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Nonrandom Distribution of Cabbage Aphids (Hemiptera: Aphididae) in Dryland Canola (Brassicales: Brassicaceae)

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ABSTRACT Characterization of spatial distribution patterns of pests in large-scale agricultural fields is important because these patterns affect the sampling effort needed to accurately detect and estimate their population density. In this study, we conducted experimental releases of alate cabbage aphids (*Brevicoryne brassicae* L.) into centers of small plots of canola (*Brassica napus* L.), and their gradual spread over a 7-wk period was characterized. The small-plot experiment demonstrated gradient effects from plot centers and a nonrandom vertical distribution, with initial colonization occurring on the abaxial side of lower canopy leaves and, later, highest numbers of cabbage aphids occurring on racemes. We also conducted large-scale distribution analyses of cabbage aphid infestations in two commercial canola fields, using visual inspection and sweep net sampling. We used canola plant phenological and landscape features as explanatory variables of the spatial distribution of cabbage aphid counts. These large-scale experiments showed strong edge effects with negative associations between cabbage aphid counts and distance to crop edges, including tree lines and contour banks. Cabbage aphid distribution was more effectively displayed using logistic regression than ordinary regression, Spatial Analysis by Distance IndicEs, or both. Based on the study findings, a nonrandom or optimized inspection approach is proposed to focus monitoring efforts on canola plants within 20 m from field edges with particular attention to the abaxial side of lower-canopy leaves. Detection of advanced cabbage aphid infestations should target the racemes within 20 m from field edges.

KEY WORDS integrated pest management, spatial distribution, targeted sampling, edge effect

One of the main pillars in "integrated" or threshold-based management of insect pests is the use of decision support tools, so that insecticide applications, other responsive actions, or both are deployed only when and where pest population density estimates exceed an economic threshold (Taylor 1984, Nansen and Ridsdill-Smith 2013). There are numerous possible downstream advantages of threshold-based pest management, including less use of insecticides, reduced risk of environmental contamination, better performance of natural enemies, and reduced risk of insecticide residues in food and livestock feed. However, compared with calendar-based insecticide applications, the significant challenge associated with threshold-based management is that it is only effective if the pest population density can be estimated with high enough accuracy. Without reliable and feasible means to accurately assess the pest population density, growers are inclined to follow a "rather safe than sorry" approach and apply insecticides, irrespective of whether or not insecticide applications are needed (Nansen et al. 2011). Clearly, there is a positive relationship between numbers of samples collected (sampling effort) and the accuracy of the pest population density estimate, but the value of increasing the sampling effort diminishes, and sampling must be feasible for the practitioner. Therefore, approaches like sequential sampling plans are used to calculate the minimum sampling effort needed to obtain a pest population density estimate associated with a user-defined level of accuracy (Pedigo and Buntin 1993). Several sequential sampling plans have been developed for pests in large-scale agricultural systems, including: *Ceutorhynchus obstrictus* Marsham (Coleoptera: Curculionidae) (Cárcamo et al. 2007), *Oebalus pugnax* F. (Hemiptera: Pentatomidae) (Espino et al. 2008), *Pseudatomoscelis seriatus* Reuter (Hemiptera: Miridae) (Parajulee et al. 2006), and *Aphis glycines* Matsumura (Hemiptera: Aphididae) (Hodgson et al. 2004).

Sampling theory, such as that associated with sequential sampling plans, outlines how proportionally more sampling effort is needed to accurately estimate a low population density compared with a high population density (Pedigo and Buntin 1993). Hence, a possible problem with use of sequential sampling plans in commercial agriculture is that they become unpractical because of unreasonable sampling requirements, when

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both the action threshold and the level of acceptable error are comparatively low. This is a particular concern when sampling is labor-intensive. Another concern is that most statistically based approaches to insect pest population density estimates are based on an assumption of random sampling of independent observations. This is a concern, as many data sets of arthropod pests have shown that observations were spatially autocorrelated over considerable distances (Liebhold and Sharov 1998, Badenhausser et al. 2012). Here, we argue that the above-mentioned concerns represent important practical constraints for the widespread adoption of threshold-based pest management. In addition, we argue that growers and crop consultants are often less concerned about the actual pest population density, but rather with identifying the locations of emerging pest infestations. If such "hot spots" of emerging pest populations can be detected early, then responsive actions (i.e., insecticide spray application or release of natural enemies) may be required merely in a small portion of a given field. Additional benefits of such a spatially targeted management approach include less insecticides applied, less labor and fewer resources involved in insecticide applications, and potentially higher insecticide spray volumes to increase coverage within targeted areas (Nansen et al. 2015). We argue that an in-depth insight into the three-dimensional distribution (i.e., spatial as well as vertical within a crop canopy) of the target pests is important to improve sampling plans and to identify "hot spot" areas in fields, in which insect pest infestations are most likely to occur. Moreover, if target pests predominantly show aggregated spatial distributions, it seems intuitively reasonable to optimize sampling efforts by focusing on monitoring of such hot spot areas.

On large spatial scales (i.e., >1 ha), most agricultural insect pests show distinct spatial aggregations, including economically important aphid species (Hemiptera: Aphididae) (Kennedy and Booth 1951, Helson 1958, Trumble 1982, Feng and Nowierski 1992, Powell et al. 2006). Such nonrandom spatial distributions are driven by a wide range of factors, including: plant phenology, such as growth stage (Ferguson et al. 2003) and leaf age (Kennedy and Booth 1951), distance from crop edge (Winder et al. 1999, Nansen et al. 2005b), land topography (Hill and Mayo 1980), host plant chemistry (Olsson and Jonasson 1994, Scheirs et al. 2003, Nowak and Komor 2010), and host plant sensory cues (Heard 2000, Powell et al. 2006).

The cabbage aphid (*Brevicoryne brassicae* L.) is arguably the most economically important of the late season aphid pests in dryland canola (*Brassica napus* L.; Berlandier 2004, Aslam et al. 2005), the second largest dryland crop in Australia (Australian Bureau of Agricultural and Resource Economics and Sciences [ABARES], 2013). Based on insecticide treatments, aphid management in canola in Australia costs over US$5 million annually (Murray et al. 2013). Canola is particularly vulnerable to direct feeding damage by invertebrate pests from the onset of its reproductive phase (here, considered as "late season infestation"; Berlandier and Baker 2007). Studies have highlighted considerable variability in development stage between canola plants sown at the same time (Nansen et al. 2012), leading to a range of host plant choices for aphids. However, little is known about cabbage aphid preference in relation to canola plant phenology, how this affects their spatial distribution, and implications for using host choice information in the development of sampling methodology.

In this study, we conducted a small-scale analysis of how experimentally released alate cabbage aphids colonized and spread from known release points. In this experiment, the main objective was to characterize and quantify the initial colonization and progressive spread based on careful weekly assessments of individual plants over a 7-wk period. In addition, we conducted large-scale distribution analyses of cabbage aphid infestations in commercial canola fields using two sampling techniques (sweep net and counts of cabbage aphids per plant) and sampling at two spatial resolutions (field-wide and field-edge grids). Sweep netting was included as a comparative sampling method because it is the recommended method of sampling canola fields for other important pests of canola (Berlandier and Baker 2007, Gu et al. 2008) and, if suitable, would simplify overall crop monitoring efforts (compared with visual inspection of canola plants). As part of the large-scale distribution analyses, we collected a wide range of plant phenological data and landscape characteristics, and we hypothesized that a combination of these variables could be used to predict the spatial distribution of cabbage aphids in dryland canola fields. Spatial Analysis by Distance IndicEs (SADIE) and logistic and ordinary regression techniques were applied to the small-scale, field-edge, and field-wide data sets, and it was predicted that one or more of these methods would indicate spatial aggregation of cabbage aphids in canola.

Materials and Methods

Small-plot Experiment. This experiment was conducted in two irrigated tunnel-houses, constructed of insect-proof polyethylene mesh (0.0267 by 0.0818 cm opening with 0.24-mm thread and 80% light transmission), at Shenton Park Field Station, The University of Western Australia (−31.949227° S, 115.792431° E). Canola ('Tanami') was hand sown with 10 cm between plants in straight rows spaced at 25 cm apart (four rows, 2 m in length) and to a depth of 9 mm using a wooden plank sowing aid at early (10 May), mid- (24 May), and late (7 June) sowing times during 2013. Each plot was 2 by 1 m^2 with a block consisting of three plots with different sowing times and being separated by 13 m of bare ground and a 1 by 6 m^2 strip of canola as a buffer. Sowing dates were based on recommendations for Western Australia (Oilseeds Industry Association of Western Australia [OIAWA], 2006). Seedlings were thinned postemergence to establish an optimal plant density of 40 plants m^{-2} (Seymour 2011). The design was a complete randomized block with six replications of three sowing times ($N = 18$ plots), with three replications in each of two tunnel houses.

Granular fertilizer (50 g m^{-2} NPK Blue Special, CSBP Limited, w/w 12% N, 5.2% P, 14.1% K, 6% S, 4.3% Ca, 0.01% Zn, 1.2% Mg, and 0.02% B) was broadcast by hand at sowing, then again on 15 and 29 July 2013. Fertilizer rates were based on local recommendations; applications were repeated to ensure optimal plant health in sandy soil (OIAWA, 2006). Weeds were initially controlled using a post-sowing preemergent spray of atrazine at 990 g a.i. ha^{-1}. Later in the season, weeds in plots were pulled by hand and the surrounding areas were sprayed with glyphosate to remove weeds throughout the tunnel houses. Bifenthrin (2 EC) was sprayed at 12.5 g a.i. ha^{-1} in all plots postsowing, prior to emergence, to control redlegged earth mites [*Halotydeus destructor* Tucker (Acarina: Penthaleidae); Australian Pesticides and Veterinary Medicines Authority [APVMA], 2014]. Plots were irrigated using overhead sprinklers for 5 min applying ~5 mm of water, three to four times per week except during rainy periods.

Alate cabbage aphids were obtained from a culture maintained on a range of cabbage plants inside rearing cages at the Shenton Park Field Station, The University of Western Australia. The cabbage aphid colony was 1 yr old originating from canola plants near Pingelly, Western Australia (−32.534044° S, 117.084140° E). The cabbage aphids were released on 18 August 2013 at noon in each plot. Cabbage aphid release consisted of a transparent plastic vial containing 10 alates that was attached to a bamboo pole placed at the plot center at a height of 1 m above ground, and the lid was removed to allow cabbage aphid dispersal. The date of cabbage aphid release was when a minimum of 50% of canola plants had attained flowering in the late sowing plots. At this date, early, mid-, and late sowing treatments displayed growth stages 4.5–5.5, 4.2–5.2, and 3.6–4.5 (Edwards and Hertel 2011), respectively. That is, 50% of buds flowering and 50% of potential pods >2 cm in length, 20% of buds flowering and 20% of potential pods >2 cm in length, and first flower stalks extending to 50% of buds flowering, respectively. This time point was chosen, as it is comparable with the development stage at which commercial canola fields commonly become infested with cabbage aphids. Of the total 180 alates released in the experiment, 8 alates remained in vials (dead) after 24 h. Hobo data loggers (Onset Computer Corporation, Bourne, MA) were used to record temperature and relative humidity every hour within tunnel houses during the 7-wk duration of the experiment. Environmental conditions (daily) during the 7-wk period were as follows: mean temperature: 16.8 ± 0.5°C (SE), maximum temperature: 22.8 ± 1.3°C, minimum temperature 12.2 ± 0.9°C, and relative humidity 75.6 ± 3.2%.

Each of the 80 plants per plot was inspected after 1, 2, 3, 4, 5, and 7 wk following cabbage aphid releases. At week 7, plants within tunnel house 1 (replicates one to three) had begun to senesce and almost all cabbage aphids had died except for scattered numbers on remaining green pod and main stem plant tissue. Consequently, these data were not included in the analysis. Cabbage aphids on leaves at week 2 were considered as cabbage aphid "colonization," and cabbage aphids on racemes at weeks 4, 5, and 7 were treated as representing "established populations."

Commercial Field Sites. Two commercial canola fields in Western Australia infested with cabbage aphids were selected for the field study. They differed in terms of within-field "noncrop" features, i.e., contour banks (the York field) and patches of remnant native vegetation (the New Norcia field). The York field (−31.965961° S, 116.677463° E) was 60 ha and had the cultivar 'Stingray' sown on 3 May 2013, while the New Norcia field (−31.031743° S, 116.204944° E) was 92 ha of 'Crusher' that was sown on 10 May 2013. At the time of sampling, the canola plants were at the 3.0–5.5 (budding, flowering, and podding) stages (Edwards and Hertel 2011), and thus were comparable with canola plants in the small-plot experiment throughout the sampling period. The above range in growth stage was chosen because it is the stage in which cabbage aphids are most likely to cause economic damage to canola crops in Australia (OIAWA, 2006, Gu et al. 2007) and, therefore, the most important time regarding crop scouting and deciding upon insecticide application. Sampling occurred during the periods 17–21 and 28–31 August for New Norcia and York, respectively.

Sampling points in commercial canola fields were geo-referenced (Garmin eTrex10; accuracy <3 m) along transects, which were selected to maximize scattering of sampling points and also to include field edge locations and varying distances from field edges (Fig. 1). At each sampling point, a 1-m stick was placed on the ground, and 10 canola plants were inspected sequentially along the crop row to count the number of cabbage aphids per plant. In addition to counts of cabbage aphids per plant, an insect sweep net (38-cm-diameter internal hoop) sample was taken at each sampling point by sweeping 1 m row of plant canopy adjacent to the assessed row. Wingless cabbage aphids were counted in sweep net samples at York, while total aphids (wingless and alates) were counted at New Norcia because the majority were alates and differentiation of species is difficult under field conditions (i.e., stereoscope required).

We established the distance of each sampling point to crop edges, including within-field noncrop areas such as contour banks and tree lines. Contour banks are soil embankments that contour according to the slope of arable land to reduce water erosion. Tree lines are here referred to any area of land that is unable to be cropped because of the presence of woody vegetation such as bushes and trees. In addition to counting cabbage aphids per plant, we collected the following canola plant phenological traits: 1) stem base diameter; 2) primary stem height (from soil to the tip of the primary raceme); 3) primary stem growth stage (recorded as one of the following five categories: budding 1], budding and flowering without pods 2], budding, flowering and podding 3], flowering and podding with no buds remaining 4], or podding only 5]); 4) plant density (based on number of plants counted along a 2 m row); 5) number of leaves per plant; and 6)

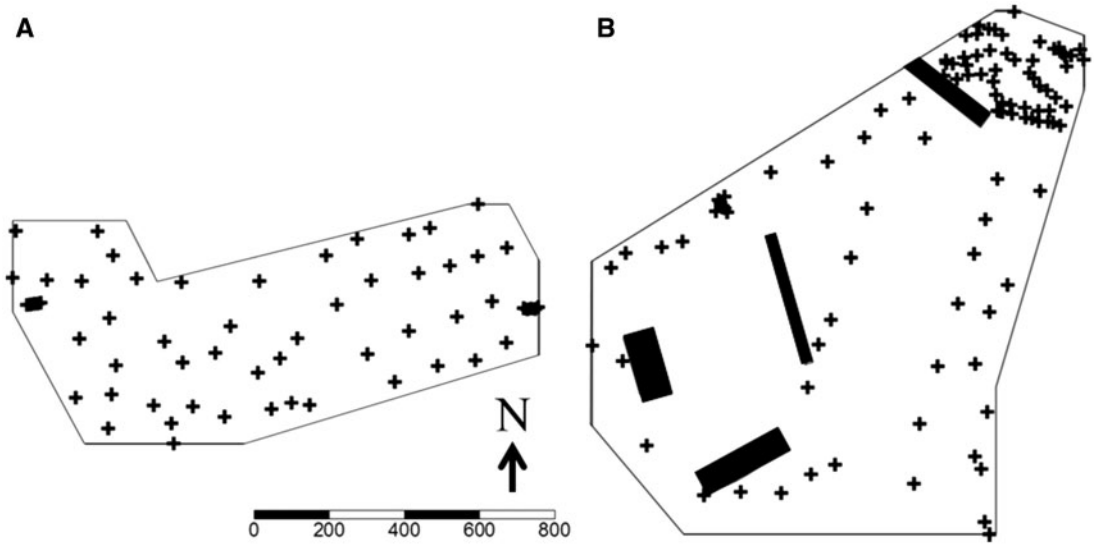

Fig. 1. York (A) and New Norcia (B) canola fields showing 59 and 100 sampling points, respectively. Black rectangles represent tree lines (i.e., noncrop regions containing woody plants) (scale in meters).

number racemes per plant. Elevation data for each location were retrieved from Schneider (2013).

Commercial Field Edge Grids. High-resolution sampling was conducted at one west and one east field edge in both commercial fields (four in total) where cabbage aphid infestations had been detected. At these locations, cabbage aphid colony length per raceme, number of infested racemes and number of infested plants were recorded for each square meter in a 400-m^2 sampling area, which was 10 m parallel along the field edge to 40 m inwards (i.e., perpendicular) from the field edge.

Data Analyses. All data analysis was conducted using Genstat for Windows v.15 (VSN International Ltd., Hemel Hemstead, United Kingdom). Unbalanced analyses of variance were conducted for the small plot data to explore associations between sowing treatments and cabbage aphid counts on leaves and racemes; chi-squared tests were used to compare the frequencies of cabbage aphids which colonized the leaves and racemes. We used logistic regression to examine the relationship between distance from edge (or plot center) and cabbage aphid presence, for all three experiments (i.e., small-plot experiment, field-wide and field-edge grids). In addition, we conducted ordinary regression analysis after removing the zero values and using $\ln(x+1)$ transformation, similar to that described by Fletcher et al. (2005). Only replicates 4–6 within the small plot trial were included in regression analyses because no data were available at week 7, which is when cabbage aphid populations were highest. For field-wide data, multiple logistic and ordinary regression with backward elimination was performed using the plant and landscape variables listed in Table 1 against the response variables of cabbage aphid counts on leaves, racemes, and sweep net.

SADIE (Perry 1995) was performed using SADIE-Shell (v.1.22; Rothamsted Research Institute, Harpenden, United Kingdom), a freely available software package that is used to characterize spatial distribution patterns of insect counts (Ferguson et al. 2003; Cocu et al. 2005; Nansen et al. 2005a,b; Mankin et al. 2014; Reay-Jones 2014). Using SADIE, an index of aggregation (I_a) was calculated. This index is a quantitative measure of the "effort" needed to theoretically move counts to the most uniform spatial distribution. The observed I_a was compared with I_a's generated from 1,000 randomizations of the actual data. The observed I_a is considered to indicate significant spatial aggregation if >950 (>95%) of the I_a's generated from 1,000 randomizations are greater than 1. SADIE was applied to counts of experimentally released cabbage aphids on leaves of individual plants in 39 combinations of: time of planting (3) × week of sampling (1–5) × replicate (2–6). These were the combinations in which counts of experimentally released cabbage aphids were found during four to five of the six weekly sampling events, and which, therefore, enabled quantitative assessment of change in spread of cabbage aphid infestations over time. In addition, SADIE was applied separately to counts of cabbage aphids on racemes of individual plants in 21 combinations of: time of planting (3) × week of sampling (3) × replicate (2–3). These were the combinations in which "established populations" (i.e., weeks 4, 5, and 7) of cabbage aphids were present on racemes for all three weeks for replicates 4–6 only; no data were available for replicates 1–3 for week 7. SADIE was also used to analyze spatial distribution patterns of counts of cabbage aphids on plants in commercial fields and field edge grids.

Cabbage aphid colony lengths were applied to regression analyses. However, SADIE is designed for counts rather than colony length measurements, so the

Table 1. Summary of plant, insect, and topographic data collected from multiple locations at York (28–31 August) and New Norcia (15–21 August) in 2013

	Description	Sample size	York			New Norcia		
			Locations	Mean	SE	Locations	Mean	SE
A	Stem base diameter (mm)	10 plants	59	6.58	0.15	26	9.90	0.36
B	Primary stem height (cm)	10 plants	59	80.05	1.76	26	73.42	3.62
C	Primary stem growth stage	10 plants	59	3.95	0.11	100	1.74	0.05
D	Plants per square meter	2-meter row	59	61.83	2.24	100	61.20	2.16
E	Leaves per plant	10 plants	59	5.86	0.15	67	10.87	0.11
F	Racemes per plant	10 plants	59	5.89	0.20	100	3.55	0.15
G	Elevation above sea level (m)	Single point	59	357.07	1.63	100	213.50	0.84
H	Distance from field edge (m)	Single point	59	60.64	7.61	100	64.32	9.28
I	Distance from vegetational edge (m)	Single point	59	33.81	4.54	100	39.93	4.25
J	Cabbage aphid colony length on racemes per plant (cm)	10 plants	59	0.40	0.24	100	0.51	0.10
K	No. cabbage aphids on leaves per plant	10 plants	59	3.45	3.25	100	0.60	0.25
L	No. cabbage aphids in insect sweep net	Single sweep	59	8.24	4.74	*	*	*
M	Total no. aphids in insect sweep net	Single sweep	**	**	**	100	24.73	5.14
N	Percent plants with cabbage aphids on racemes	10 plants	59	7.97	2.13	100	20.20	2.88

*Mostly unidentifiable winged aphids, total counts performed in "M".
**species counted separately in "L".

colony lengths on racemes were converted to cabbage aphid counts. To achieve this, 40 canola racemes infested with cabbage aphids, ranging from 3.2 to 134.1 mm colony length, were cut and placed into separate vials containing 70% ethanol at the York field. Fifteen of the samples were randomly selected, and 20 cabbage aphids were randomly removed, dried, and weighed using microscales to determine the average dry weight per cabbage aphid. The 40 cabbage aphid samples were dried and weighed. Cabbage aphid sample mass was multiplied by average dry weight per cabbage aphid to obtain cabbage aphid counts per sample. Through regression analyses, comparing cabbage aphid colony lengths against calculated cabbage aphid counts as the response variable ($F = 360.10$; $P < 0.001$; $R^2 = 0.90$), cabbage aphid counts were estimated using the colony lengths in millimeter multiplied by 6.17, according to the regression model.

Results

Small-plot Experiment. Of the 18 plots subjected to experimental infestations, cabbage aphids established successfully in 8. Here, establishment is defined as cabbage aphids being detected in at least four of the six weekly sampling events, including the final sampling event at week 7. Spread from central release points in small plots during the seven consecutive weeks followed fairly similar patterns across the three sowing treatments (Figs. 2 and 3). Most predominant infestations on leaves occurred during the initial three weeks and, overall, significantly more cabbage aphids colonized the leaves on primary stems than the racemes ($\chi^2 = 15.7$; df = 1; $P < 0.01$). Very modest spread occurred within the first four weeks of plot infestation. In weeks 4 and 5, there appeared to be a marked shift in host plant foraging, as cabbage aphids became most predominant on racemes and this coincided with a marked increase in cabbage aphid population density. Early and mid-sowing treatments had significantly more cabbage aphids on the racemes at week 7 than the late sowing ($F = 15.00$; df = 2,237; $P < 0.01$), with mean cabbage aphid colony lengths of 12.5 ± 1.98, 12.6 ± 1.59, and 4.9 ± 0.84 cm per plant, respectively. In addition, cabbage aphids were found exclusively on the abaxial sides of canola leaves, and the frequencies of colonized leaves among the lower five leaves were not significantly different ($\chi^2 = 8.91$; df = 4; $P = 0.06$), 3). Frequencies of colonized leaves among early, mid-, and late sowing treatments were not significantly different ($\chi^2 = 4.46$; df = 2; $P = 0.11$), and all alate cabbage aphids colonized the lower five leaves on the primary stem.

Regarding spatial distribution analyses (SADIE) of counts on racemes, we found that cabbage aphids were significantly aggregated at week 7 across all combinations of sowing treatments (I_a values ranged from 1.36 to 1.81 and $P < 0.05$). However, spatial distribution analyses of all weekly cabbage aphid counts on leaves of primary stems and on racemes during the initial five weekly counts suggested that cabbage aphids were randomly distributed (I_a values ranged from 0.71 to 1.11 and $P > 0.05$). Logistic regression analyses showed that cabbage aphid presence was negatively associated with distance from plot centers for all three sowing treatments and four canola growth stages tested, except for mid-sowing at week 7 (see Table 2). Ordinary regression of cabbage aphid counts (i.e., positive data only) at weeks 2 (leaves), 4 (racemes), and 5 (racemes) showed no significant association between distance from plot centers and cabbage aphid counts. However, by week 7, significant negative associations between distance from plot centers and cabbage aphid counts were evident across all three sowing treatments: early ($F = 32.81$; $P < 0.001$; $R^2 = 0.226$), mid- ($F = 45.18$; $P < 0.001$; $R^2 = 0.205$), and late ($F = 39.37$; $P < 0.01$; $R^2 = 0.275$). In summary, ordinary regression of presence data and SADIE yielded significant results for week 7 only, while logistic regression detected significant spatial trends in all data sets.

Commercial Field Sites. Of the 590 canola plants sampled at 59 sampling points at York and 1,000 plants

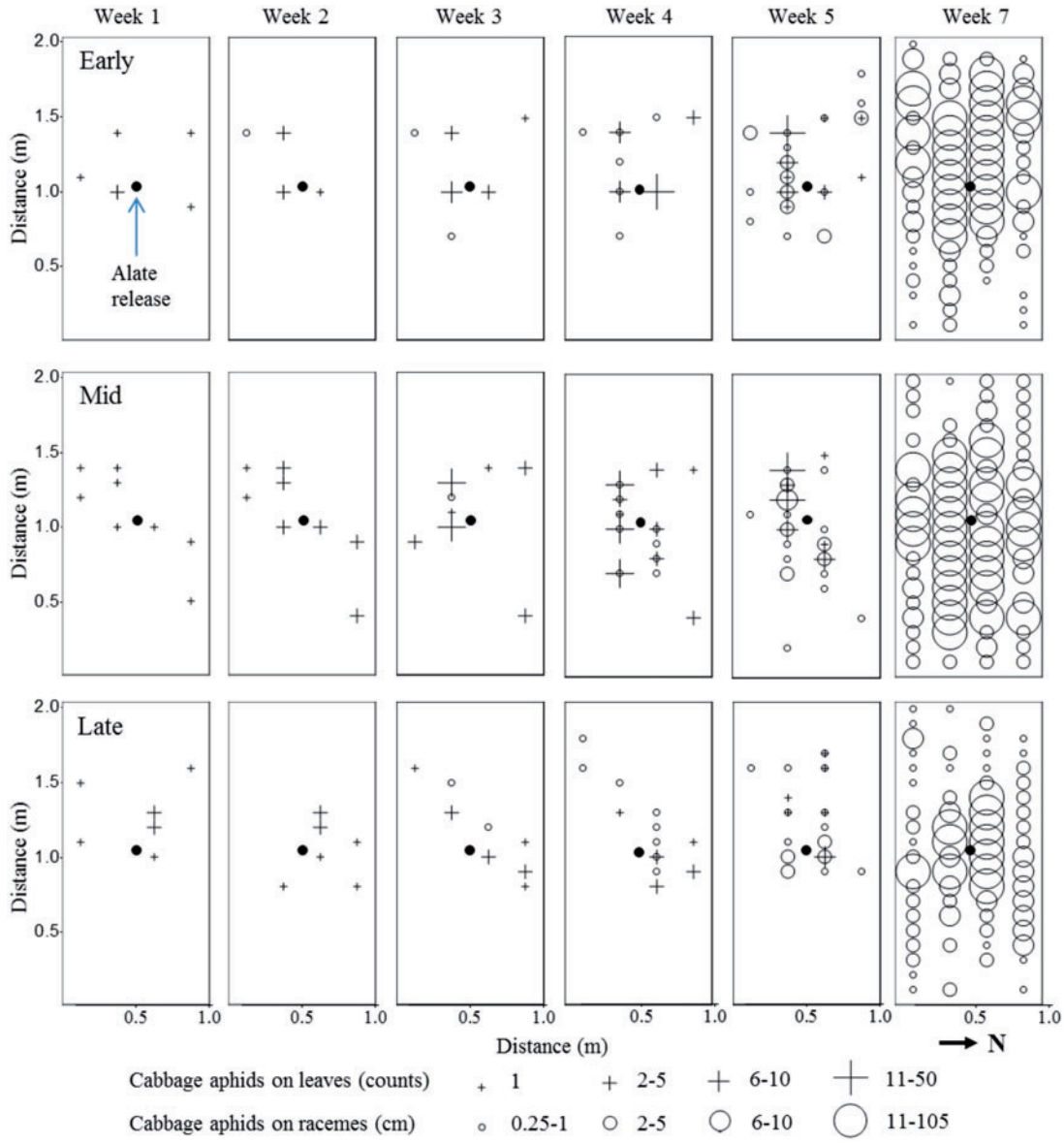

Fig. 2. Distribution of cabbage aphids on primary stem leaves (+; counts) and racemes (o; colony length in centimeters) of canola grown in irrigated plots within insect-proof tunnel houses at Shenton Park Field Station, Western Australia. Treatments consisted of three sowing times: early (10 May), mid- (24 May), and late (7 June) with six replicates. Symbols represent aphid counts or colony length averaged across the six replicates for each grid-referenced plant location.

sampled at 100 points at New Norcia field sites, cabbage aphids were detected on leaves on only 9 (York) and 4% (New Norcia) of the total plants sampled. Thus, even without taking the spatial distribution of canola plants into account, there was a highly aggregated frequency distribution of cabbage aphids on canola leaves. Canola plants with cabbage aphids on leaves were distributed across 36 (York) and 16% (New Norcia) of the total sampling points. Likewise, cabbage aphids were detected on racemes at York and New Norcia on only 8 and 20% of total plants sampled and these were distributed across 32 and 50% of sampling points, respectively. The average percentages of plants infested with cabbage aphids were $8.0 \pm 2.1\%$ and $20.2 \pm 2.9\%$ at York and New Norcia, respectively (Table 1).

For field-wide sampling, SADIE results suggested no significant aggregation at York ($I_a = 1.02$; $P = 0.41$) or New Norcia ($I_a = 0.79$; $P = 0.79$). Cabbage aphids were most commonly detected within 20–30 m of the crop edge and rarely detected further inwards (Fig. 4). Cabbage aphids detected further into the field were initially considered "outliers." However, it was evident that the locations were near either a tree line or

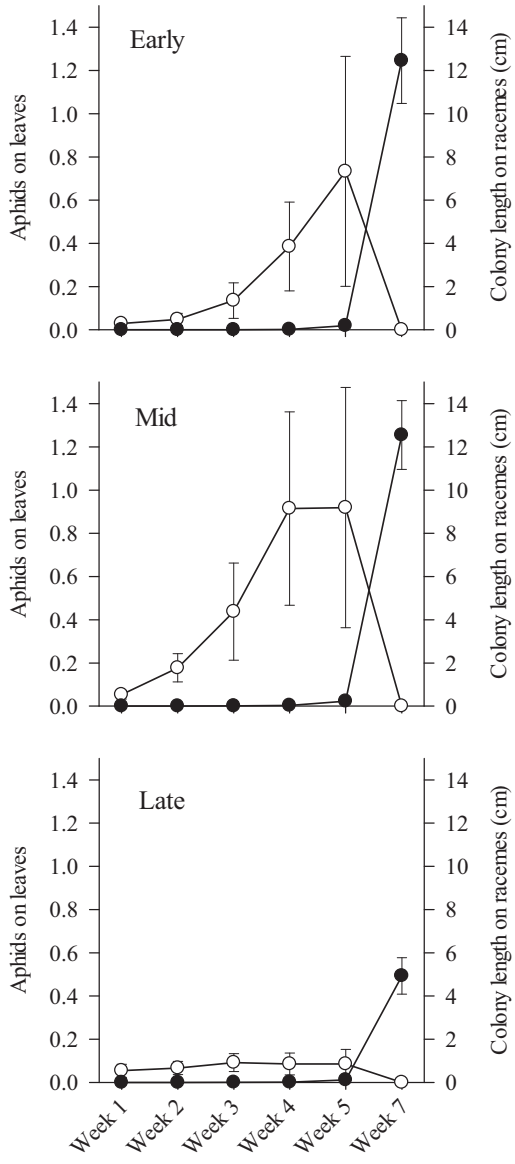

Fig. 3. Average number of cabbage aphids on primary stem leaves (○; left y-axis) and colony length (cm) on racemes (●; right y-axis) for early (10 May), mid- (24 May), and late (7 June) sowing at week 1 (26 August), 2 (02 September), 3 (09 September), 4 (16 September), 5 (23 September) and 7 (7 October) after aphid release. Bars represent SE of the mean cabbage aphids from 80 plant locations averaged across six replicates per treatment.

contour bank, and these were considered as within-field crop edges. Logistic regression analyses revealed that distance to crop edges (i.e., including within-field noncrop regions such as tree lines and contour banks) was a significant factor in determining the presence of cabbage aphids on racemes for both York and New Norcia canola fields (Table 3) (Figs. 4a and d). Distance to crop edges was also important in determining the presence of cabbage aphids in sweep net samples at York and the presence of cabbage aphids on leaves at New Norcia. The number of plants per square meter was a significant factor in determining the presence of any (i.e., unidentified) aphids in sweep net samples at New Norcia, but this was not significant at the York site (Table 3). With regards to ordinary regression of cabbage aphid counts, significant albeit weak relationships existed for New Norcia only; these were between distance from crop edges and cabbage aphid colony length counts on racemes ($F = 12.88$; $P < 0.01$; $R^2 = 0.195$) and distance from crop edges and total aphids in sweep net samples ($F = 28.16$; $P < 0.01$; $R^2 = 0.247$).

Field Edge Grids. Distance to crop edges was a significant factor in predicting both cabbage aphid counts and probability of cabbage aphid presence, when modeled for all four field-edge locations (Table 4). Mean cabbage aphid colony lengths showed a logistic decrease with increasing distance to field edges at both sites (Fig. 4b, c, e, and f). SADIE analyses showed significant indices of aggregation ($P < 0.05$) for all field-edge grids at both fields for total racemes infested, total plants infested and total cabbage aphids and colony lengths per square meter (Table 5). The sevenfold higher I_a values for total cabbage aphids per square meter for York east compared with York west field-edge grids is most likely because of the much higher populations of cabbage aphids at the York east edge (Fig. 4b and c).

Discussion

A lack of reliable and practically feasible sampling is one of the main constraints in widespread adoption of threshold-based pest management (Taylor 1984, Nansen and Ridsdill-Smith 2013). This is evident in canola cropping systems in which growers and their advisors have limited knowledge about how to accurately and cost-effectively estimate cabbage aphid densities late in the canola season. New insight into the spatial and temporal distribution pattern of cabbage aphids in canola was gained in the current research and will be beneficial in the development of optimized monitoring and detection procedures.

Spread From Release Points. The spatial distribution of alate cabbage aphids in the small-plot experiment was aggregated in relation to distance from plot centers when released from a single point source, indicating limited alate flight distance in relation to the source location. Powell et al. (2006) explained that very few alate aphids migrating from a host plant locate suitable hosts because they are 1) mostly specialized to specific host species, 2) susceptible to desiccation given their small size and soft cuticle and, therefore, require minimal periods of time between feeding to survive, and 3) relatively weak flyers and can only control speed and direction in low-wind conditions. Where there is a particular host preference or prevailing wind, aphids are known to display a gradient effect from the initial "invading" population (Helson 1958).

Table 2. Small-plot experiment: logistic regression statistics for cabbage aphids on primary stem leaves or racemes in relation to distance from plot centers for early (10 May), mid- (24 May), and late (7 June) sowing treatments

Treatment	Position: date	Parameter	Estimate	SE	*t*	Significance
Early	Leaves: week 2	Constant	−0.05	1.34	−0.04	0.968
		Distance from center	−0.11	0.05	−2.04	0.042
	Racemes: week 4	Constant	−1.12	0.96	−1.17	0.243
		Distance from center	−0.05	0.02	−2.08	0.037
	Racemes: week 5	Constant	−0.07	0.66	−0.1	0.921
		Distance from center	−0.05	0.02	−3.22	0.001
	Racemes: week 7	Constant	3.88	0.65	5.99	<0.001
		Distance from center	−0.05	0.01	−5.33	<0.001
Mid	Leaves: week 2	Constant	−1.34	0.95	−1.42	0.157
		Distance from center	−0.06	0.03	−2.22	0.027
	Racemes: week 4	Constant	1.00	0.74	1.34	0.179
		Distance from center	−0.10	0.03	−4.02	<0.001
	Racemes: week 5	Constant	1.17	0.59	1.97	0.049
		Distance from center	−0.08	0.02	−4.91	<0.001
	Racemes: week 7	Constant	2.42	0.43	5.64	<0.001
		Distance from center	−0.02	0.01	−3.89	<0.001
Late	Leaves: week 2	Constant	−0.46	1.61	−0.28	0.777
		Distance from center	−0.11	0.07	−1.68	0.093
	Racemes: week 4	Constant	−0.87	0.84	−1.04	0.299
		Distance from center	−0.05	0.02	−2.35	0.019
	Racemes: week 5	Constant	0.11	0.87	0.12	0.904
		Distance from center	−0.08	0.03	−2.92	0.003
	Racemes: week 7	Constant	4.35	0.68	6.36	<0.001
		Distance from center	−0.06	0.01	−6.08	<0.001

This gradient effect was evident in the small plot trial, and the location and size of the initial population of alates is clearly an important factor in determining the subsequent distribution. The small-plot experiment demonstrated how cabbage aphid density estimates (i.e., mean counts) are, in fact, misleading unless spatial aggregation is considered. In the small-plot experiment, for example, plot mean (per plant) cabbage aphid densities were low until week 7, although several plants in certain portions of plots contained 2–10 cm of cabbage aphid colonies prior to week 7 (Fig. 2). Conversely, we found high plot mean cabbage aphid densities at week 7, but plants in portions of the plots contained no or very few cabbage aphids. Spatially aggregated herbivorous insects may cause greater economic damage than equivalent populations with a more random or uniform distribution, as pest aggregations may increase the risk of over-coming crop plants' ability to tolerate or compensate for infestation levels (Bardner and Fletcher 1974, Hughes and McKinlay 1988). At the same time, spatial aggregations of pest infestations may reduce the ability of natural enemies to locate their prey. Alternatively, plants may be able to compensate for damage caused by aggregated populations of aphids because of production of more racemes or pods (Lamb 1989). Spatial aggregations of cabbage aphids within and between canola plants may explain why previous research conducted in Western Australia often reported no significant yield losses attributed to cabbage aphid feeding (i.e., 16 of 17 trials), even where cabbage aphid populations were considered to be high (Berlandier 2002).

Within-plant Distribution. Many insect pests are known to be nonrandomly distributed within single plants (Kennedy and Booth 1951, Liu and Sengonca 1997, Mo et al. 2008, Martini et al. 2012, Kumar et al. 2014). Cabbage aphid colonies in the small plot trial were spatially aggregated vertically, starting on the abaxial side of leaves in the bottom portion of the canopy and moving to the racemes over the 7-wk period. It was evident that leaves on the primary stem started senescing at the onset of flowering and progressively fell off, starting from basal leaves, with few leaves remaining on the primary stem at week 7. This phenological change wherein leaves drop off, which is portrayed by Papantoniou et al. (2013), would explain the lack of cabbage aphids on leaves at week 7. Importantly, this indicates that the vertical distribution of cabbage aphids is strongly influenced by plant growth stage. Almost all cabbage aphids colonized the underside of lower canopy leaves in the small-plot experiment. Therefore, sampling of cabbage aphids on the abaxial surface of lower canopy leaves may be a reliable means of detecting early or "invading" populations, but unreliable for detecting and estimating cabbage aphid densities in canola crops where they have established because established populations, such as those sampled at York and New Norcia (and weeks 4–7 in the small-plot experiment), are mostly aggregated on raceme terminals. This confirms the current recommendation for sampling of cabbage aphid-infested canola that is based on inspection of racemes, while the leaves are disregarded (Berlandier and Valentine 2001, Berlandier 2004, Bellati et al. 2010, Berlandier et al. 2010).

Large-scale Spatial Distribution Patterns. Ferguson et al. (2003) demonstrated that particular insect pests of canola in the United Kingdom were associated with plant density and growth stage of the primary stem, and that these characteristics could be used in the prediction of their spatial distributions and used in targeted sampling. Field-wide data, which are summarized in Table 1, showed considerable spatial variability

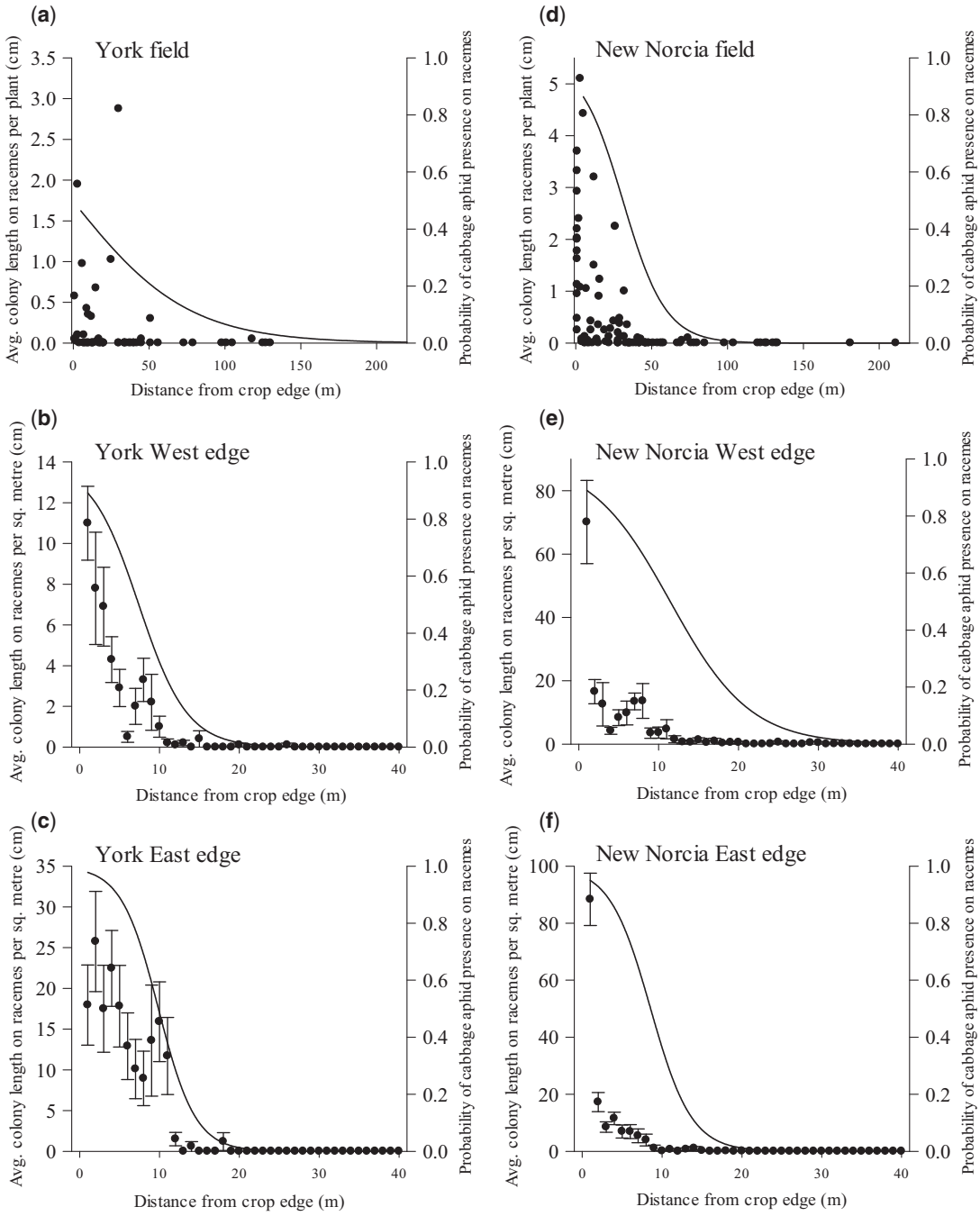

Fig. 4. Plots of average cabbage aphid colony length (cm) on racemes per plant against distances from vegetational edges for field-wide sampling at York (a) and New Norcia (d); average cabbage aphid colony length (cm) on racemes per square meter for York west (b) and east (c) and for New Norcia west (e) and east (f) field edge grids with bars showing SE of mean. All lines within graphs are fitted logistic regressions ($P < 0.05$) and represent the probability of cabbage aphid presence (right, y-axis) on racemes at distances from vegetational edges.

within the measured variables (e.g., plant density and growth stage), which was "on offer" for migrating cabbage aphids. However, this study was unable to demonstrate that distributions could be explained by the plant phenological traits. Moreover, an "edge effect," or gradient in infestation, as described by Fleischer et al. (1999) and Nansen et al. (2005b), was evident for both York and New Norcia canola crops, in which cabbage

Table 3. Field-wide sampling: significant logistic regression statistics ($P < 0.05$) for plant and landscape variables tested as explanatory variable against cabbage aphids on leaves, racemes and in sweep net

Variable	Parameter	Estimate	SE	*t*	Significance
York					
Cabbage aphids on racemes	Constant	−0.01	0.42	−0.03	0.972
	Distance to noncrop	−0.03	0.01	−1.98	0.048
Cabbage aphids in sweep net	Constant	0.03	0.41	0.08	0.934
	Distance to noncrop	−0.02	0.01	−1.98	0.048
New Norcia					
Cabbage aphids on racemes	Constant	2.20	0.49	4.53	<0.001
	Distance to noncrop	−0.07	0.02	−4.66	<0.001
Cabbage aphids on leaves	Constant	−0.50	0.40	−1.26	0.209
	Distance to noncrop	−0.05	0.02	−2.72	0.007
Total aphids in sweep net	Constant	−0.11	0.85	−0.13	0.896
	Plants per square meter	0.03	0.02	2.04	0.041

Table 4. Field-edge grids: logistic and ordinary regression statistics for cabbage aphids on racemes tested against distance from field edge

Location	Parameter	Logistic regression				Ordinary regression of presence data					
		Estimate	SE	*t*	Significance	Estimate	SE	*t*	Significance	*N*	R^2
York west	Constant	2.44	0.40	6.10	<0.001	2.17	0.12	18.34	<0.001	71	0.260
	Distance from edge	−0.33	0.04	−7.95	<0.001	−0.08	0.02	−5.06	<0.001		
York east	Constant	4.24	0.57	7.43	<0.001	3.02	0.17	17.80	<0.001	95	0.055
	Distance from edge	−0.43	0.05	−8.15	<0.001	−0.06	0.02	−2.54	0.013		
New Norcia west	Constant	2.29	0.31	7.33	<0.001	2.84	0.13	21.62	<0.001	112	0.298
	Distance from edge	−0.20	0.02	−9.64	<0.001	−0.08	0.01	−6.93	<0.001		
New Norcia west	Constant	3.34	0.48	6.92	<0.001	3.32	0.16	20.34	<0.001	82	0.442
	Distance from edge	−0.39	0.05	−8.03	<0.001	−0.18	0.02	−8.07	<0.001		

Table 5. Overall indices of aggregation (I_a) for west and east field-edge grids assessed at York and New Norcia

Measurement	York		New Norcia	
	West	East	West	East
Infested racemes per square meter	6.38	8.18	6.48	6.27
Infested plants per square meter	7.56	8.22	7.85	7.07
Total cabbage aphids per square meter	10.20	77.72	>99	>99
Total colony length (mm) per square meter	6.22	6.66	6.41	6.14

$I_a > 1$ indicates clustering; $P < 0.05$ for all values.

aphids were most commonly found within 20–30 m of the crop edge and rarely detected further inwards (Fig. 4). It is also interesting to note that the gradient "steepness" of the edge effect at York (Figs. 4b, c) and New Norcia (Figs. 4e, f) differed with a much higher aggregation of cabbage aphids within the first 1 m from crop edge at New Norcia. It is likely that cabbage aphids originated from peripheral sources such as roadside weeds, and that these insects were driven by prevailing winds, as suggested by Helson (1958).

Infestation of cabbage aphids, detected further into the crop, were initially considered "outliers," as most infested sites were found near the crop edges. It was noted, however, that the locations were either near a tree line or contour bank that harbored alternative hosts for cabbage aphids. For example, an infestation detected >200 m into the crop at New Norcia most likely originated from the cabbage aphid populations identified on wild radish (*Raphanus raphanistrum* L.) growing within the nearby tree line. Infestations detected >50 m into the crop at York were close to contour banks, where wild radish, which was present at the time of sampling, may have been the source of the initial infestations. This association between cabbage aphid detection and within-field "vegetational edges" highlights the importance of weed control within noncropped areas in fields to prevent within-field sources of cabbage aphids. These within-field edge effects also emphasize that tree lines and contour banks should be included in targeted sampling efforts, as they are likely to provide habitat for invading populations of cabbage aphids. Furthermore, fields without noncrop areas may be "safer" in that they are much less likely to contain within-field sources of cabbage aphids given appropriate weed control measures, and this information may aid in field selection.

It should be noted that data represented in this study was collected from one growing season, and that cabbage aphid populations may be much higher in other growing seasons (Dedryver et al. 2010). However, the two fields were sampled at growth stages in which cabbage aphids are most likely to cause economic damage to canola crops in Australia (OIAWA, 2006, Gu et al. 2007) and, therefore, the most important time regarding crop scouting and insecticide application. Furthermore, the edge effects evident in this study will aid in the development of an improved sampling plan for cabbage aphids in canola, which takes into account variable cabbage aphid populations and multiple growing seasons.

Spatial Resolution Analyses. Three spatial resolutions were used to assess cabbage aphid densities, and the two regression methods varied in their suitability to model the data effectively. Low (field-wide), high (square-meter), and very high (per plant) resolutions, as represented by the York and New Norcia crops, field-edge grids and small-plot experiment, respectively, all displayed nonrandom distributions of cabbage aphids. Logistic regression showed that distance from plot centers was negatively associated with cabbage aphid presence for almost all combinations of sowing time and sampling time. It is evident, however, that the test for probability of presence was unsuitable for mid-sowing at week 7 because 99% of plants contained cabbage aphids. Ordinary regression of cabbage aphids on leaves at week 2 and colony length on racemes at week 4 showed no significant association between distance from plot centers and cabbage aphid counts (Table 2). This is not surprising given that early, mid-, and late sowing treatments displayed positive data from few plant locations at this sampling time. Ordinary regression of presence data, however, consistently gave significant edge effects for all four field edge grids but was unable to show significant results, where 1) positive data was low (e.g., very high resolution) and 2) cabbage aphid densities were too variable in relation to distance from crop edge (e.g., low resolution). Therefore, the test for probability of cabbage aphid presence proved to be the most robust in this study because it consistently modeled the three spatial resolutions with statistical significance, except where the percent plants infested was very high. Thus, presence of cabbage aphids on racemes, rather than cabbage aphid colony length counts, is perhaps the most reliable method for predicting cabbage aphid distribution and for targeting sampling efforts.

Sampling Method. Numerous studies have highlighted concerns about sampling being practically challenging and, therefore, proposed improved sampling methods for detection of insect pests in field crops (Nansen et al. 2010, Martini et al. 2012). Sweep net sampling was included in this study as a comparison to counts of cabbage aphids per plant because it is the recommended method of sampling canola fields for other important pests of canola (Berlandier and Baker 2007, Gu et al. 2008) and, if suitable, would simplify the overall crop monitoring efforts. Although the sweep netting technique did not give consistent results between fields, further research is warranted in the use of the insect sweep net, given its established importance for other pests and to complement visual plant inspections to help in the development of a spatially dependent sampling program. It is important to note that sweep netting, which collects insects from the top canopy of canola plants, would not detect cabbage aphids where they have colonized the lower canopy leaves and would therefore only be suitable in detecting already established populations.

In conclusion, reduced sampling effort and increased detection of emerging infestations of cabbage aphids in canola may be achieved by targeting sampling points and plant parts where they are most likely to occur. So, rather than sampling randomly throughout a canola crop, results from this study clearly showed that cabbage aphids are most likely to be detected early on the abaxial side of leaves in the bottom portion of the crop canopy and on plants within the first 10–20 m of crop edge or other noncrop areas, such as weedy patches within or adjacent to canola fields. Therefore, weed control within and around the peripheral of canola crops is highlighted as a potential management strategy to reduce risks of cabbage aphid infestations.

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