Effects of different pesticide management options on the population dynamics of aphids, *Lipaphis erysimi pseudobrassicae* (Davis) and *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), their natural enemies and the yield of cabbage

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ABSTRACT

Cabbage is a popular vegetable grown in Ghana and it serves as an important source of livelihood for small-scale farmers. Aphids are major pests of cabbage in the field and as such, farmers have resorted to the indiscriminate use of insecticides which have had adverse environmental and health implications. The current study sought to investigate the effect of commonly used management options on the population of aphids, *Lipaphis erysimi pseudobrassicae* (Davis) and *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), their natural enemies and the yield of cabbage. Cabbage seedlings were planted during the major and minor seasons of 2015 in 3 x 3 m plots and the treatments used included Chlorpyrifos, Lambda-cyhalothrin, hot pepper, *Capsicum futescens* fruit extract, neem, *Azadirachta indica* seed extract, solution of local soap (*alata samina*) with water as a control. Ten cabbage leaves per treated plot were randomly sampled weekly into 70% alcohol to obtain actual counts of aphids and their natural enemies. The least number of aphids was recorded in the neem treated plots, while Lambda-cyhalothrin treated plots recorded the highest number of aphids. The control and biopesticide treated plots recorded the highest numbers of the natural enemies (hoverflies, ladybirds and spiders). The highest yield and marketability was recorded in the neem treated plots for both seasons. The yield and marketability of cabbages obtained from plots sprayed with *alata samina* and pepper was also higher than that obtained from the control, Lambda-cyhalothrin and Chlorpyrifos treated plots, with the insecticide treated plots recording the least number of marketable heads. It offered the most promising solution. The current findings suggest that the crude neem seed extract, and to some extent local soap, *alata samina*, and pepper, are effective and safe options for managing aphids on cabbage.

Keywords: Pesticides, Mustard aphid, Green peach aphid, Neem, Natural enemies

Introduction

Cabbage, *Brassica oleracea* var. *capitata* L. (Brassicaceae) is a popular and very important vegetable grown in Ghana. It is a cold temperate crop that also thrives in other climates throughout the world (Nieuwhof, 1969; Dickson and Wallace 1986; Mochiah *et al.*, 2011a). It has been identified by the Food and Agriculture Organization (FAO) as one of the top twenty vegetables and an important food source globally (FAO, 1998). Cultivation of this crop serves as a source of employment for most of the rural and peri-urban population in Ghana (Abbey and Manso, 2004). Cabbage is usually consumed raw or cooked in stews. This cruciferous vegetable provides important nutrients such as vitamins, dietary fibre, iron, potassium, manganese and magnesium for healthy body development (USDA, 2009). Despite these benefits, cabbage has been ravaged by several insect pest species. Among them, the aphids: *Brevicoryne brassicae* L., *Lipaphis erysimi erysimi* Kalt., *Lipaphis erysimi pseudobrassicae* (Davis) and *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) cause devastating losses in the production of cabbage worldwide (Müller, 1986; Ronquist and Ahman, 1990; Mc Cullum *et al.*, 1992; Sæthre *et al.*, 2011; Fening *et al.*, 2013; Vidogbéna *et al.*, 2015). All the stages of these insects feed on the phloem, and their feeding results in stunted plants with little or no yield (Hughes, 1963; Mochiah *et al.*, 2011b). They cause indirect damage by transmitting viral diseases to the cabbage plant during feeding (Blackman and Eastop, 1984; Flint, 1991). Also, the excretion of honeydew supports the growth of sooty mould which decreases yield and marketability of cabbage heads (Blackman and Eastop, 1984; Amoabeng *et al.*, 2013).

Fortunately, these pests are attacked by several natural enemies, including the ladybird beetle *Cheilomenes* spp., *Coccinella* spp., (Coleoptera: Coccinellidae), the hoverflies *Paragus borbonicus* (Diptera: Syrphidae), spiders (Araneae) and the braconid parasitoid *Diaeretiella rapae* (Stary) (Hymenoptera: Braconidae) (Fening *et al.*, 2011, 2014; Liu *et al.*, 2014). These natural enemies can reduce the rate of population increase of the aphids or even wipe out infestations (Mandal and Patnaik, 2008; Liu *et al.*, 2014). Despite its effectiveness, this natural control is often considered inadequate, and this situation, combined with the growing craving for damage-free cabbages (vegetables), makes farmers often overuse insecticides to meet this demand (Obeng-Ofori *et al.*, 2002; Ntow *et al.*, 2006; Osei *et al.*, 2013). However, several authors have attested that these chemicals often adversely affect the health of people, the environment and especially the natural enemies, which serve as a natural control measure for these pests (Obeng-Ofori *et al.*, 2002; Ntow *et al.*, 2006; Fernandes *et al.*, 2010; Fening *et al.*, 2011, 2014). It is therefore necessary to seek alternative, sustainable methods of managing cabbage pests. This study sought to assess the effect of some management options on aphids, their natural enemies and the yield of cabbage, in order to provide sustainable options for managing these insect pests.

Materials and method

Study site

The study was carried out at the University of Ghana Soil and Irrigation Research Centre, Kpong (00 04' E, 60 09' N), located within the lower Volta basin of the Coastal Savannah agro-ecological zone of Ghana. The study hsite has an annual rainfall of between 700 and 1100 mm, an average annual temperature of 28 °C and relative humidity of between 59%-93%. The main soil type is the vertisols (black clay soil). The experiments were conducted from May to August and September to December, 2015 in the major and minor seasons, respectively.

Land preparation, transplanting and application of treatments

The land used was cleared of weeds, ploughed, harrowed and ridged. Seeds of certified healthy hybrid white cabbage (*B. oleracea* var. *capitata*) (*cv. oxylus*) obtained from AGRIMAT Ltd in Accra were sown on raised beds in the field. The young seedlings were protected from pest attack with mosquito-proof netting (1.2 mm ×1. 2 mm of mesh size). Appropriate agronomic and cultural practices such as weed control and watering were employed regularly throughout the growing period. The experimental design was a randomized complete block with six treatments and three replicates. Cabbage seedlings were transplanted 30 days after germination. Spacing was 0.5 x 0.75m and each plot measured 3 m x 3 m, giving a total of 30 plants per plot. Inter-plot and inter-block distance was 2m to prevent drift between adjacent plots and blocks. NPK 15-15-15 (5g/plant) and Sulphate of Ammonia (3g/plant) were applied in a ring form around each plant 10 and 42 days respectively after transplanting.

Treatments used were neem *Azadirachta indica* seed extract (50g/L of water), hot pepper *Capsicum frutescens* fruit extract (20g/L of water), local soap (*alata samina*) solution (7g/L of water), two commonly used synthetic insecticides, Conpyrifos® (Chlorpyrifos 480g/L, applied at 2ml/L of water), Lambda M® (Lambda-cyhalothrin, 25g/L, applied at 2ml/L of water) and tap water as control. For the hot pepper, ripe fruits were obtained from a local market and the required weight obtained using an electronic balance. The weighed fruits were homogenised using an electric blender. The required amounts of dry neem seeds were also weighed and pounded in a wooden mortar using a wooden pestle. The homogenate was mixed separately with 1L tap water, and a few drops of liquid soap (Madar Renzo®) and vegetable oil were added to enhance its delivery and stickiness onto the leaf surfaces of the cabbage plant. The resultant mixture was left overnight, and later sieved through a fine linen material. The mixtures were further diluted with the required volume of water for spraying. The required amount of *alata samina* was also weighed and dissolved in the required volume of water. Treatments were applied using a 15L capacity knapsack sprayer on the top and the underside of leaves. Applications commenced 14 days after transplanting the seedlings for both the major and minor seasons and continued weekly thereafter until cabbage heads were fully mature, about 14 days before harvesting. There were seven applications for each season.

Data collection

Sampling for aphids was modified from the method according to Hughes (1963). Ten leaves per plot were randomly sampled into 70% alcohol to obtain actual counts of aphids. Natural enemies were also separated and counted. In addition, weekly field observations were made to determine the number of natural enemies per plot. For yield assessment, a total of 12 cabbage heads in the three inner rows (4 cabbages per row) was harvested and weighed, and the mean for each treatment calculated. Mean yields were extrapolated into tonnes/hectare. The cabbage head damage was assessed by using a standard scoring scale of 0-5 (Aboagye, 1996): zero (0) = no head damage, 1= 1-15% head damage, 2= 15-30% head damage, 3=30- 45% head damage, 4= 45-60% head damage, 5= 60-100% head damage, and categorised into marketable and unmarketable heads.

Identification of pests and their natural enemies

The aphids and their natural enemies collected in this study were identified using reference specimens at the Insect Museum of the Department of Animal Biology and Conservation Science, University of Ghana, Accra. Samples of the immature stages of coccinellids and syrphids were cultured in the laboratory to the adult life stage to allow identification by comparison with labelled specimens in the insect museum. Voucher specimens of all the insect species collected were also deposited in the insect museum. The aphid species were identified using taxonomic keys by Blackman and Eastop (1984).

Data analysis

Count data for aphids and natural enemies were square root transformed and subjected to repeated measures of ANOVA. Mean cabbage head weight was analysed using ANOVA. Significant differences in means were separated using SNK test ($P \leq 0.05$). All analyses were carried out in GENSTAT V12.

Results

Generally, the neem was very effective in controlling the aphids *Lipaphis e. pseudobrassicae* and *M. persicae* for the two seasons, even more than the synthetic insecticides (Figs. 1-4). *Lipaphis e. pseudobrassicae* infestation started in the first sampling week for the two seasons and increased progressively throughout the sampling period. The population of *Lipaphis e. pseudobrassicae* was at its peak in the third and fourth week for the major season and the fifth week for the minor season of 2015 (Figs. 1 and 2). Lambda-cyhalothrin treated plots recorded the highest number of *Lipaphis e. pseudobrassicae* for both the major and minor seasons. Infestations in the botanical treated and Chlorpyrifos treated plots were minimal. Neem however recorded the least number of *Lipaphis e. pseudobrassicae* for both seasons. There was a significant difference in the effect of the different treatments on *Lipaphis e. pseudobrassicae* for both seasons ($F_{5,125}$ = 3.69; P = 0.0380, and $F_{5,125}$ = 5.58; P = 0.010, respectively). There was also a significant difference in the effect of each treatment on the population of *Lipaphis e. pseudobrassicae* among the weeks of sampling for both seasons ($F_{6,125}$ = 21.54; P < 0.001 and $F_{6,125}$ = 9.82; P = < 0.0010). However, the interaction between the spray formulations and weeks of sampling of *Lipaphis e. pseudobrassicae* was not significant for the major season ($F_{30,125}$ = 1.75; P = 0.1340) but significant for the minor season ($F_{30,125}$ = 3.03; P = 0.008).

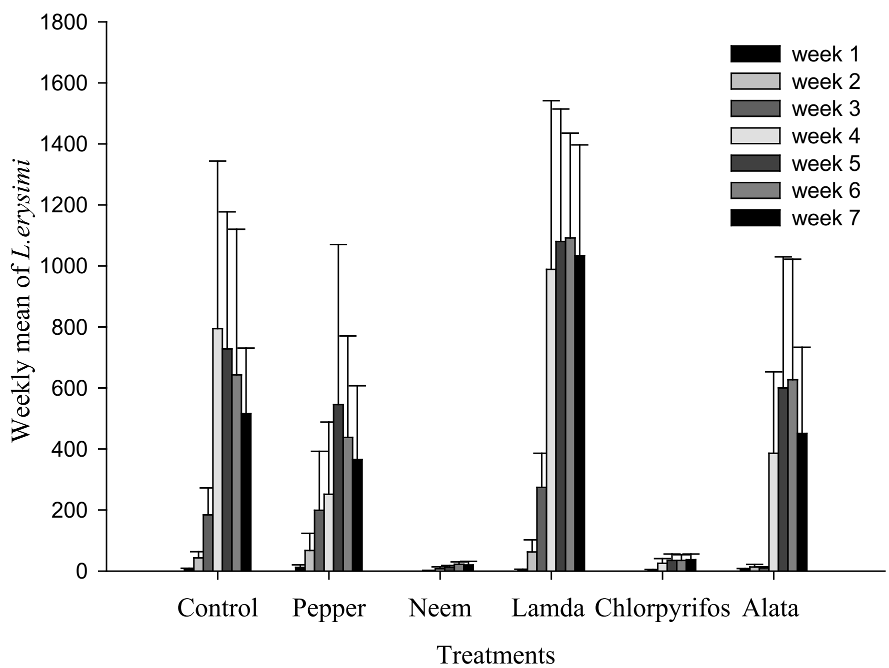

Fig. 1: Effects of treatments on mean (± *SE*) weekly count of *Lipaphis e. pseudobrassicae* per cabbage plant during the major season, 2015 in Kpong, Ghana.

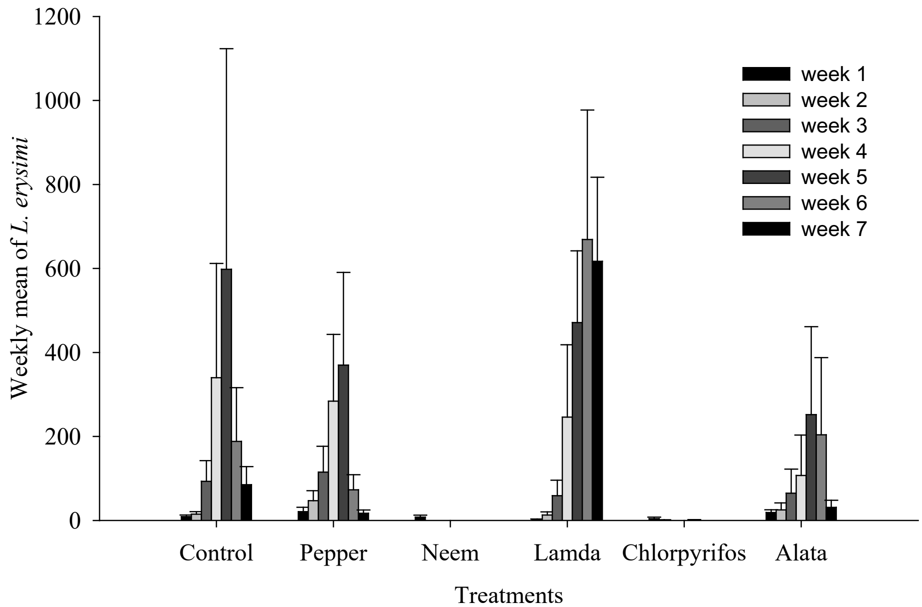

Fig. 2: Effects of treatments on mean (± *SE*) weekly count of *Lipaphis e. pseudobrassicae* per cabbage plant during the minor season, 2015 in Kpong, Ghana.

Myzus persicae infestation started in the first week of sampling, depending on the treatment for the major season, and in the fourth week of the minor season, and increased progressively throughout the sampling period of 2015 (Figs. 3 and 4). Infestation by this pest was generally low throughout the sampling period for both seasons. Plots sprayed with botanical insecticides and water had very minimal infestation for the major season compared to the synthetic insecticides. In the minor season, infestation was minimal in the botanical treated and Chlorpyrifos treated plots. Highest *M. persicae* numbers were recorded in the Lambda-cyhalothrin treated plots for the major season and the control plots for the minor season. However, neem treated plots recorded no *M. persicae* for both seasons. There was no significant difference in the *M. persicae* population among the treatments for both seasons ($F_{5,125} = 1.67$; $P = 0.2290$ and $F_{5,125} = 0.71$; P = 0.6310). The effect of treatments on the *M. persicae* population among the sampling weeks was significant for the major season ($F_{6,125} = 12.55$; $P = 0.0030$) but not for the minor season ($F_{6, 125} = 2.10$; $P = 0.170$). However, the interaction between the treatments and the sampling time for the *M. persicae* population was not significant for both seasons ($F_{30, 125} = 1.54$; $P = 0.2400$ and $F_{30, 125} = 0.79$; $P = 0.5850$).

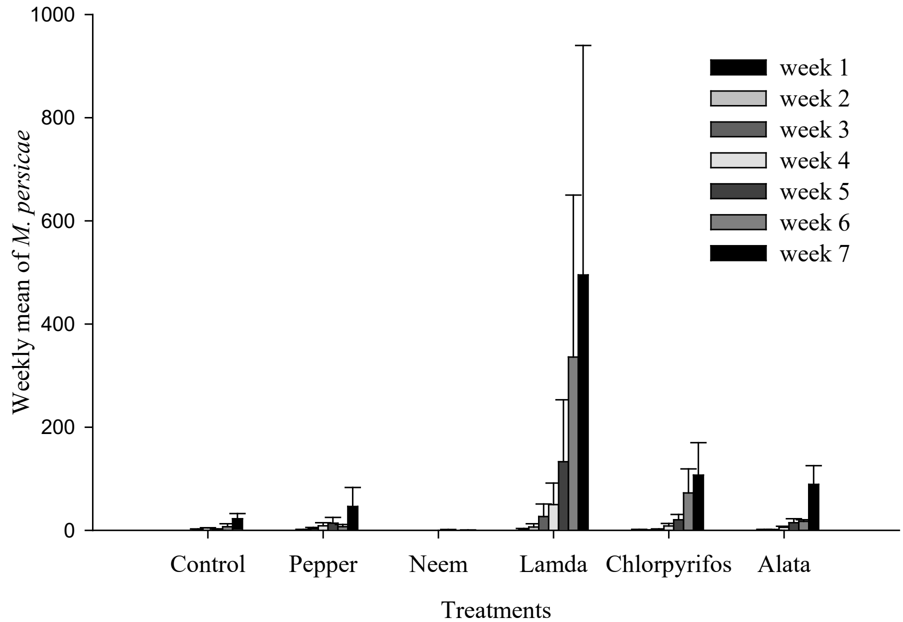

Fig. 3: Effects of treatments on mean (±SE) weekly count of *M. persicae* per cabbage plant during the major season, 2015 in Kpong, Ghana

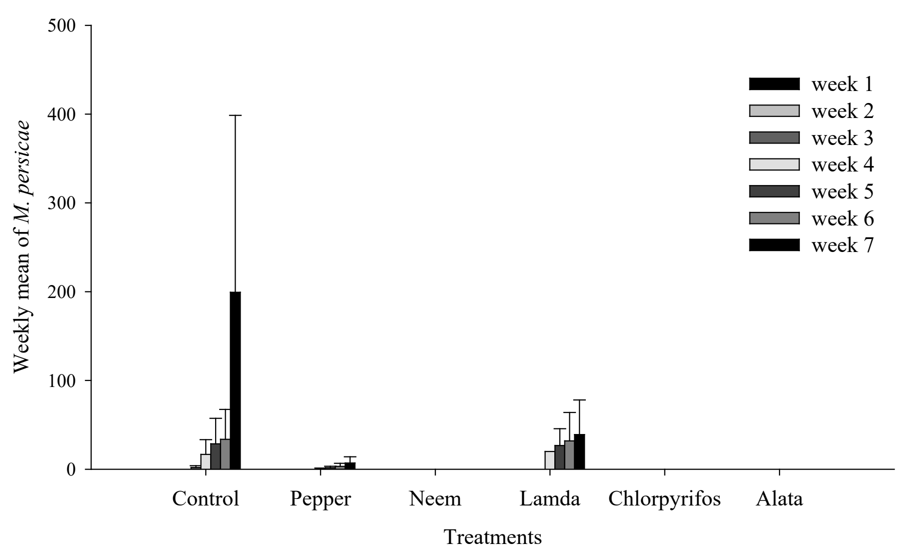

Fig. 4: Effects of treatments on mean (±SE) weekly count of *M. persicae* per cabbage plant during the minor season, 2015 in Kpong, Ghana.

The incidence of hoverfly, *P. borbonicus* was recorded in the first week of sampling and increased progressively until it reached its peak population in the fifth week of sampling for the control plots for both seasons during 2015 (Figs. 5 and 6). Plots sprayed with neem, Lambda-cyhalothrin and Chlorpyrifos had the least number of hoverflies for both seasons. Control plots recorded the highest number of hoverflies, followed by the pepper and *alata samina* treated plots. The number of hoverflies was significant among the treatments for both seasons ($F_{5,125} = 5.23$; $P = 0.0130$ and $F_{5, 125} = 4.17$; $P = 0.0260$). There was also a significant difference in the effect of treatments on the hoverfly population in the different weeks of sampling for the major season ($F_{6,125} = 13.00$; $P < 0.0010$) but no significant difference during the minor season ($F_{6,125} = 2.63$; $P = 0.0920$). The interaction between the treatments and sampling time was significant for the major season ($F_{30,125} = 2.30$; $P = 0.0260$) but not for the minor season ($F_{30,125} = 1.82$; $P = 0.1090$).

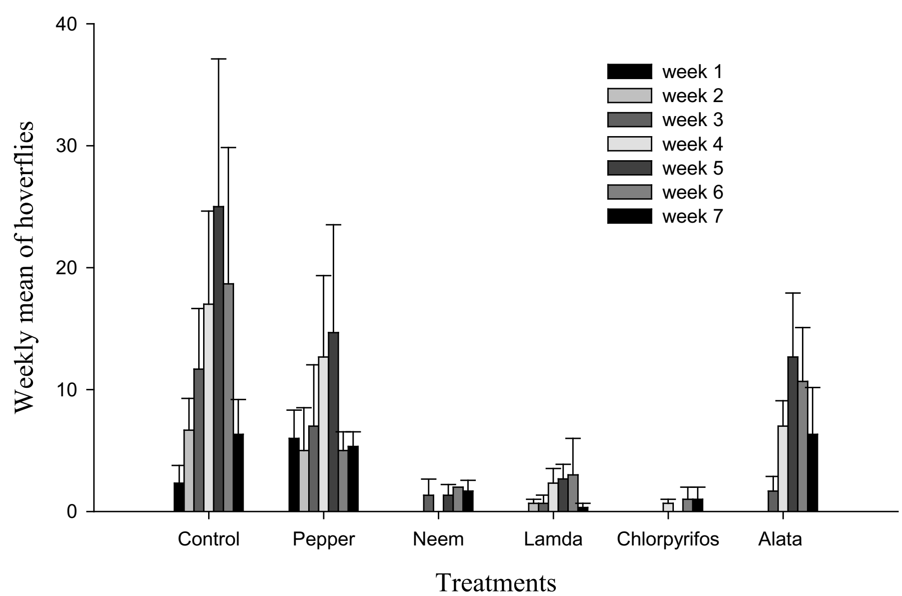

Fig. 5: Effects of treatments on mean (± *SE*) weekly count of the hoverfly, *P. borbonicus*, per cabbage plant during the major season, 2015 in Kpong, Ghana.

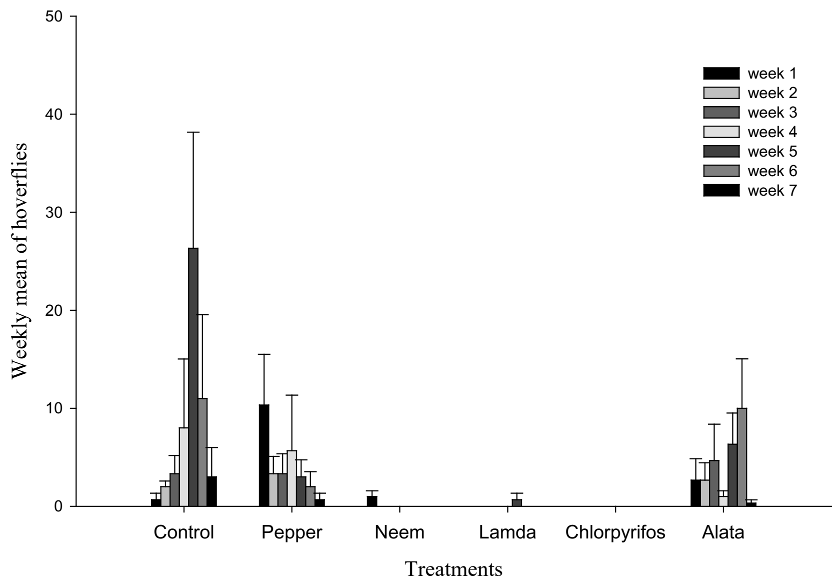

Fig. 6: Effects of treatments on mean (± *SE*) weekly count of the hoverfly, *P. borbonicus*, per cabbage plant during the minor season, 2015 in Kpong, Ghana.

The occurrence of ladybird, *Cheilomenes* spp. started in the first week of sampling and reached its peak population in the fifth and fourth week of sampling for the major and minor seasons of 2015 respectively (Figs. 7 and 8). Control plots, pepper-treated plots and *alata samina* treated plots recorded the highest number of ladybirds for both seasons. The neem, Lamda-cyhalothrin and Chlorpyrifos treated plots recorded the least number of ladybirds for both seasons. There were significant differences in ladybird abundance among the treatments for the major season ($F_{5,125} = 3.92$; $P = 0.0310$), but no significant difference in the minor season ($F_{5,125} = 1.82$; $P = 0.1960$). There was also a significant difference in the effect of each treatment on the ladybird population among the weeks of sampling for the major season ($F_{6,125} = 12.87$; $P < 0.0010$) but no significant difference in the minor season ($F_{6,125} = 1.47$; $P = 0.2520$). The interaction between the treatments and sampling time was not significant for both seasons ($F_{30,125} = 1.69$; $P = 0.1530$ and $F_{30,125} = 0.69$; $P = 0.7060$).

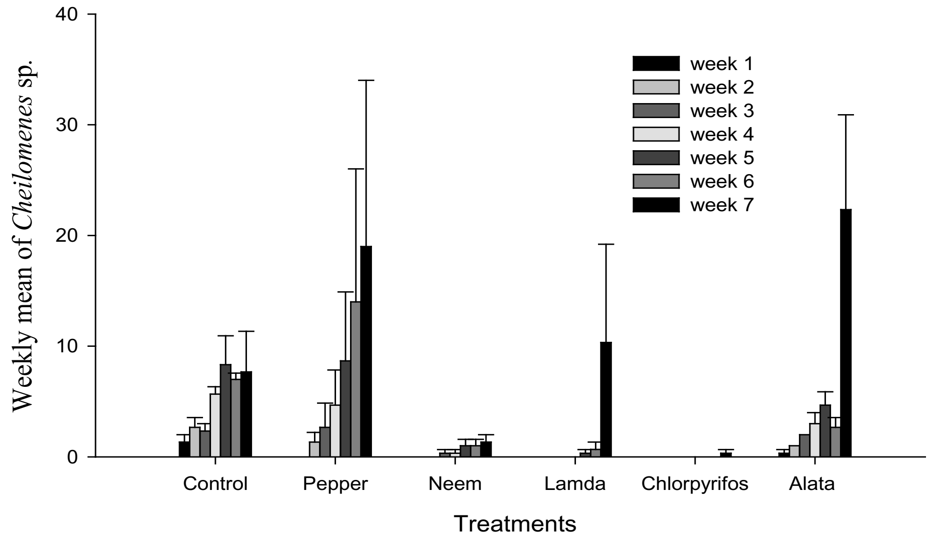

Fig. 7: Effects of treatments on mean (± *SE*) weekly count of the ladybird beetle, *Cheilomenes* spp., per cabbage plant during the major season, 2015 in Kpong, Ghana.

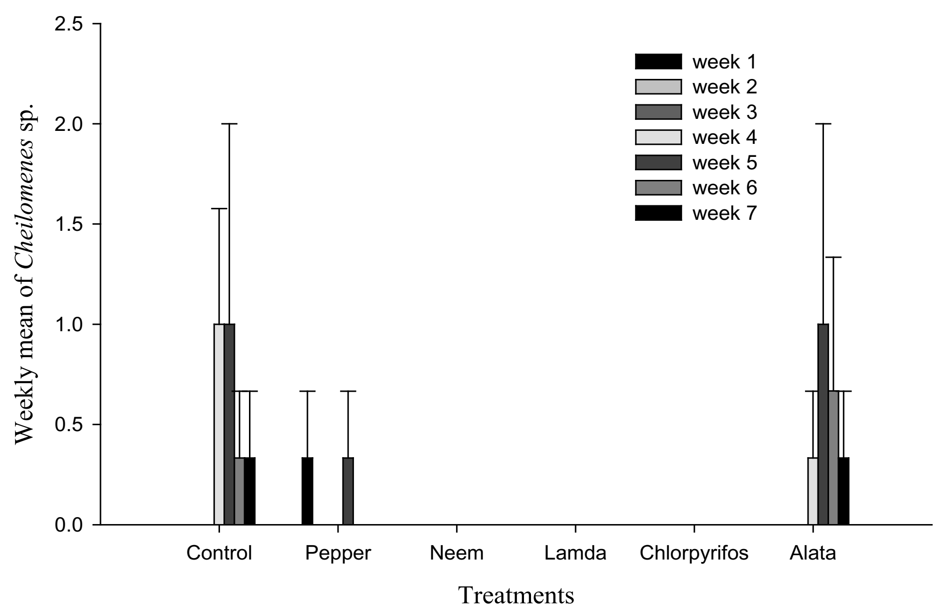

Fig. 8: Effects of treatments on mean (± *SE*) weekly count of the ladybird beetle, *Cheilomenes* spp. per cabbage plant during the minor season, 2015 in Kpong, Ghana.

The occurrence of spiders started in the first week of sampling and continued increasing until its peak in the fifth week of sampling for both seasons (Figs. 9 and 10). Control plots recorded the highest number of spiders, followed by the botanical treated plots for both seasons. Plots sprayed with synthetic insecticides recorded the lowest number of spiders for both seasons. There was a significant difference among the different treatments in controlling the spiders for both seasons ($F_{5,125} = 21.27$; $P < 0.0010$ and $F_{5,125} = 61.95$; $P < 0.0010$). The effect of each treatment on the spider population among the weeks of sampling for both seasons was also significantly different ($F_{6,125} = 12.30$; $P < 0.0010$ and $F_{6,125} = 55.91$; $P < 0.0010$). However, the interaction between the sampling weeks and treatment was not significant for the major season ($F_{30,125} = 1.68$; $P = 0.0670$), but significant for the minor season ($F_{30,125} = 4.40$; $P = 0.0010$).

Populations of the cabbage aphid parasitoid, *D. rapae* were very low throughout the sampling period for the major season. Most treatments recorded no *Diaeretiella rapae* for the entire season. Only control plots and pepper treated plots recorded *D. rapae*. The different treatments showed no significant difference for the *D. rapae* populations ($F_{5, 125} = 1.82$, $P = 0.1960$). The effect of the treatments on the weekly sampling of *D. rapae* was not significant for the major season ($F_{6, 125} = 1.70$, $P = 0.2070$). The interaction between the sampling weeks and treatments on *D. rapae* numbers was also not significant ($F_{30, 125} = 1.26$, $P = 0.3140$). *D. rapae* was absent in the minor season.

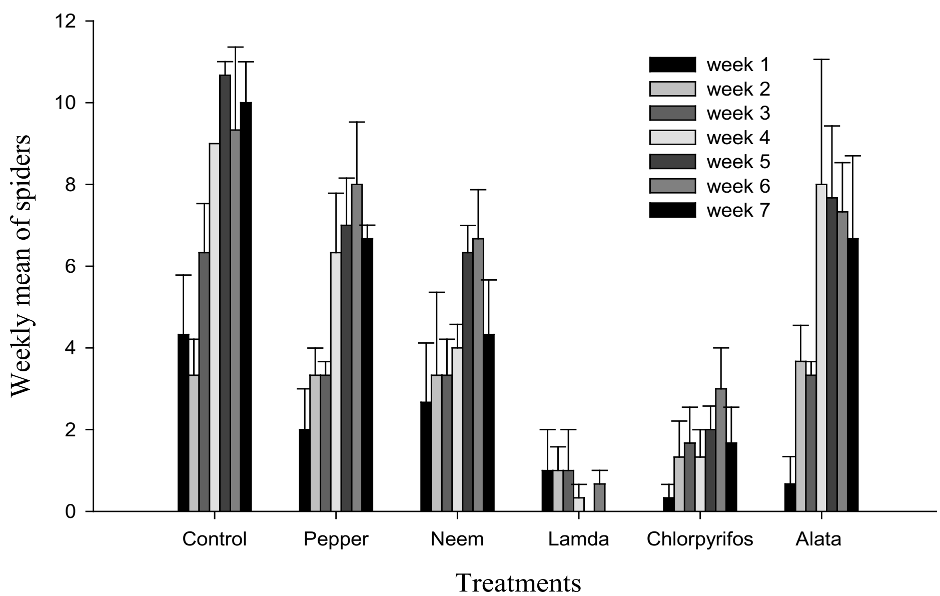

Fig. 9: Effects of treatments on mean (± *SE*) weekly count of the spiders (Araneae) per cabbage plant during the minor season, 2015 in Kpong, Ghana.

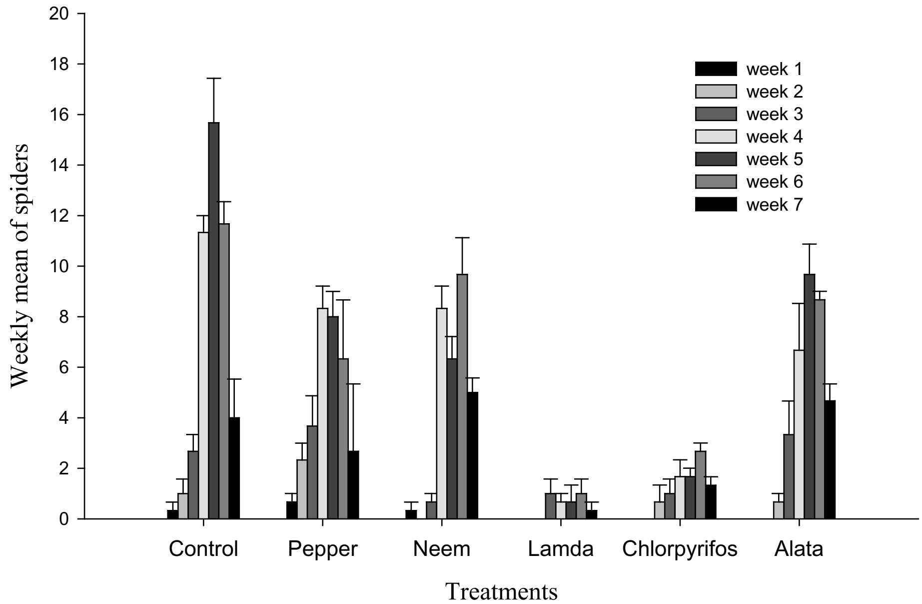

Fig. 10: Effects of treatments on mean (± *SE*) weekly count of the spiders (Araneae) per cabbage plant during the minor season, 2015 in Kpong, Ghana.

The mean yield among the treatments was significantly different for the major and minor seasons in 2015. The neem treated plots had significantly higher yields than the Lambda-cyhalothrin treated plots, but it was not significantly different from the rest of the treatments during the major season (Table 1). However, during the minor season, the highest yield was obtained in the neem sprayed plots, followed by the *alata samina* treated plots. Damage on cabbage heads was highest in the synthetic insecticide treated plots (damage 5 category). Cabbage heads from botanically treated plots were lower (damage 0-2 categories). Within the different treatments, the neem recorded the highest number of marketable heads for both seasons (Figs. 11 and 12). Lambda-cyhalothrin, however, did not record any marketable head for the major season. For the minor season, Chlorpyrifos, control and Lambda-cyhalothrin did not record any marketable head. The yield of cabbage during the major season was significantly higher than that of the minor one for the control and pepper treated plots. However, the yield of the neem treated plot was significantly higher during the minor than the major season.

Table 1: Mean (± *SE*) yield of cabbage under different treatments during the major and minor seasons of 2015, Kpong, Ghana.

Treatment	Mean yield (tonnes/hectare)		*t*-value	*P*
	Major season	**Minor season**		
Water (Control)	12.37 ±1.27ab	0.59 ± 0.07c	8.94	0.0120*
Pepper	12.37 ± 1.30ab	6.50 ± 0.74c	3.93	0.0170*
Neem	17.80 ± 2.61a	28.36 ± 0.97a	4.08	0.0150*
Lambda-cyhalothrin	6.03 ± 2.08b	5.07 ± 2.81c	0.27	0.7970
Alata samina	14.57 ± 2.75ab	15.05 ± 3.05b	0.12	0.9120
Chlorpyrifos	13.40 ± 1.99ab	10.02 ± 3.70bc	0.80	0.4660
F	3.47	22.14		
P	0.0359*	< 0.0010*		

Means with the same letter(s) are not significantly different within ($P < 0.05$, SNK test) within columns. Means between the same row, for both seasons, were compared using *t* test ($P < 0.05$).

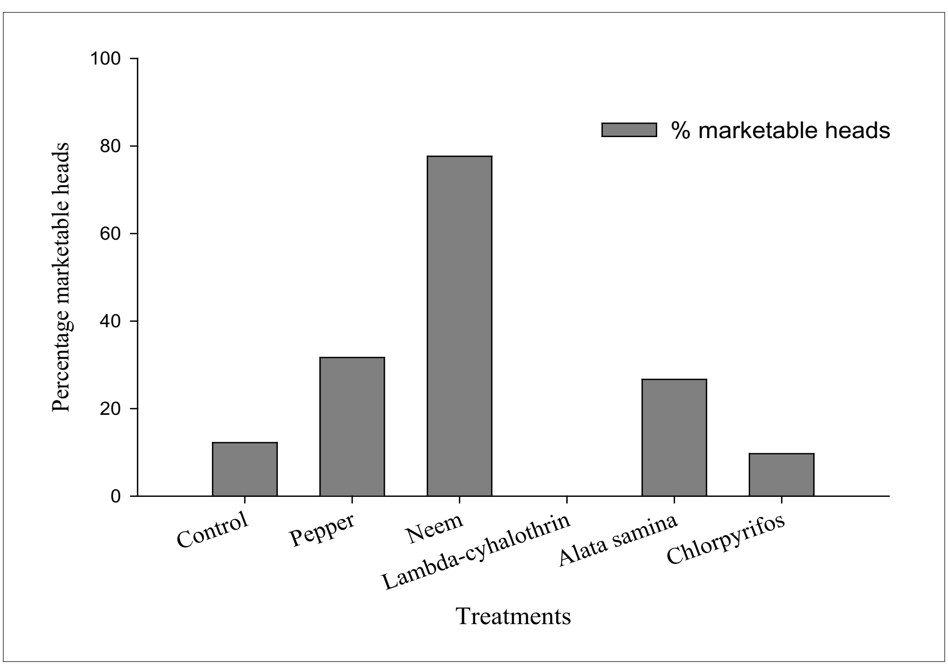

Fig. 11: Mean percentage marketable heads for different treatments for the major season of 2015, Kpong, Ghana.

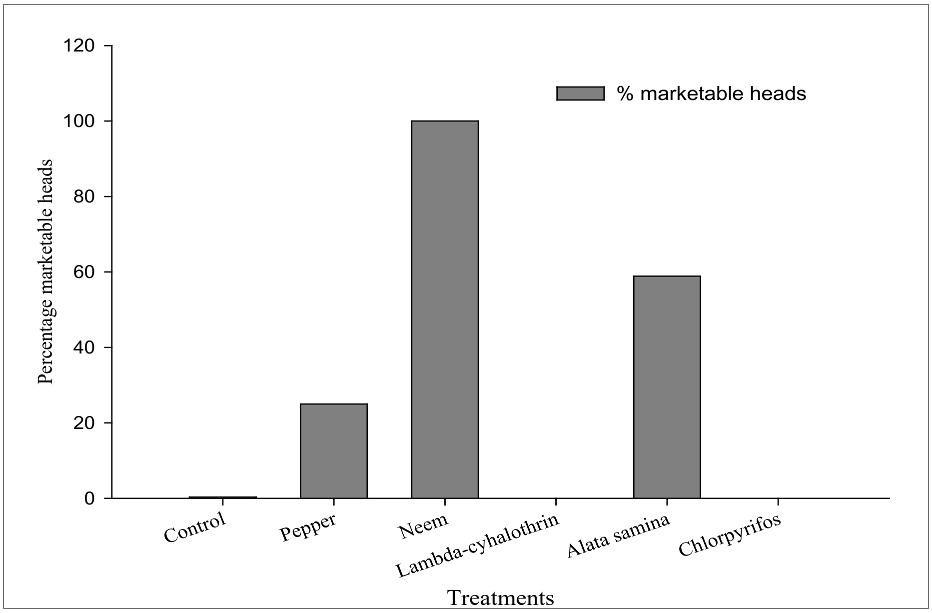

Fig. 12: Mean percentage marketable heads for different treatments for the minor season of 2015, Kpong, Ghana.

Discussion

The main species of aphids identified during the study were *Lipaphis erysimi pseudobrassicae* and *Myzus persicae.* The two species and have been observed to be the main aphids occurring on crucifers in the Hangzhou suburbs in China (Liu *et al.*, 1997). *Lipaphis erysimi* is known to be the specialist aphid on cabbage in Benin and Mali (James *et al.*, 2010; Sæthre *et al.*, 2011), but this is the first report of its presence on cabbage in Ghana. *Myzus persicae*, however, is a polyphagous aphid and has already been reported in Ghana (CIE, 1979). This study has shown that neem is very effective in managing the population of the aphids, *L. e. pseudobrassicae* and *M. persicae* on cabbage, while conserving the natural enemies, especially spiders. However, the abundance of the main aphid predators (hoverflies and ladybird) was very low or absent throughout the sampling period on the neem treated plots. This could be attributed to the fact that the predators' main prey, the aphids, were absent due to their effective control, leading to the low numbers or absence of their predators. However, the spider, being a generalist predator, was found in the neem plot throughout the sampling period, because of the availability of other sources of prey. This implies the neem treatment did not really have any detrimental effect on the natural enemies, including the ladybirds and hoverflies.

The efficacy of the neem is in line with previous work done by other authors. The neem oil formulation was proven effective against *L. erysimi* and did not have any detrimental effect on its hoverfly predator, *Ischiodon scutellaris* (F.) (Diptera: Syrphidae) (Boopathi and Pathak, 2011). The application of 3% neem seed kernel extract also was reported to be effective in reducing the aphid population on cabbage (Patel *et al.*, 1996). According to the current study, the highest yield was recorded in the neem treatment, which supports earlier work done by Baidoo and Adam (2012) that reported improved cabbage yield when the neem was used against insect pests.

This contrasts with the Lambda-cyhalothrin plot which had a continuous build-up of aphids and a detrimental effect on the natural enemies. A similar observation was made in a field experiment in Ghana in which Lambda-cyhalothrin failed to control aphids on cabbage, leading to low yields compared to plots sprayed with garlic, chili pepper and Attack (Fening *et al.*, 2013; 2014). Amoabeng *et al*. (2013) also observed poor control of aphids on cabbage by Lambda-cyhalothrin in a field cage experiment. The lack of control by these insecticides was attributed to the reduction of natural enemies: hoverflies, *Cheilomenes* spp. and spider, and also the resistance of this pest to Lambda-cyhalothrin. This is also likely to have been the case in the present study. Lambda-cyhalothrin is a pyrethroid with a broad spectrum action which could be harmful to non-target organisms such as natural enemies of aphids (Devotto *et al*., 2007). Though Chlorpyrifos (organophosphate) controlled the aphids better than Lambda-cyhalothrin, it also had a negative effect on the natural enemies. Organophosphates are broad spectrum insecticides and are known to be highly toxic to predators (Fernandez *et al*., 2010). For example, Chlorpyrifos 20% EC was found to be highly toxic to the maggots of *I. scutellaris* (Boopathi and Pathak, 2011).

Pepper and *alata samina* also reduced pest populations more than Lambda-cyhalothrin, with no effect on the natural enemies. This observation is confirmed by earlier findings of Zehnder *et al*. (1997) and Fening *et al*. (2013) that pepper controlled aphids on cabbage and conserved its natural enemies better than the insecticides Lambda-cyhalothrin. The ability of pepper to kill or repel pests is speculated to be associated with the presence of capsaicinoid elements in the extract, although this has not been proven (Antonious *et al*., 2006; Fening *et al*., 2013). *Alata samina* has insecticidal properties and is thus considered as an insecticidal soap. The soap is composed of potassium salts of several fatty acids whose mode of action is not well understood, but it is believed to disrupt the cellular membrane of pests, especially soft bodied insects, resulting in the loss of cellular contents, and hence, death (Osborne and Henley, 1982). A lower dose of *Alata samina* is recommended for pest control, as a high dose could have a phytotoxic effect on the plant (Organic Resource Guide, 2010).

Control plots (plots sprayed with only water) had higher yields than Lambda-cyhalothrin in the major season. This was likely to be a result of high natural enemy abundance (spiders, ladybirds and hoverflies) which offered natural control as opposed to Lambda-cyhalothrin. Despite the high numbers of natural enemies in the control plot, the attack by the aphids was very severe due to their large numbers, leading to very low yields in the minor season. This shows that the control of pests solely by natural enemies was inadequate. The addition of botanicals such as neem and pepper will therefore offer a synergy between the two strategies to reduce the population of aphids in the field and improve yields.

Conclusion

The current study has revealed that the crude neem seed extract is an effective option for managing aphids on cabbage. The method of preparation is not very difficult and can easily be adopted by resource-poor farmers, especially for small scale production of cabbage. Cabbage is often eaten raw and using the neem as a management option for aphids will contribute to food safety and further prevent contamination of produce by insecticide residues.

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