is to grow CMV-resistant cultivars. Although resistant cultivars are not available, Griffiths (2007) has traditionally bred several CMV-multigenic resistant lines by crossing accessions of scarlet runner bean, *P. coccineus*, with *P. vulgaris*. These lines must still be backcrossed into a commercial line to improve their agronomic characteristics.

The possibility of transforming snap bean to express the coat protein of CMV as a means of conferring resistance to the virus also has been discussed (Fuchs 2006).

Until CMV-resistant cultivars are commercially available, identifying cultivars that are tolerant to CMV could be useful to mitigate potential yield loss. Taylor and Shail (2006) reported a range in susceptibility to CMV among commercially available cultivars. More research is needed to determine whether the level of tolerance observed will be robust enough to protect the crop under stressful environmental conditions (e.g., hot and dry). Cultivars that are resistant or tolerant to CMV could be grown during the second half of the season when yield-limiting levels of CMV are most likely to occur. Processing snap bean acreage is contracted, cultivars are selected, and planting dates are scheduled months before the growing season begins. Thus, it is impossible to know if resistant or tolerant cultivars will be needed as a preventative measure against CMV. For this reason, cultivars that are resistant or tolerant to CMV, but also have a high yield potential in the absence of CMV, will be highly preferred by growers and the processing industry.

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