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How natual [i.e. natural] enemy and cabbage aphid populations affect organic broccoli harvest

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HOW NATUAL ENEMY AND CABBAGE APHID POPULATIONS AFFECT ORGANIC BROCCOLI HARVEST

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ABSTRACT

HOW NATUAL ENEMY AND CABBAGE APHID POPULATIONS
AFFECT ORGANIC BROCCOLI HARVEST

by Diego J. Nieto

The cabbage aphid (*Brevicoryne brassicae* L.) is the primary broccoli (*Brassica oleracea* L.) pest in Monterey County. Their ability to contaminate a broccoli head has sometimes led to zero-tolerance spray thresholds, thereby causing ecological harm. To improve upon these management practices, aphid arrival time, within-plant colony location, and abundance of natural enemies were tested against the organic broccoli harvest. Cabbage aphids predominately colonized the outer leaves of a broccoli plant. These colonies, however, did not significantly influence the broccoli harvest. Aphid arrival time into a field was strongly correlated with harvest, with early arriving aphids being less likely to infest a head. This was in part due to natural enemies, particularly syrphid larvae (Syrphidae), which were in greatest abundance in response to early aphid colonizers. Therefore, future research efforts should focus on management practices that encourage the early establishment of natural enemies.

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CHAPTER 1

Introduction

THE PRODUCTION OF BROCCOLI (*Brassica oleracea* L.) is heavily concentrated in California. Of the 141,000 total U.S. domestic acres produced in 2001, 129,000 (91.5%) originated from California (Brunke 2002). California broccoli acreage nets $516 million annually, with Monterey County accounting for 52% of California's total broccoli production, worth $266 million (CDFA 2003).

The cabbage aphid (*Brevicoryne brassicae*) is the primary broccoli pest in Monterey County (Pure Pacific Organic, personal communication). Cabbage aphid colonies are capable of rapid population growth, as parthenogenetic, winged (alate) aphids migrate into cultivated fields and establish colonies of wingless (apterous) aphids; each capable of producing 30-50 offspring (Hughes 1963). Population densities are greatest during seasons with moderate or cool temperatures, which are characteristic of Monterey County summers (Trumble 1982a). Cabbage aphids have been found typically to colonize the youngest, uppermost broccoli leaves (Trumble 1982a, 1982b, 1982c; Hopkins et al. 1998), yet have also been found concentrated on middle and lower leaves (George 1957). We have found that in Monterey County, cabbage aphids are more likely to be found on the outermost, mature leaves of a broccoli plant (unpublished data).

Cabbage aphids cause economic loss by infesting, and thereby contaminating a broccoli head, which is the only marketable portion of a broccoli plant (Kennedy and Oatman 1976; Pickel et al. 1983; Costello and Altieri 1995). This has led to a zero-tolerance approach regarding the presence of aphids anywhere on a broccoli plant, once head formation has begun (UCIPM 1986). Thus, in this economically important stage of development, insecticides are typically applied upon the discovery of aphids, regardless of aphid colony size or plant location.

In California, 716,899 lb of pesticide-active ingredients were applied to broccoli fields during 2002 on 1,039,208 acre-treatments, ranking broccoli 16th in the state for pesticide use (CDPR 2003). Pesticide applications may have a deleterious affect to ecologically sensitive areas (Pereira et al. 1996). With an important array of wetlands, sloughs and rivers, along with the Monterey Bay Sanctuary, the ecology and biodiversity of Monterey County may be particularly susceptible to pesticide-derived water pollution (Hartz et al. 2004).

Utilizing organic agriculture in this region may reduce such sources of pollution. In 2002, Monterey County had 8,690 acres in organic broccoli production, which generated over $6 million (Monterey County Crop Report 2002). In these systems, an aphid zero-tolerance spray threshold is typically not used, as organically acceptable sprays are relatively expensive and only moderately effective. Therefore, insect predators and parasitoids (natural enemies) may be of greater importance in determining the harvest potential of a broccoli head, and have been recorded in higher abundances in organic versus conventional systems (Dritschilo and Wanner 1980; Letourneau and Goldstein 2001).

In terms of aphid control, parasitic wasps and aphidophagous predators may effectively suppress aphid populations in kale crops (Hughes 1963). For instance, the aphidiid wasp *Diaeretiella rapae* (McIntosh) is capable of laying up to 135 eggs as an adult, and while typical parasitism rates vary between 1-5%, rates of over 90% have also been recorded (Mackauer and Chow 1986; Wilson and Lambdin 1987). Additionally, aphidophagous syrphid larva (Syrphidae) can consume 200-600 aphids from egg-hatch to pupation (Hughes 1963). Syrphid larvae are often considered the most important control agent in an aphid dominated system, such as broccoli (Cheney 2004; Colfer 2004).

Some important aspects of cabbage aphid biology have not been studied. Particularly, how aphid arrival time into broccoli fields, and colony location on the plant, may relate to broccoli harvest, which is the subject of this study. Documenting these factors, in addition to the effect of natural enemies on organic broccoli, may serve as a first step in modifying the zero-tolerance spray threshold used in conventional systems, as well as improving control success in organic systems, and thereby improving cabbage aphid management practices.

This study seeks to answer four questions: (1) How do aphid arrival time, colony plant location, and abundance and efficacy of natural enemies each correlate with broccoli head harvest? (2) Do early season aphid arrivals correspond with larger aphid densities, which might, therefore, be more likely to infest a broccoli head? (3) Are aphid colonies closest to the broccoli head more likely to impact broccoli harvest, relative to aphid colonies located on the older, outermost leaves? (4) Do populations of aphid natural enemies, particularly parasitic wasps (*D. rapae*) and syrphid flies, substantially impact broccoli harvest?

CHAPTER 2

Methods and Materials

Field experiments were conducted to determine how aphid arrival time, colony location (with respect to the broccoli head), and the presence of natural enemies contribute to broccoli head infestation. Caged experiments were also performed to test aphid arrival time and impact of natural enemies on broccoli harvest.

Field Experiment. Four different organically certified farms in Monterey County were sampled in the summers of 2002 and 2003 (Table 1). Sites A, B, C, and D are located in the Salinas Valley, and are characterized by warm temperatures in the summer and strong southern winds in the late afternoons. Site D is located on the coast, and experiences much cooler temperatures, with coastal fog occurring frequently in the mornings and late afternoons. Strong eastward winds off the coast are often present.

These farms used 1-mo-old Maritime broccoli plug transplants, except for Site B in 2002, which used Arcadia broccoli. Fields were arranged in 0.56 m wide double-row beds, spaced 1.02 m, and utilized overhead sprinklers for irrigation.

Quadrats were established on four double-row beds per broccoli site (Fig. 1). Each of the four double-row beds was separated by approximately 20 double-row beds, both interiorly, and away from any edge of the field, to minimize potential edge effects. Within the four double-row beds sampled, four quadrats were flagged, and spaced approximately equidistant from each other, for a total of 16 quadrats. Each quadrat consisted of four plants, labeled A, B, C, and D for a total of 64 plants sampled per field.

Each plant was divided into five sampling sections based on its spatial location relative to the head of the plant. These sections were categorized as follows:

Center - youngest leaves and developing head on the apical portion of the plant
Leaf 1 - the first mature leaf growing closest to the center of the plant
Leaf 2 - the second closest mature leaf to the center
Middle Leaves - subset of leaves that are located in the middle portion of the plant, which are older, larger, and farther away from the head than the previous 2 leaves
Outer Leaves - the oldest and largest leaves, which are farthest away from the plant's center; offshoots were also included in this category

Since immature broccoli plants do not provide vegetative parts for all the sample categories, within-plant location labels were limited to the center and outer leaves during early season analyses (1-4 wk after transplant). Late season observations (5-10 wk after transplant) adopted all five within-plant location labels.

Wilson et al. (1983) suggested that the extensive time requirements necessary to count individual aphids would not be efficient. Consequently, a categorical appraisal of aphid densities was used. Alate aphids were counted only when present in colonies of 10 or fewer aphids, in order to investigate a colony's possible origins and initial development.

Aphid and beneficial insects were counted weekly on each plant sampled through harvest. Beneficial insects included syrphids (adults and larvae), coccinellids (adults and larvae) and the parasitoid *D. rapae*. Voucher specimens of beneficial insects were deposited in the J. Gordon Edwards Entomology Museum at San Jose State University.

Parasitized mummies were counted on a particular leaf by placing twist-ties on the leaf, and noting the current number of mummies present. During successive samplings, additional mummies counted were added to determine a cumulative total per plant location.

Prior to harvest, a final notation was made to indicate harvest result. Plants that had no aphids in their head were considered harvestable, while broccoli heads with one or more aphids were not considered harvestable. This standard was adopted from the growers at Pure Pacific Organics, who use this criterion to determine if a broccoli head is commercially acceptable.

Caged Experiment. Data were collected at the Center for Agroecology and Sustainable Food Systems (CASFS) at the University of California, Santa Cruz, during the summer of 2003. Two adjacent, double-row planting beds, 64 m long, were utilized for experiments on this organic farm. Only the inner two rows of these beds were sampled, and treatments were randomized with respect to location within the beds. One-mo-old Maritime broccoli plugs were cleaned before transplant with a soft-bristle paintbrush to remove any possible insects. Square cages (0.06 m^3), constructed with PVC pipe and insect netting (AGRIBON AG-19, Peaceful Valley, Grass Valley, CA) were then placed around individual broccoli plants, and prevented immigrating aphids, other herbivores, or natural enemies from influencing, or altering the aphid populations being tested. Aphid arrival times were simulated by inoculating broccoli plants at three different times. Early season inoculations were performed shortly after the transplant date (5 August 2003), when plants were approximately 5 weeks-old. Mid-season inoculations began 9 weeks into the season, while late season inoculations began at 14 weeks into the season. A single alate aphid was collected from an infested broccoli plant and transferred with forceps to a treatment plant. Once inoculated, monitoring was undertaken to detect aphid mortality.

Early season inoculations included 27 plants, 17 of which were caged with 10 un-caged plants serving as treatment controls to study the effects of natural enemies. Mid-season inoculations consisted of 40 plants, including 30 caged plants and 10 un-caged control plants. Late season inoculations included 34 plants, with 24 caged plants and 10 un-caged plants. All un-caged plants were cleaned to remove previously established insects before inoculations were made.

Statistical Analyses. To determine how variables influenced the harvest of a broccoli head, a binary logistic regression analysis was utilized, which provided a simple, yes or no predictive model for harvest.

A repeated measures ANOVA was used to detect any significant differences in insect abundance with regards to within-plant location. To normalize aphid distribution data, a log (X+1) transformation was implemented, as recommended by Hayman and Lowe (1961). Dunnett's T3 post-hoc analyses for distribution data was used to directly compare the abundance data of one within-plant location (outer leaves) against all others.

A log linear analysis was performed to determine any potential relationships between two inoculation treatments and harvest for the caging experiment. An *a posteriori* chi-square analysis was then conducted to illustrate any differences between such treatments, in which a Dunn-Sidax alfa transformation was implemented.

Percent aphid parasitism was measured using the equation:

$$\Sigma\ mummies\ /\ [\Sigma\ mummies + \Sigma\ aphids]$$

This equation was applied to each broccoli plant without differentiating within-plant location, and was employed per sampling date. All analyses were performed on SPSS 11.5 (SPSS Inc. 2002).

CHAPTER 3

Results

Field Analyses. Aphid abundance was three times greater in 2003, relative to 2002, while aphid parasitism was half in 2002 than in 2003. Mean aphid abundance per plant was 11.48 ± 0.97 and 35.48 ± 1.75 for 2002 and 2003, respectively, and yearly mean mummy abundance per plant was 0.49 ± 0.04 and 4.44 ± 0.29 for 2002 and 2003, respectively. Mean syrphid adult and larvae abundance per plant was 0.01 ± 0.00 and 0.01 ± 0.00 in 2002, and 0.02 ± 0.00 and 0.06 ± 0.01 in 2003, respectively. Aphid percent parasitism was 31.95% and 17.48% for 2002 and 2003, respectively.

Aphid arrival time was correlated with both colony size and harvest. Aphids that arrived mid-season in field trials generated larger colony sizes (Fig. 2) and were more likely to infest a broccoli head than those that arrived earlier. The mean values for arrival time in 2002 were 6.29 ± 0.09 weeks for non-harvestable plants and 4.07 ± 0.08 weeks for harvestable plants. In 2003, the arrival time means were 4.44 ± 0.09 weeks for non-harvestable plants and 2.85 ± 0.07 weeks for harvestable plants. There were also differences in arrival time frequencies, such that most aphids arrived and colonized plants during mid and late seasons in 2002, and early in 2003 (Fig. 3). Syrphid larvae were also present in higher numbers earlier in a growing season (Fig. 4).

The binary logistic regression analysis had an overall correct predictive value of 63.6% for the 2002 growing season (Table 2). Within this model, both aphid arrival time and aphids located on center leaves had a highly significant negative impact on broccoli harvest ($P < 0.001$). Positive or negative influence on harvest was determined by the B values in Table 2. Both natural enemies *(D. rapae*, syrphids, and coccinellids) and the presence of parasitized aphids (mummies) were not significantly correlated with harvest ($P > 0.05$).

ANOVA repeated measures for the early 2002 growing season showed differences in insect abundance with regards to within-plant location (Table 3). Post-hoc analyses demonstrated that both aphid abundance and the presence of aphid mummies on the outer leaves were significantly higher than a plant's center location ($P = 0.03$ and $P < 0.001$ respectively) (Fig.5). Moreover, during the late 2002 growing season, aphid colony size and the number of aphid mummies found were highest on outer leaves when compared to center, first, second and middle leaves ($P < 0.001$) (Fig. 5).

In 2003, the binary logistic regression analysis had an overall correct predictive value of 73.2%. Again, both aphid arrival time and aphids located on center leaves had a highly significant negative impact on broccoli harvest ($P < 0.001$). However, the presence of syrphid adults and larvae had a significant positive effect on broccoli harvest ($P < 0.05$). Aphid mummy presence was also significant; having a positive effect on broccoli harvest when located on the outer leaves ($P < 0.05$) and negative impact when located on center leaves ($P < 0.01$). The presence of coccinellids and adult *D. rapae* were not significantly correlated with broccoli harvest (Table 2).

In contrast to 2002, the early 2003 growing season showed that aphid abundance was not significantly different between outer and center leaves ($P = 0.274$), although significantly more aphid mummies were found on outer leaves relative to center leaves ($P < 0.001$) (Fig. 6). During the late 2003 growing season, aphid colony size was significantly higher on outer leaves when compared to center ($P = 0.001$), first ($P < 0.001$), second ($P < 0.001$) and middle leaves ($P = 0.001$). Aphid mummy densities were also significantly highest on outer leaves when contrasted with center ($P = 0.002$), first ($P = 0.001$) and second leaves ($P = 0.002$). However, no difference in mummy abundance was detected between outer and middle leaves ($P = 0.932$) (Fig. 6).

Caged Analyses. The log-linear analysis performed for the natural enemy exclusion (caging) experiment showed no significant three-way interactions between caging, inoculation time and harvest, however, two-way interactions were highly significant ($P < 0.001$) (Table 4). Dunn-Sidak corrections for the chi-square *a posteriori* cage tests produced an adjusted P-value of 0.017. Thus, harvest rates for caged plants were 31% lower than un-caged plants ($P = 0.002$). Moreover, harvest rates for early-season inoculations were diminished by 37% when compared to mid-season inoculations ($P = 0.003$), and 84% lower than late-season inoculations ($P < 0.001$). Harvest rates for inoculations made during mid-season were also reduced by 49% relative to those made during late season ($P < 0.001$).

CHAPTER 4

Discussion

The caging experiment illustrates two points. First, the time at which an aphid colonizes a plant plays an important role in the probability of a broccoli head being harvestable. Caged plant results suggest the earlier an aphid arrives on a plant, the less likely that plant will be harvested. We attribute this effect to increasing aphid densities overtime as the plant matures, resulting in broccoli head infestation. Second, caged broccoli plants had a harvest rate of 31% less than un-caged plants, which we attribute to natural enemy exclusion in caged plants. Thus, natural enemies likely play a key role in preventing head infestation. How these two factors (aphid arrival time and the presence of natural enemies) interact to ultimately affect broccoli harvest is difficult to assess, but our field results provide some insights.

As in the caging experiment, aphid arrival time in field trials was strongly associated with harvest, and along with aphids colonizing the central part of the plant, was the most important determinant of broccoli harvest. However, whereas harvest rates diminished with earlier arrival times in the caged experiment, aphids that colonized plants in mid-season field trials generated larger colony sizes and were more likely to infest a broccoli head than those that arrived earlier or later. For both the 2002 and 2003 seasons, the highest number of aphids counted on broccoli plants at the end of harvest tended to be found on those plants colonized during the middle (four to seven weeks after transplant) of the growing season (Fig. 2). Two possible reasons exist as to why early arriving aphid colonizers had little impact on broccoli head harvest; proportionally low numbers of early aphid arrivals in 2002, and high efficacy of natural enemies in correspondence with the high proportion of early aphid arrivals in 2003.

In 2003, the presence of natural enemies (syrphids and aphid mummies) had a significant positive impact on broccoli harvest (Table 2). Syrphid larvae abundance, for example, was greatest when aphids arrived early in the growing season and progressively decreased with middle and late season aphid arrival times (Fig. 4). This coincided with high aphid colonization rates early in the season, when over 50% of the broccoli plants were colonized within 3 weeks after transplant (Fig. 3). It appears that elevated natural enemy populations prevented those colonies from reaching high population levels, which were consequently less likely to infest a head. Both syrphids and *D. rapae* are reported to have higher activity and fecundity rates that correspond to higher aphid densities (Hughes 1963; Akinlosotu 1978; Mackauer and Chow 1986). Thus, early aphid colonizers may allow beneficial insects to establish sufficient population increases and contain aphid population levels below economic thresholds.

This was not the case in 2002, when natural enemies were not significantly correlated with harvest, which may have been the result of low numbers during the early season of both aphid colonizers and natural enemies. In contrast to 2003, the majority of aphid colonization of broccoli plants did not take place until after 5 weeks, when over 50% of the plants were colonized. This may explain why, although syrphid larvae populations were highest corresponding to early season aphid arrivals, their abundance was generally too low for active suppression. Also, mid season aphid colonizers still have sufficient time to increase colony size enough to infest an entire plant. With the bulk of plants colonized in the middle part of the season, natural enemies may not have time to build up their numbers and control rapidly rising aphid populations that may spill over and infest a broccoli head.

However, in general there appears to be great potential for natural enemy induced aphid suppression in organic or low insecticide-stress systems. Percent parasitism in our field trials (32% in 2002 and 17% in 2003) were considerably higher than the 1-5% parasitism that is typically recorded for conventionally managed fields (Trumble 1982a, 1982c; Mackauer and Chow 1986). This discrepancy is most likely attributable to a lack of pesticide applications in organic systems (Theiling and Croft 1998).

Our data strongly support the notion that location on a plant where aphids colonize also has a significant impact in determining harvest. In field trials, aphids were most abundant on the outer leaves of most broccoli plants, which were not significantly correlated with harvest. Only aphids located on center leaves, which were found in lower densities and on fewer plants, had a significantly negative correlation with harvest for both field seasons. Based on logistic regression field models, aphid thresholds exceeding 0.2 and 1.0 insects in the center of broccoli plants produced a 63.6% and 73.2% probability that the broccoli head would not be harvestable for 2002, and 2003, respectively. Thus, although very low industry-based economic thresholds for aphid numbers exist regarding a broccoli head, most cabbage aphids reviewed in our study were found primarily on the outer portion of the plant, and did not affect harvest.

The conclusion that cabbage aphids were found in significantly higher numbers on the outer-most leaves of a broccoli plant supports previous work by George (1957), but is not consistent with studies conducted by Trumble (1982a, 1982b, 1982c) and Hopkins *et al.* (1998), who found that cabbage aphids were mostly associated with the center of the plant. The differences between these distribution patterns might possibly be attributed to the organic soil management practices used in our trials. For example, by using compost and other natural soil amendments, broccoli plants might uptake and distribute nutrients differently than conventionally applied fertilizers, thereby providing cabbage aphids with a different nutritional feeding environment. Studies in tomatoes found that varied soil management practices (organic vs. conventional) generated treatment differences in plant nitrogen concentrations and consequent herbivorous feeding behavior (Letourneau *et al.* 1996). Similar soil comparisons were made in corn, where it was determined that *Ostrinia nubilalis* had higher fecundity rates on corn grown in conventional soils when compared with organic soils (Phelan *et al.* 1995).

An alternate explanation for the differing aphid distribution results is that our fields were colonized only by cabbage aphids. Trumble (1982a, 1982b, 1982c) recorded four different aphid species in their broccoli fields. The green peach aphid (*Myzus persicae*), was the most abundant and colonized the plants the earliest. Therefore, it might be possible that when competing aphid species are absent, cabbage aphids alter their distribution patterns to colonize the outer leaves (Trumble 1982b).

Regardless of these possibilities, aphid mobility from outer plant-locations was apparently limited, such that aphids colonized furthest from the head were not likely to travel towards the head of the plant. These colonies were not associated with head infestation. It would, therefore, be advantageous to integrate spray policies in conventionally managed systems, which recognizes aphid location as an important contributor to broccoli harvest, rather than utilizing a presence-absence or zero-tolerance threshold once heading has begun.

To expand on this body of work, future research efforts should focus on techniques to enhance early season establishment of natural enemy populations, which is of course strongly correlated with early colonization of aphid populations. Therefore, a landscape approach to field management, which would integrate harvest time, field location (in relation to neighboring fields), wind direction, and aphid/natural enemy suite compatibility between cropping fields, might advance growers' ability to influence the arrival times of aphids and their corresponding natural enemies. Additional efforts to encourage the early establishment of natural enemies could utilize non-crop vegetation, such as insectary plantings, which might provide natural enemies with a secondary aphid species before cabbage aphids are established in a broccoli field. Alternately, the pollen and nectar resources provided by such micro-habitats might also sufficiently attract beneficial insects before a crop has become colonized by aphids.

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APPENDIX

Tables and Figures

Table 1. Monterey County broccoli sample sites.

Year	Location	Acres Sampled	Transplant Date	Harvest Date	Total Sampling Dates
2002	A	8	21 June	10 Aug.	9
	B	8	14 June	7 Aug.	10
	C	8	15 Aug.	22 Oct.	10
	D	8.8	7 Aug.	10 Oct.	8
2003	A	6	1 Sept.	6 Nov.	9
	B	8	1 July	29 Aug.	7
	C	6	6 Aug.	24 Sept.	10
	D	8.7	1 July	5 Sept.	11

Table 2. Contributions to broccoli harvest in field studies resulting from binary logistic regression analysis.

	B	Wald	P
2002			
Center (aphids)	-0.642	49.237	< 0.001
Arrival Time	-0.1119	22.654	< 0.001
Leaf 2 (aphids)	-0.203	4.476	0.034
Lady Bird Beetles (adults)	1.212	3.651	0.056
Middle Leaves (alate)	-0.653	3.221	0.073
Outer Leaves (aphids)	0.057	2.226	0.136
Leaf 1 (alate)	21.491	< 0.001	0.999
Constant	-19.898	< 0.001	0.999
2003			
Arrival Time	-0.961	90.164	< 0.001
Constant	1.79	75.388	< 0.001
Center (aphids)	-0.226	17.931	< 0.001
Center (mummies)	-0.458	7.089	0.008
Syrphid Adults	1.234	6.085	0.014
Outer Leaves (mummies)	0.017	4.821	0.028
Syrphid Larvae	0.492	4.256	0.039
Center (alate)	0.516	3.638	0.056
Leaf 1 (alate)	1.107	3.624	0.057
Leaf 2 (alate)	-1.332	2.460	0.117
Leaf 1 (aphids)	-0.084	2.311	0.128

Significance based on $P < 0.05$; i.e. 99.9% of plants with center-located aphids in 2002 were not harvestable.
B values determined whether the effect was positive (harvestable) or negative (not harvestable). The Wald statistic demonstrated the relative strength of the effect.

Table 3. Analysis of variance testing differences in insect abundance between within-plant locations.

Source	df	F	P
Aphids			
Location (early '02)	1	4.739	0.030
Location (mid/late '02)	4	38.523	< 0.001
Location (early '03)	1	1.201	0.274
Location (mid/late '03)	4	26.031	< 0.001
Mummies			
Location (early '02)	1	24.285	< 0.001
Location (mid/late '02)	4	41.756	< 0.001
Location (early '03)	1	24.856	< 0.001
Location (mid/late '03)	4	9.654	< 0.001

Location, within-plant location.
Significance based on $P < 0.05$.

Table 4. Log-linear analysis from caging experiment, illustrating two-way interactions.

Variables	df	L.R. Chi-Square	P
Caged (Y/N) x Harvest (Y/N)	2	44.636	<0.001
Inoc. Time (E/M/L) x Harvest (Y/N)	4	10.618	0.031
Inoc. Time (E/M/L) x Caged (Y/N)	2	37.94	<0.001

Significance based on $P < 0.05$.
Inoc., inoculation; (Y/N), yes or no; (E/M/L), early, mid or late.

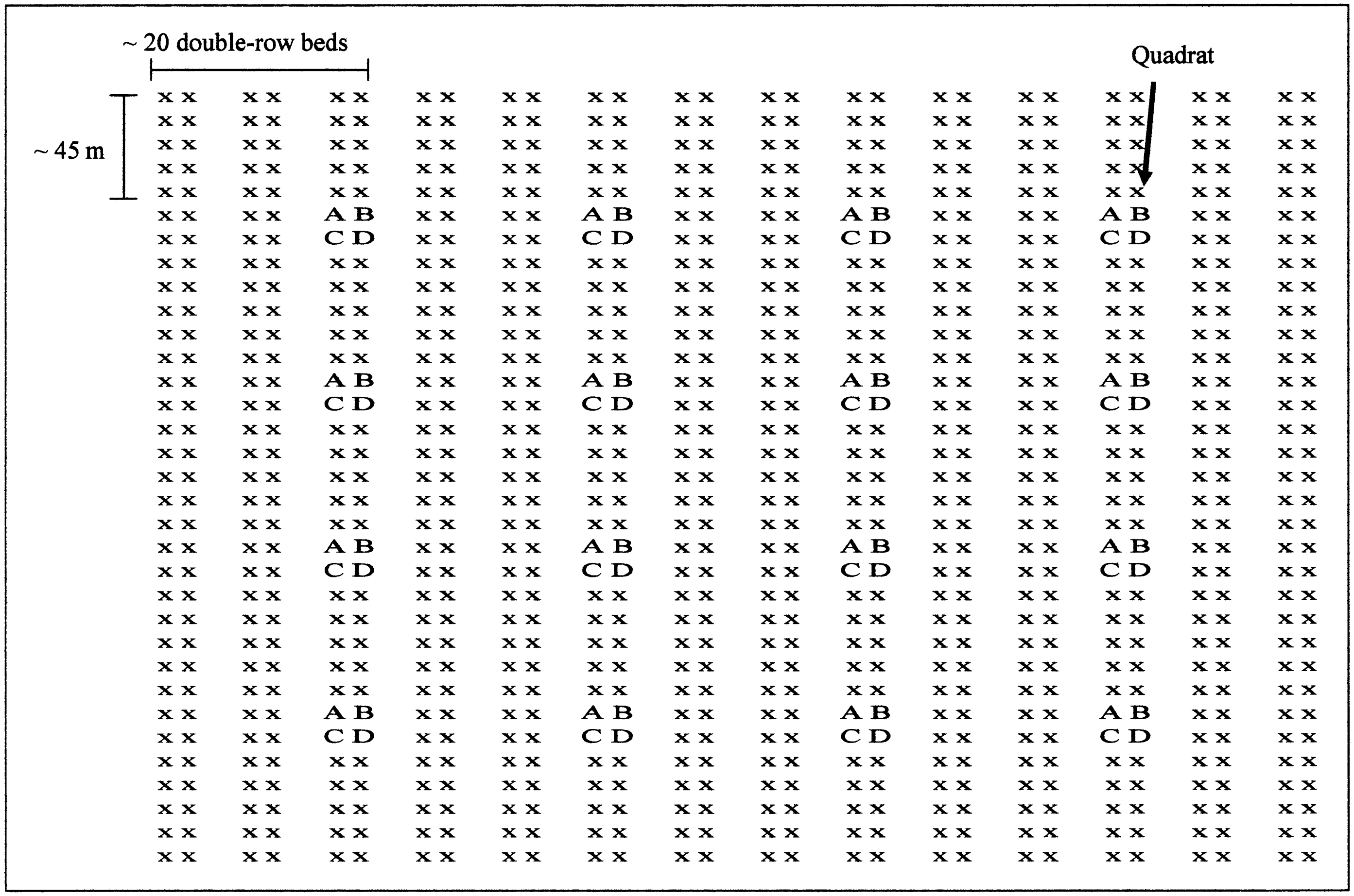

Fig. 1. Broccoli field with quadrats on four double-row beds spaced equidistantly. Beds with quadrats were seperated by approximately 20 beds, while quadrats on the same bed were seperated by approximately 45 m. Diagram not to scale.

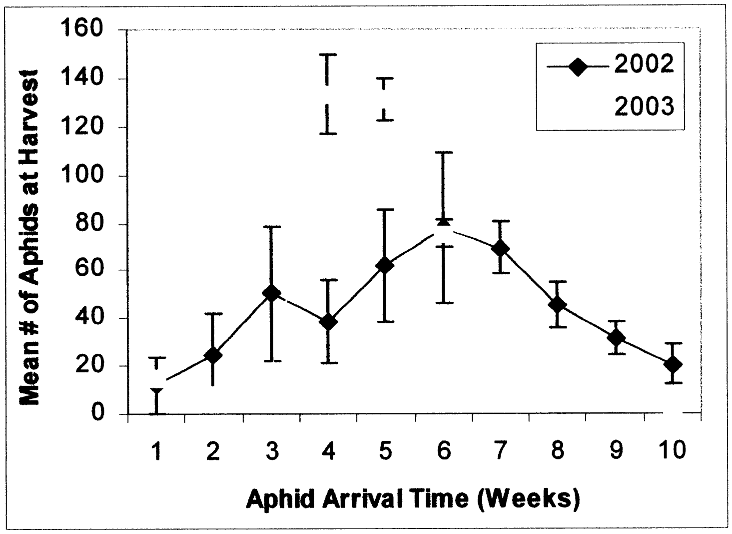

Fig. 2. Aphid abundance at harvest based on arrival time. Plants with mid-season aphid arrivals were associated with the highest densities. Arrival times were based on initial aphid recordings on a broccoli plant, and were measured by the number of weeks after broccoli plugs were transplanted.

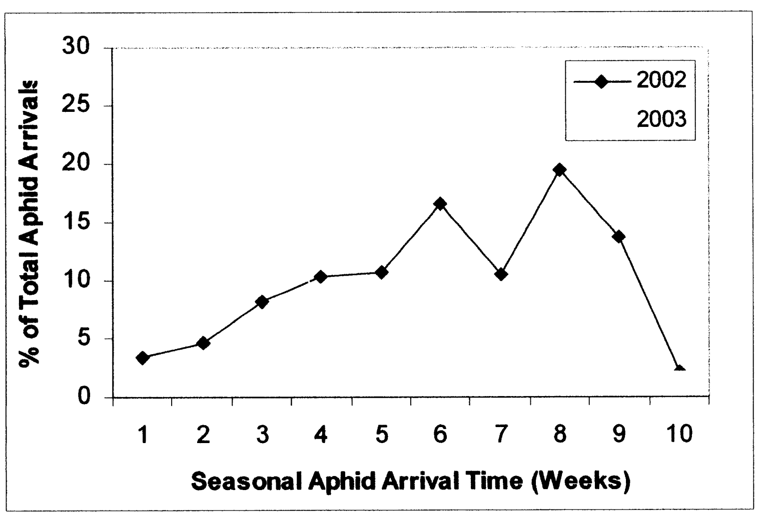

Fig. 3. Percentage of total aphid arrivals at successive weeks in a growing season. Weeks are based on time after broccoli-plug transplant. Percentages are derived from frequency data.

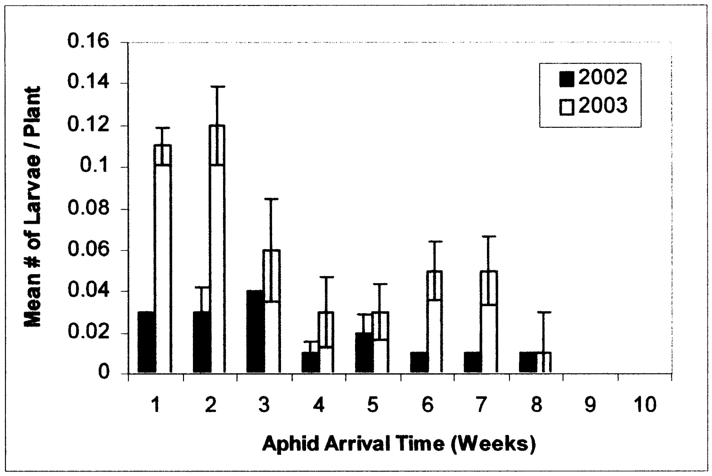

Fig. 4. Syrphid larvae abundance based on aphid arrival time. Arrival times were based on initial aphid recordings on a broccoli plant, and were measured by the number of weeks after broccoli plugs were transplanted.

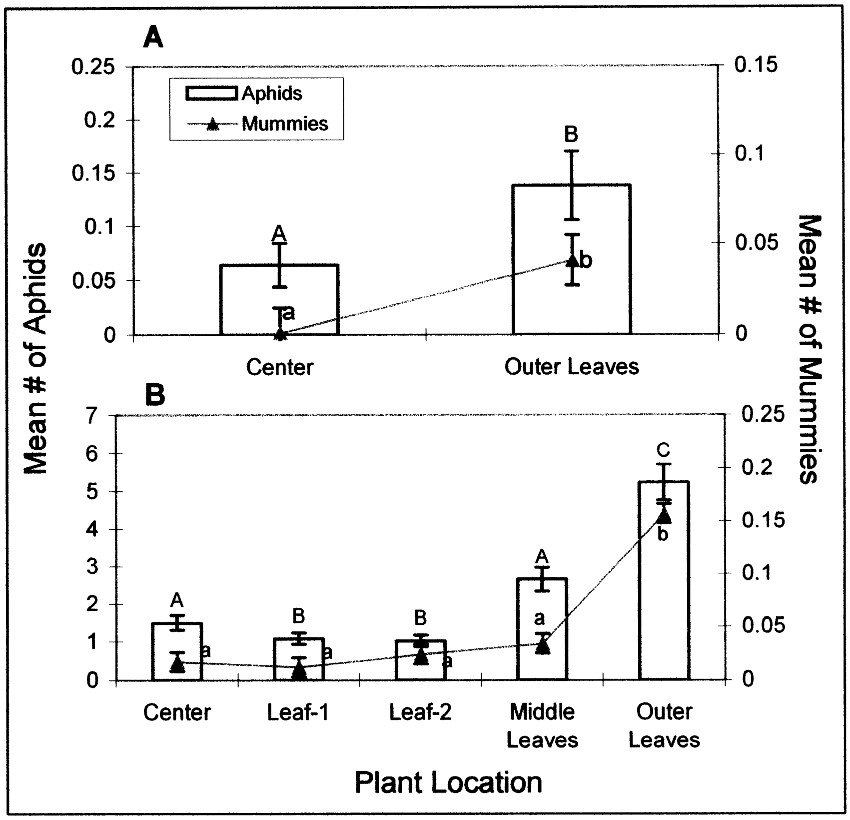

Fig. 5. Mean aphid and aphid mummy abundance based on within-plant location for early (A) and late (B) season broccoli plants in 2002. Individual categories with differing letters are significantly different (P < 0.05) based on repeated measures ANOVA.

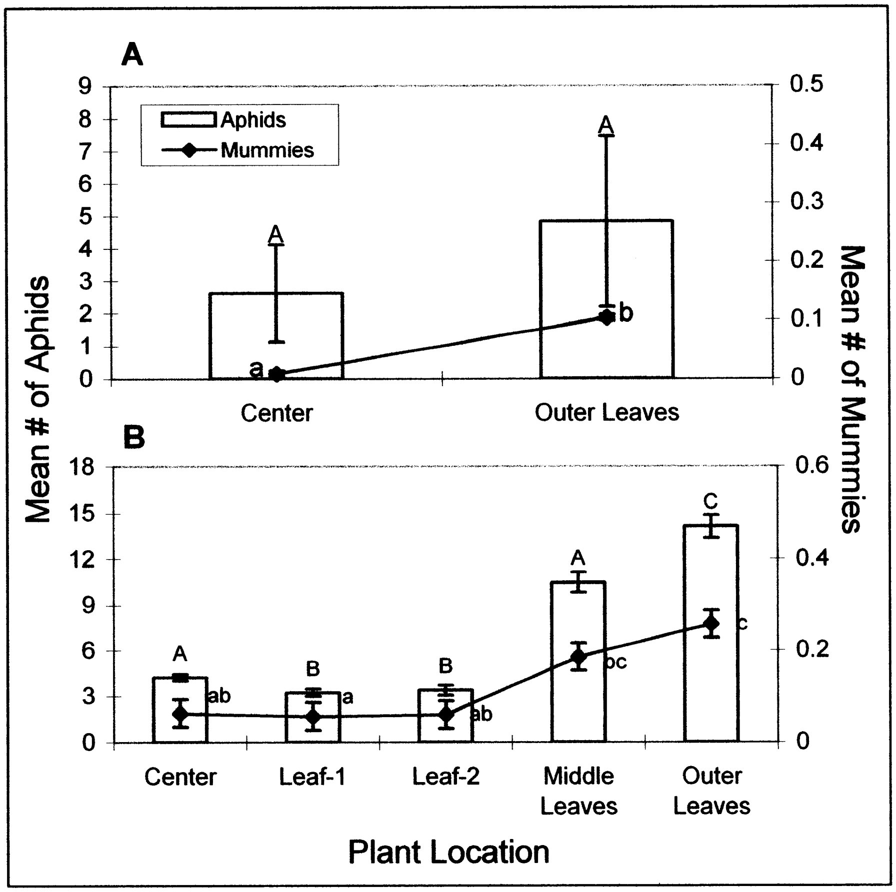

Fig. 6. Mean aphid and aphid mummy abundance based on within-plant location for early (A) and late (B) season broccoli plants in 2003. Individual categories with differing letters are significantly different ($P < 0.05$) based on repeated measures ANOVA.