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LABORATORY OF ENTOMOLOGY

**Effects of variation in plant quality
on densities and sizes of herbivores, primary and
secondary parasitoids**

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ABSTRACT

To investigate the effects of variation in host quality on densities and sizes of three levels of consumers, a cabbage-aphid-parasitoid foodweb was analyzed. Three close related cabbage populations were studied: *Brassica oleracea* var. *gemnifera* cv. Cyrus, a feral *Brassica oleracea* and a wild cabbage type Old Harry as source of variation in host plant quality. A field experiment were established in Wageningen, The Netherlands to measure the effects on densities of herbivores. Aphids and lepidopteran species were monitored weekly during eight weeks on fifteen randomized plants within each plot. Parasitism in aphids and numbers of predators (coccinelids and syrphids) were also estimated. Repeated Measures Analysis of Variance using a Mixed Model was used to compare insect densities on different cabbage populations in each spatial arrangement. Mummies were also collected from the field during the whole season. Size of mummies of *B. brassicae* and hind-tibia length of the emerged parasitoids were determined to investigate the effects on sizes. Moreover, the parasitoid was identified and sex determined. To analyze mummy sizes and parasitoid sizes a General Linear Model (ANCOVA) was used, with fixed factors (cabbage population and spatial arrangement) and mummy size as a covariate. Groups of treatments were made based on LSM and Tukey's post hoc correction. Effects of cabbage population were found to be significant on densities of the aphid *M. persicae* and the lepidopteran species *M. brassicae*, *P. rapae*, *P. xylostella* and coccinelidae. No effects of cabbage population were found for densities of the aphid *B. brassicae*, the lepidopteran *P. brassicae*, syrphids and parasitism in *B. brassicae* and in *M. persicae*. Effects of spatial arrangement were not significant for all the species of aphids, lepidopteran, predators and parasitoids analyzed. Effects of time (week) were significant for all the species analyzed.

Effects of cabbage population on sizes were significant for overall mummy size and for sizes of mummies hosting *D. rapae*, *A. suspensus* and *Alloxysta* spp. For sizes of mummies hosting *A. vulgaris* the effects were not significant. Sizes of mummies hosting males and females of *D. rapae* and *A. vulgaris* were comparable but significant differences were found for mummies hosting males and females of *A. suspensus* and *Alloxysta* spp. Effects on overall hind-tibia length (parasitoid size) were significant for cabbage population and for sex of the parasitoid. Sizes of males and females of *D. rapae* and *A. vulgaris* were comparable. However, females of *A. suspensus* and *Alloxysta* spp. were larger than females.

These results indicate that effects of plant quality on aphid densities were different to those on lepidopteran densities. Aphids performed better in feral *Brassica* and lepidopteran better in Cyrus. Differences in plant chemistry between cabbage populations, effects mediated by content of glucosinolates very probably are playing a role in lepidopteran-cabbage interactions. Possible effects of phenological variation in host plant-food quality between the three cabbage populations can be occurring for the lepidopteran *M. brassicae*, *P. xylostella* or *P. rapae*. Differences for parasitism were not significant and for predators differences in characteristics of the physical environment possibly play a role in its abundance. The effects of host plant quality were transmitted to the second, third and fourth trophic levels as variation in body sizes. Mummies were the largest in feral *Brassica* plants, and in turn parasitoids and hyperparasitoids were also the largest. Mummies, parasitoids and hyperparasitoids in Cyrus and Old Harry were smaller.

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I. INTRODUCTION

The study of multitrophic interactions aims to a holistic understanding of insect-plant relationships and structure of insect communities. Current approaches in the ecology of insect-plant interactions aim to understand how the interaction between top-down (consumer driven) and bottom-up (producer-driven) forces impacts on structure of insect communities and how these effects may influence community level processes and population dynamics of single species (Underwood & Rausher, 2000; Teder & Tammaru, 2002). Indeed, the role of the third trophic level as part of the range of plant's defenses against herbivores must be considered to understand plant-herbivore interactions. Plants have many effects, indirect and direct, positive and negative, not only on herbivores but also on the enemies of herbivores (Price *et al*, 1980). For example, direct effects of host plant (bottom-up effects) on herbivores can occur through exploitative competition between two aphid species feeding on the same host plant (Muller & Godfray, 1999). On the other hand, insect communities can be influenced by indirect interactions (top-down effects) between organisms of the same trophic level through apparent competition when herbivores share a common predator, parasitoid or pathogen (van Veen *et al*, 2008). Indeed, aphid-parasitoid communities are likely to be more influenced by indirect interactions mediated through predators (Muller & Godfray, 1999; van Veen *et al*, 2008).

Food-plant quality often varies among genotypes of the same species (Gols, *et al* 2008) and intraspecific genetic variation in plants has been shown to extend to the third trophic level and even beyond (Poelman *et al*, 2008). A study done by Harvey *et al* (2003) has demonstrated that the effects of qualitative differences in herbivore diet are much more apparent on the fourth trophic level (the performance of the hyperparasitoid *Lysibia nana*) than in its primary host *Cotesia glomerata*, and in its secondary host *Pieris brassicae*. In the study of Fritz & Price (1988) it was found that plant genetic variation is a component of the variation in insect community structure in the field. Furthermore, the authors suggest that there could be an important influence of plant location on herbivore community structure as measured by proportional abundances of each species. In addition, Agrawal *et al* (2006) has mentioned that the strength of plant-herbivore interactions vary analogously with the variance in diversity, structure and composition of plant communities. For instance, it has been hypothesized that there is a latitudinal gradient in the intensity of herbivory, which has favored a greater diversity of unpalatable plants closer to the equator compared with other regions. However, the biological processes driving diversity and complexity of insect communities at different trophic levels are poorly understood. (Bukovinszky *et al.*, 2008). In contrast, it has been revealed how some components of the insect community are affected by spatial heterogeneity, for example, Bukovinszky *et al* (2004) showed that searching behavior of parasitoids can be affected by plant species composition of the host's habitat but many more biological mechanisms remain to be investigated.

Aphid-parasitoids systems are suitable for the study of cascading effects of variation in plant quality, because parasitoids have a tight physiological coupling with their host insects and they also feed "plugged in" to the phloem of the plant being particularly sensitive to variation in host plant quality (Teder & Tammaru, 2002; Muller & Godfray, 1999). Aphids are attacked by hymenopterous parasitoids which deposit their eggs in the aphid; the larvae normally kill the late instar or adult aphid forming a mummy (Muller *et al*, 1999). The primary parasitoids in turn, are attacked by two groups of hyperparasitoids: koinobionts, which allow their host to continue development after oviposition; and idiobionts, which paralyze or kill their hosts in the process of oviposition (Sullivan & Volk, 1999). In an aphid-cabbage system, Bukovinszky *et al*, (2008) showed that cascading effects in three trophic levels of consumers can occur mediated through variation in plant quality influencing body size and densities of herbivores and diversity of parasitoids and hyperparasitoids (Bukovinszky *et al*, 2008). The results demonstrated that plants cropped in monotypic stands- of feral *Brassica oleracea* L. population supported larger aphids

compared with *Brassica oleracea* L. var. gemnifera cv. Cyrus. Larger mummies yielded larger primary and secondary parasitoids and a higher proportion of females, affecting fitness and sex ratios, respectively. The effects of variation in plant quality have been tested in laboratory experiments but rarely in the field among brassicaceas. Gols *et al* (2008) showed effects on survival for generalists (*M. brassicae*), whereas, effects on fitness were recorded for the specialists (*P. rapae* and *P. xylostella*). Moreover, development of the specialist parasitoid *Diadegma semiclausum* was affected directly by development of the host and correlation between survival of *Diadegma defenestrata* and host performance was less clear. However, the same author suggest that to achieve a better understanding of the role that variation in plant quality has played in shaping the structure of insect communities, insect communities-plant populations should be examined in plots in which spatial heterogeneity of plants is also manipulated . Furthermore, it is unknown how insects respond to different spatial environments (homogeneous and heterogeneous). These responses can have evident consequences in foraging decisions, oviposition behavior and in turn effects on densities and sex ratios (Bukovinszky, personal communication) Thus, a wild cabbage population (Old Harry) is introduced in this study and two different spatial arrangements in the field: pure and mix stands were tested.

The aim of this study is to investigate the effects of variation in host plant quality on densities of aphids and lepidopteran species and on parasitism by hymenopterous in higher trophic levels. Furthermore, effects on host-parasitoid size relationships will be study. The effects of spatial heterogeneity will be assessed in a lesser degree. Herbivores are expected to respond differently than aphids (in densities) to variation in plant quality. Within the cabbage-aphid-parasitoid system each trophic level is expected to respond differently (both in densities and body sizes) to variation in plant quality and/or to spatial heterogeneity. To measure such effects, densities of herbivores, primary and secondary parasitoids were monitored through one season on three different populations of cabbage plants cultivated in two spatial arrangements: pure and mix stand, in the vicinity of Wageningen, The Netherlands. Furthermore, the effects of plant quality are expected to be transferred to the second and the third trophic levels in aphid and parasitoid sizes, respectively. To verify that aphid and parasitoids are affected directly by host plant quality, pair measurements of *B. brassicae* mummies and hind-tibia length of four species of parasitoids were recorded and correlated. Each species of primary and secondary parasitoid was identified and sex determined. Sexual dimorphism is expected in secondary parasitoid species but not in the primary parasitoid *D. rapae*.

II. MATERIALS AND METHODS

1. FIELD MONITORING

Experimental plots with three *Brassica* populations were established in the field within two types of spatial arrangement: pure and mix stand. The three *Brassica* populations sown were: a wild cabbage (Old Harry), a feral *Brassica* and Brussels sprouts (Cyrus) (*Brassica oleracea* L.). Eight plots of each genotype in pure stands and eight plots of the three genotypes in mix stands were sown in an experimental field located in the vicinity of Wageningen, The Netherlands. Row and plant spacing was 75 cm and 50 cm, respectively. The distance between plots was a pathway of 7 m and they are sown with grass *Poa* spp. The monitoring of the populations of herbivores during the whole season was done from 16 June to 14 September 2008. Fifteen plants in each plot were selected to estimate of the numbers of cabbage aphids (*Brevycorine brassicae* and *Myzus persicae*), larvae of Lepidoptera (*Pieris brassicae*, *Pieris rapae*, *Mamestra brassicae*, *Autographa gamma*) and numbers of parasitized aphids and lepidopteran on the three *Brassicae* genotypes. Furthermore, numbers of predators (Syrphidae and Coccinellidae) and minor

herbivores were estimated weekly. To compare insect densities on different cabbage populations in each spatial arrangement the data was analyzed with Repeated Measures Analysis of Variance using a Mixed Model. Groups of treatments were made based on LSM and Tukey's post hoc correction.

2. HOST -PARASITOID SIZE RELATIONSHIPS

Mummies were collected from each plot during the whole season and measurements were done after parasitoid emergence. Species of primary and secondary parasitoids were identified and sex determined. To correlate host size and parasitoids size, hind tibia length of parasitoids and mummy size (mm²) were measured for a number of host-parasitoid pairs. Mummy surface (mm²) was estimated with a standard curve describing the length*width of a mummy, times the constant 0.000453). To analyze mummy sizes and parasitoid sizes a General Linear Model (ANCOVA) was used, with fixed factors (cabbage population and spatial arrangement) and mummy size as a covariate. Groups of treatments were made based on LSM and Tukey's post hoc correction.

III. RESULTS

1. EFFECTS OF VARIATION IN PLANT QUALITY AND SPATIAL HETEROGENEITY ON APHIDS DENSITIES

Feral *Brasica* was the plant population which supported the highest densities and smaller densities of *B. brassicae* were found in Cyrus and Old Harry during the whole season. However, differences in aphid densities between cabbage populations were not significant ($F_{2,329} = 2.89$; $P > 0.05$). The peak recorded in feral *Brassica* in pure spatial arrangement was higher than the one in mix arrangement, however no significant differences were observed between mix and pure stands ($F_{1,329} = 0.62$; $P > 0.05$) (Fig 1).

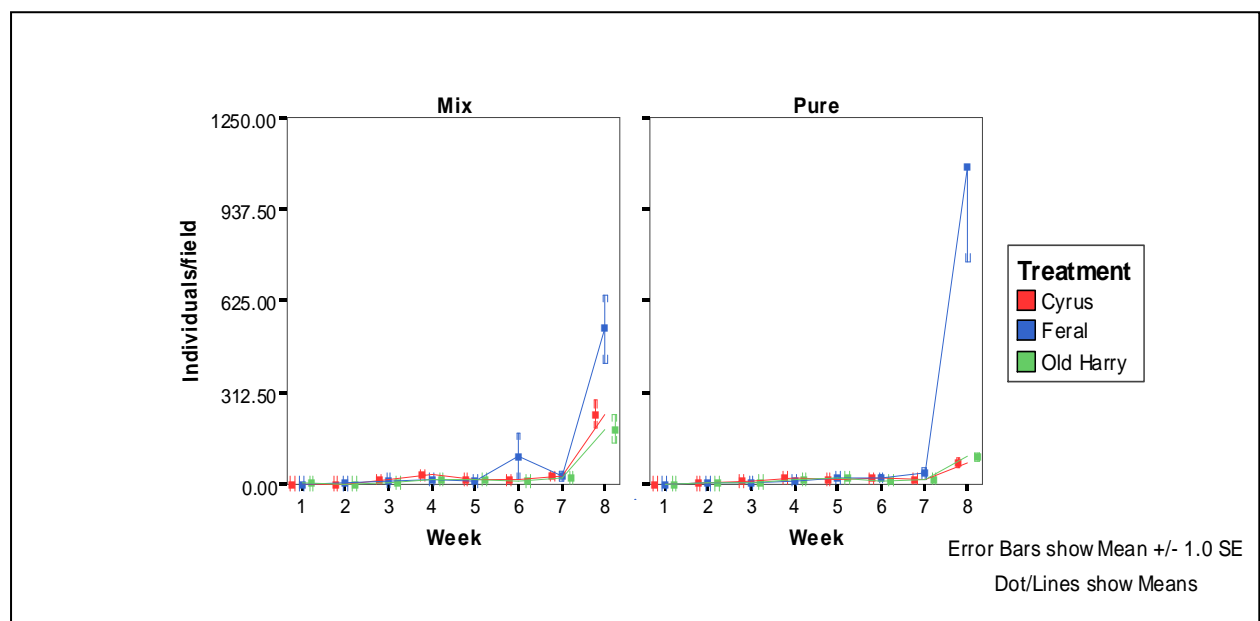


Figure 1. *B. brassicae* on three cabbage populations within two spatial arrangements.

Densities of *M. persicae* were generally higher in feral *Brassica* than in Cyrus and Old Harry and these differences were significant ($F_{2,329} = 24.99$; $P < 0.05$), densities in Cyrus and Old Harry were comparable (Fig 2). Densities in each spatial arrangement did not differ significantly ($F_{1,329} = 2.88$; $P > 0.05$).

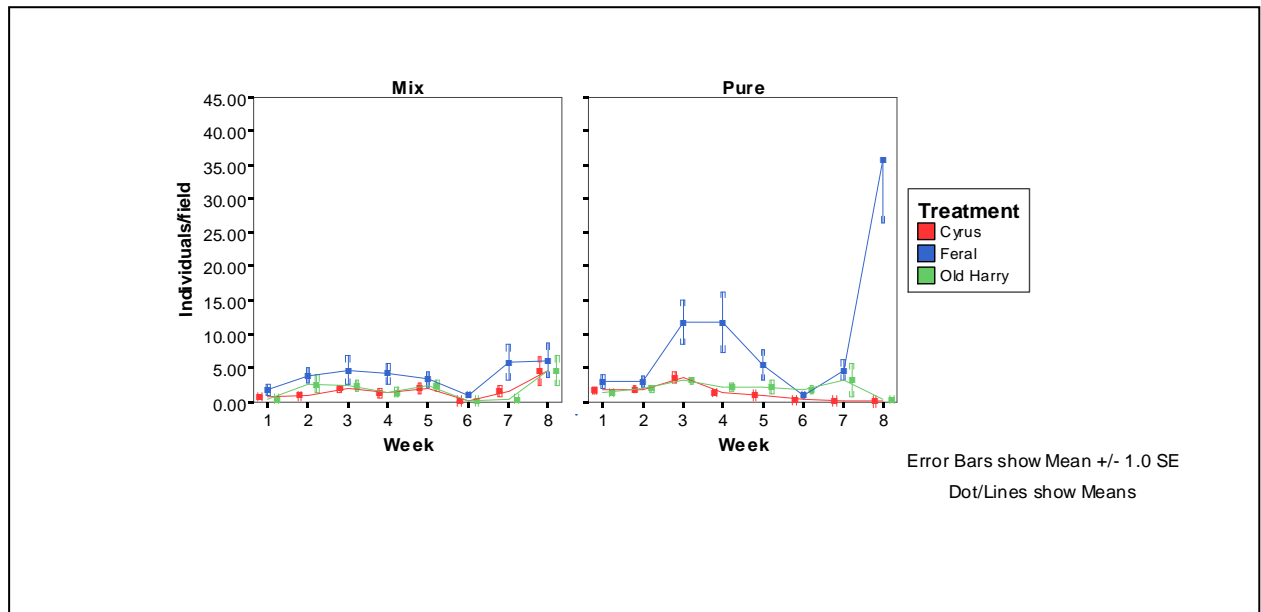


Figure 2. *M. persicae* on three cabbage populations within two spatial arrangements.

2. EFFECTS OF VARIATION IN PLANT QUALITY AND SPATIAL HETEROGENEITY ON LEPIDOPTERAN DENSITIES

P. brassicae populations presented the highest densities on Cyrus and lower densities on feral and Old Harry (Fig 3). However, densities on the three plant populations did not differ statistically ($F_{2,329} = 0.10$; $P > 0.05$). Larvae densities presented a clumped distribution were during the whole season and the effect of spatial arrangement were not significant ($F_{1,329} = 0.78$; $P > 0.05$).

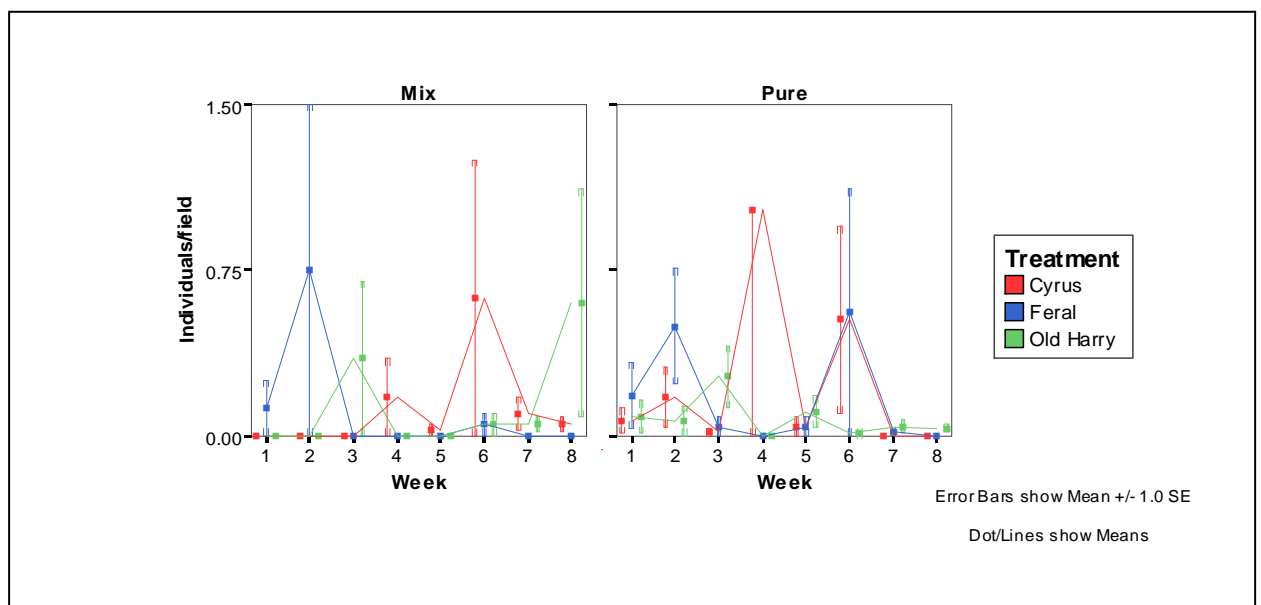


Figure 3. *P. brassicae* on three cabbage populations within two spatial arrangements.

Mamestra brassicae densities were significantly different on each cabbage population ($F_{2,329} = 6.72$; $P < 0.05$). This lepidopteran reached the highest densities in Cyrus and Old Harry supported smaller densities; the lowest densities were recorded in feral *Brassica* (Fig 4). The significant interaction between week and genotype caused that densities in each genotype vary across the season ($F_{14,329} = 2.99$; $P < 0.05$). The effect of spatial arrangement on densities of *M. brassicae* was not significant ($F_{1,329} = 1.44$; $P > 0.05$).

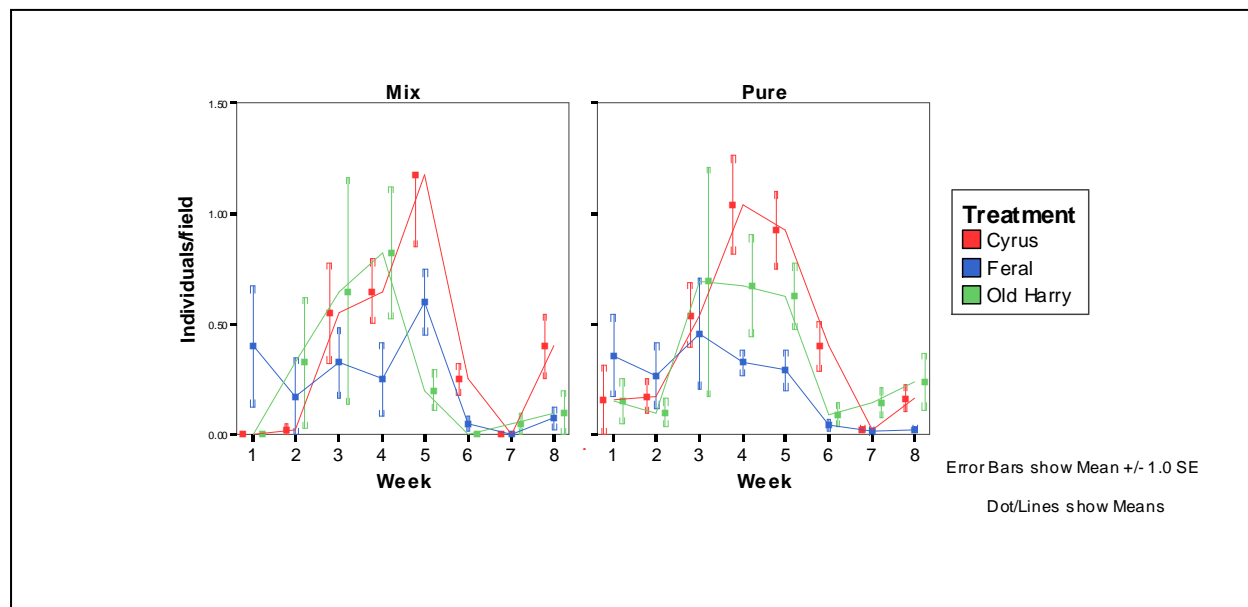


Figure 4. *M. brassicae* on three cabbage genotypes within two spatial arrangements.

Densities differed significantly between cabbage populations ($F_{2,329} = 7.04$; $P < 0.05$). The highest densities of *P. rapae* were recorded in Cyrus (Fig 5). However, densities did not differ significantly between spatial arrangements ($F_{1,329} = 0.7$; $P > 0.05$) but the interaction week and genotype was significant ($F_{14,329} = 5.62$; $P < 0.05$).

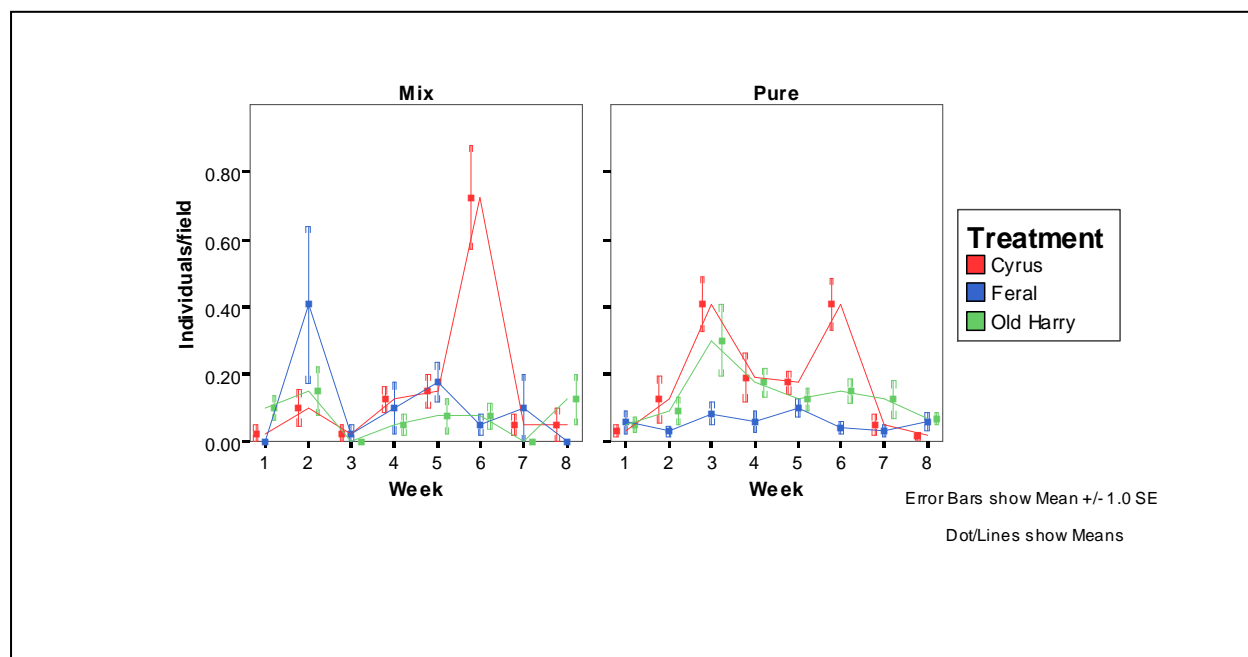


Figure 5. *P. rapae* on three cabbage populations within two spatial arrangements.

There was an effect of cabbage population on densities of *P. xylostella* ($F_{2,329} = 5.55$; $P < 0.05$). The highest densities were recorded on Cyrus and densities on Old Harry were lower. (Fig 6). The effect of spatial arrangement on *P. xylostella* densities was not significant for the three plant populations ($F_{1,329} = 0.16$; $P < 0.05$). The interaction week and cabbage population was significant ($F_{14,329} = 2.42$; $P < 0.05$)

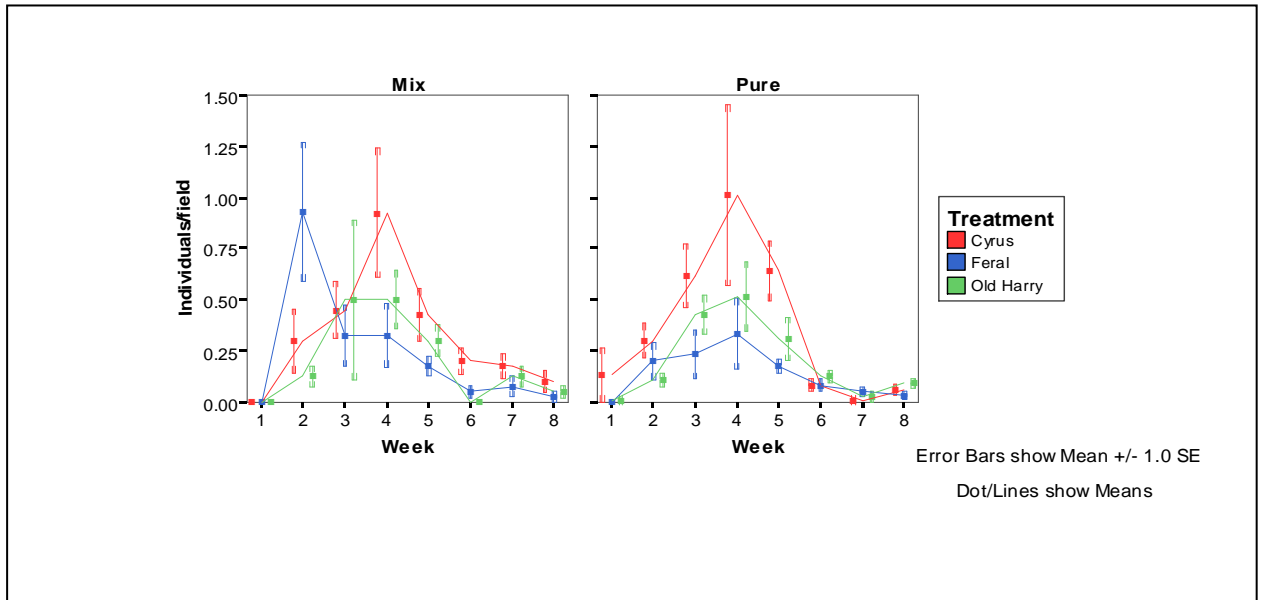


Figure 6. *P. xylostella* in three cabbage populations within two spatial arrangements.

A. gamma did not achieve important densities during the season. Furthermore, they did not differ between treatments ($F_{2,329} = 0.16$; $P > 0.05$), neither between spatial arrangements ($F_{1,329} = 0$; $P > 0.05$). However, more larvae were found in Cyrus and feral *Brassica* than in Old Harry in mix arrangement. Densities on Cyrus and Old Harry were higher than on feral *Brassica* in pure stand (Fig 7).

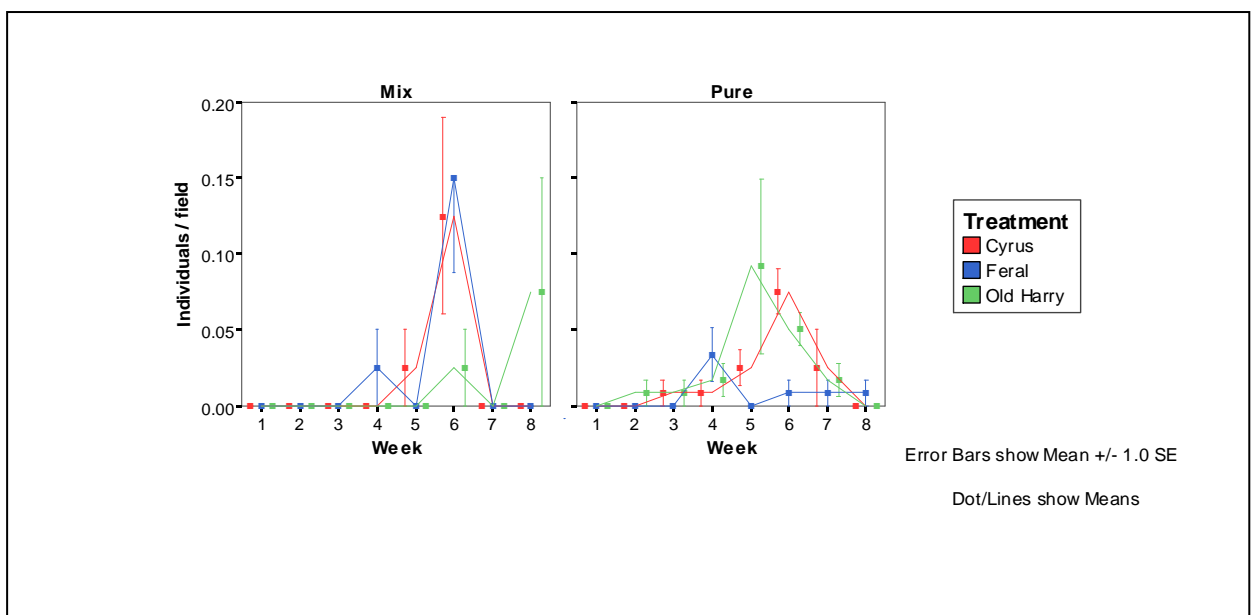


Figure 7. *A. gamma* in three cabbage populations within two spatial arrangements.

3. EFFECTS OF VARIATION IN PLANT QUALITY AND SPATIAL HETEROGENEITY ON PREDATORS POPULATIONS

Syrphids were found more on feral *Brassica* than on Cyrus and Old Harry on pure stand. However, syrphids were more abundant on Cyrus than on Old Harry and on feral *Brassica* in the mix stand (Fig 8). However, densities of syrphids were not significantly different between treatments ($F_{2,329} = 1.50$; $P > 0.05$), neither between spatial arrangements ($F_{1,329} = 0.00$; $P > 0.05$). The interaction between week and treatment were no significant also ($F_{14,329} = 1.39$; $P > 0.05$).

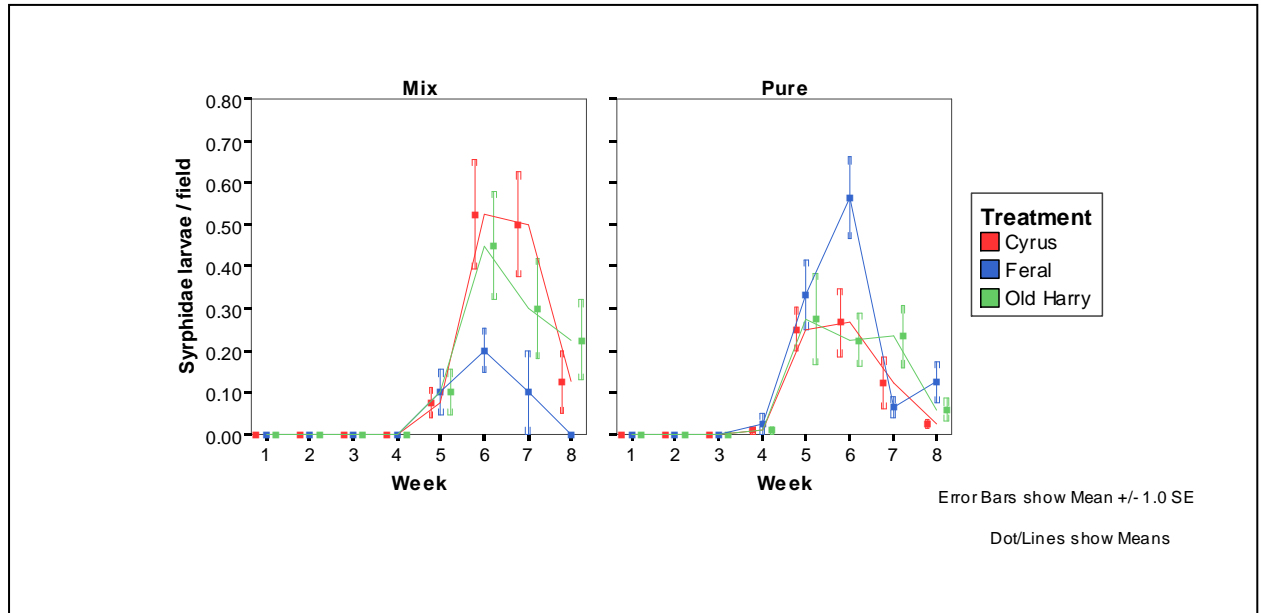


Figure 8. Syrphids on three cabbage populations within two spatial arrangements.

Densities of coccinelidae were significantly higher in feral *Brassica* ($F_{2,329} = 41.84$; $P < 0.05$) than in Cyrus and Old Harry. Coccinelidae larvae were more abundant in feral *Brassica* in pure spatial arrangement than in mix, but their densities did not differ on Cyrus and Old Harry. Indeed, densities were not different between spatial arrangements ($F_{1,329} = 0.69$; $P > 0.05$) (Fig 9).

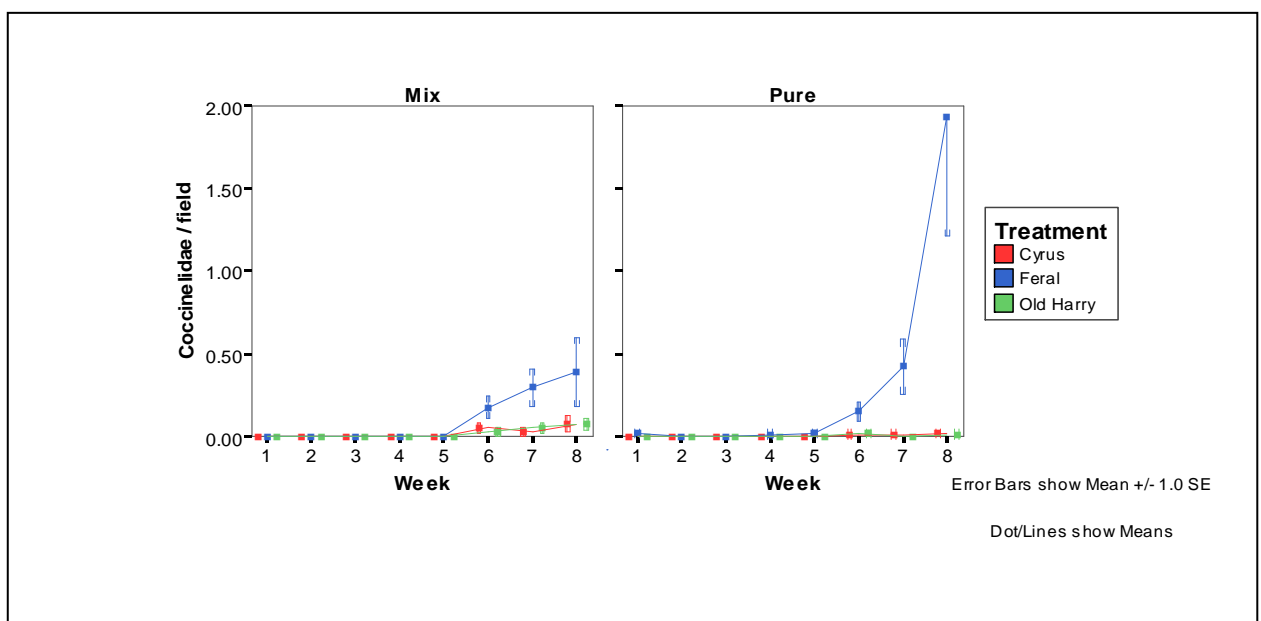


Figure 9. Coccinellidae on three cabbage populations within two spatial arrangements.

4. EFFECTS ON RATES OF PARASITISM IN HERBIVORES SPECIES

The highest rate of parasitism for *B. brassicae* was recorded in feral *Brassica* and it was lower in Cyrus and Old Harry in both spatial arrangements. However, the rate of parasitism did not differ significantly between treatments ($F_{2,329} = 0.52$; $P > 0.05$). The effect of spatial arrangement was significant ($F_{1,329} = 13.87$; $P < 0.05$) as well the effect of interaction between week and treatment ($F_{14,329} = 1.87$; $P < 0.05$).

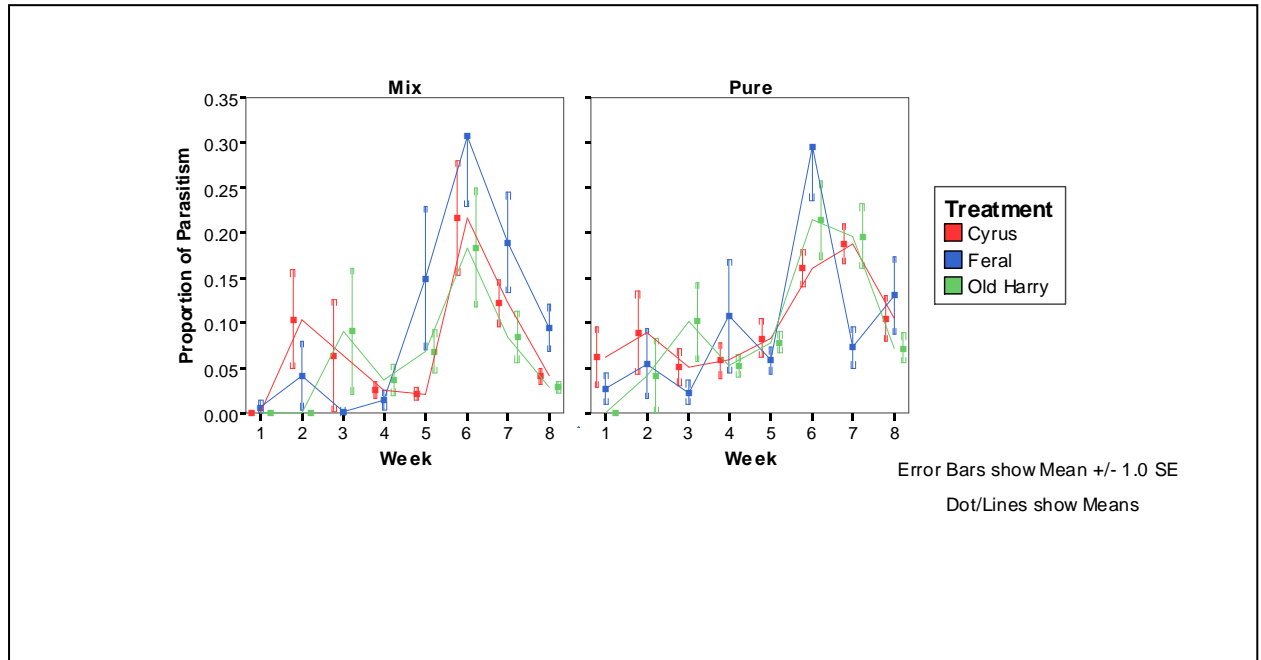


Figure 10. Proportion of parasitism for *B. brassicae* (per field).

In general, the highest rate of parasitism were achieved at the end of the season in Cyrus in both spatial arrangements (Fig 11). However, the proportion of parasitism in *M. persicae* was not statistically different between cabbages population ($F_{2,329} = 2.64$; $P > 0.05$), neither between spatial arrangements ($F_{1,329} = 3.35$; $P > 0.05$).

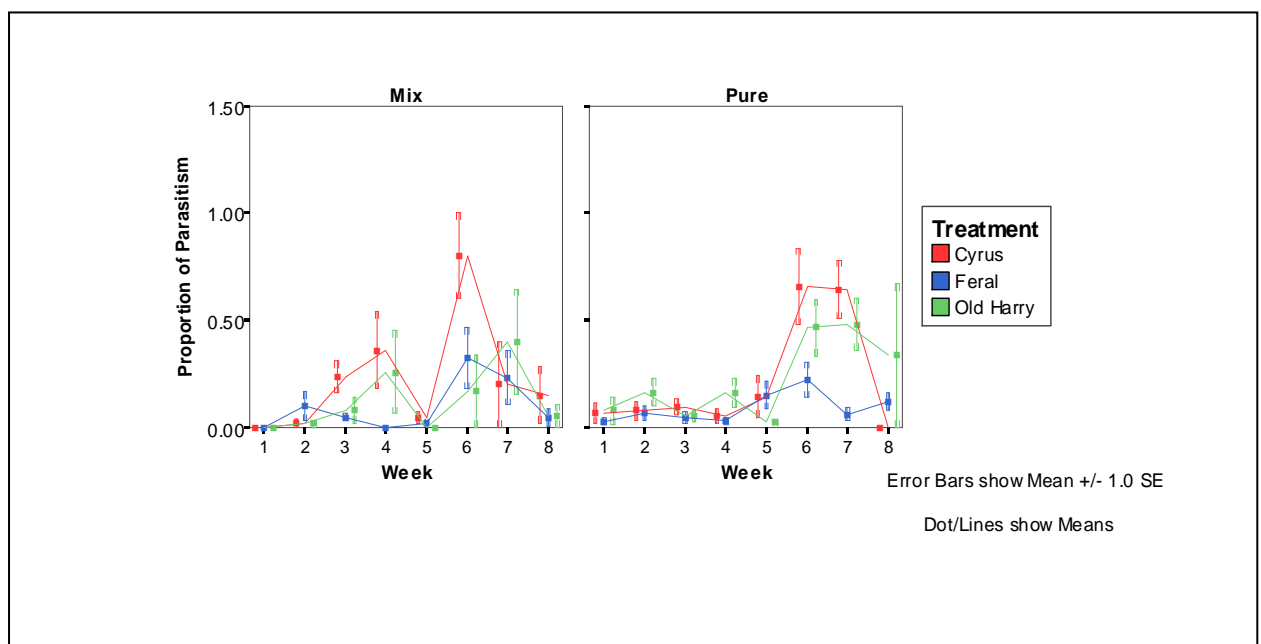


Figure 11. Proportion of parasitism for *M. persicae* (per field).

Small outbreaks in parasitism of larvae of *P. rapae* were recorded at the end of the season mainly in Cyrus and Old Harry. In feral *Brassica* no parasitism were recorded in mix stand but a slight rate of parasitism were recorded in pure stand. (Fig 12).

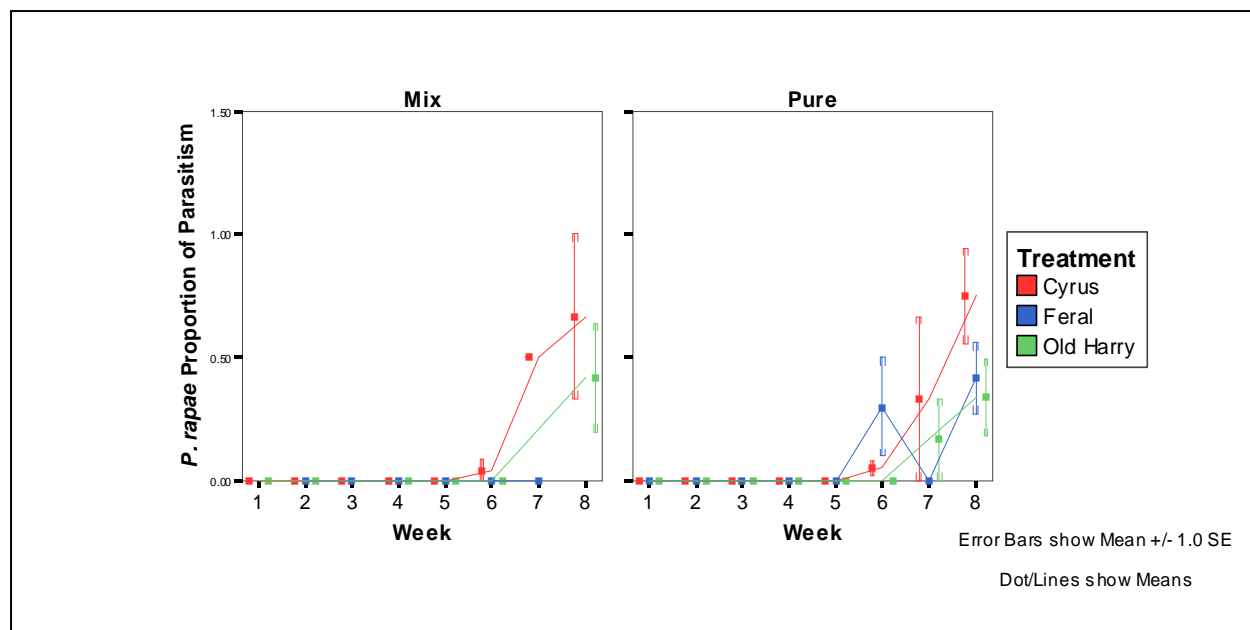


Figure 12. Proportion of parasitism for *P. rapae* (per field).

The rate of parasitism for *M. brassicae* was similar in the three cabbage populations. Moreover, parasitism tended to decrease across the season in all the populations and also in both spatial arrangements (Fig13).

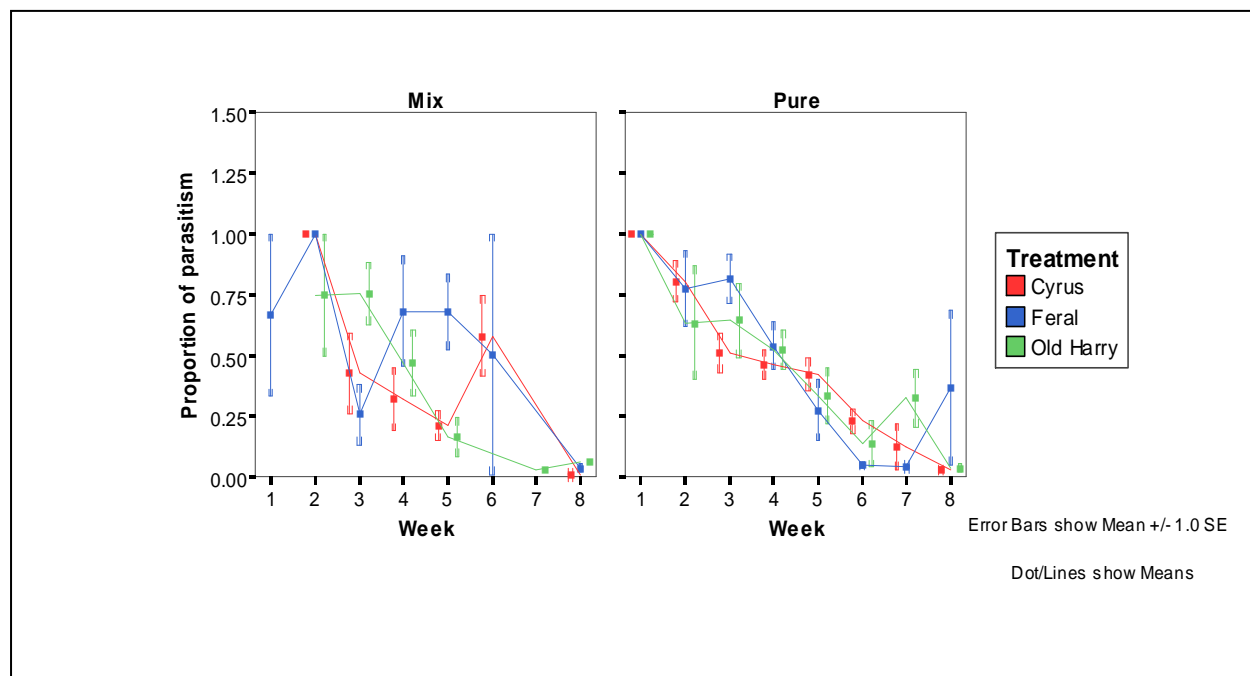


Figure 13. Proportion of parasitism for *M. brassicae* (per field).

Outbreaks in parasitism of *P. xylostella* were recorded in the three cabbage populations mainly at the end of the season. The highest rates of parasitism were recorded in Cyrus and Old Harry in pure stand and in feral *Brassica* and Old Harry in mix stand (Fig 14).

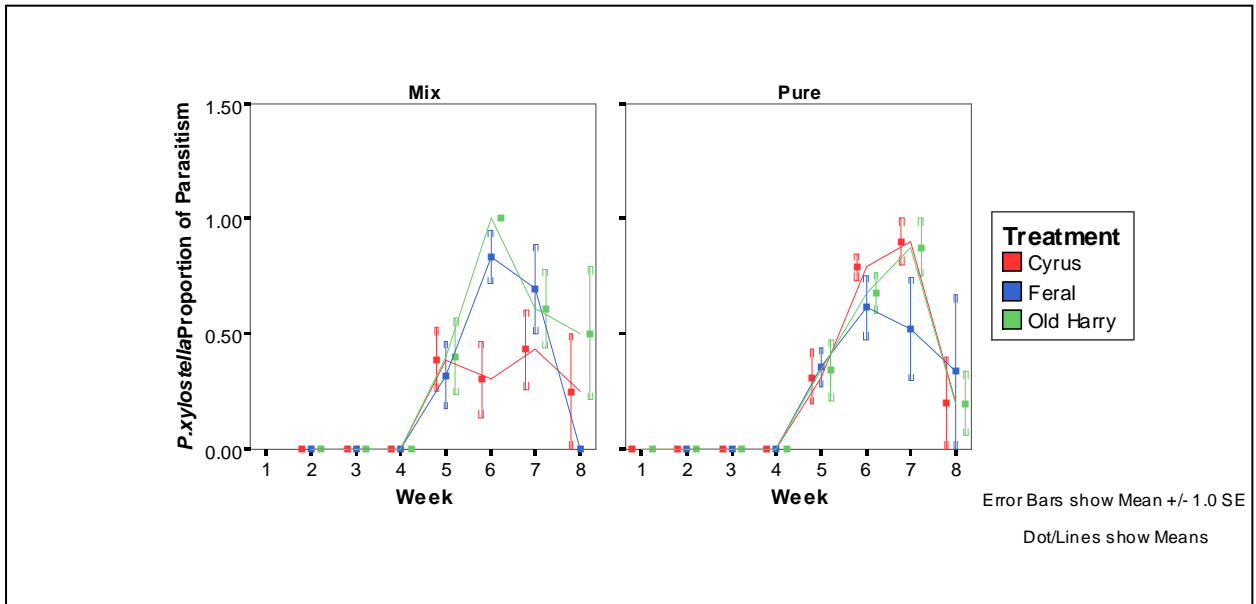


Figure 14. Proportion of parasitism for *P. xylostella* (per field).

Small rates of parasitism of *P. brassicae* were registered at the end of the season on the three cabbage populations. However, parasitized larvae of *P. brassicae* only were found in feral *Brassica* and Old Harry in the mix stand.

5. EFFECT OF PLANT POPULATION-SPATIAL ARRANGEMENT ON HERBIVORE (MUMMY SIZE)

The effect of cabbage population on overall mummy size was significant ($F_{2,685} = 61.84$; $P < 0.05$). The biggest mummies were found in feral *Brassica*. Mummies collected from Cyrus were less big than those from feral and the smallest were the mummies from Old Harry (Tukey, $P = 0.0004$). The sex of the parasitoid were significant on the overall mummy size ($F_{1,685} = 10.92$; $P < 0.05$) for all the species. (Fig 15).

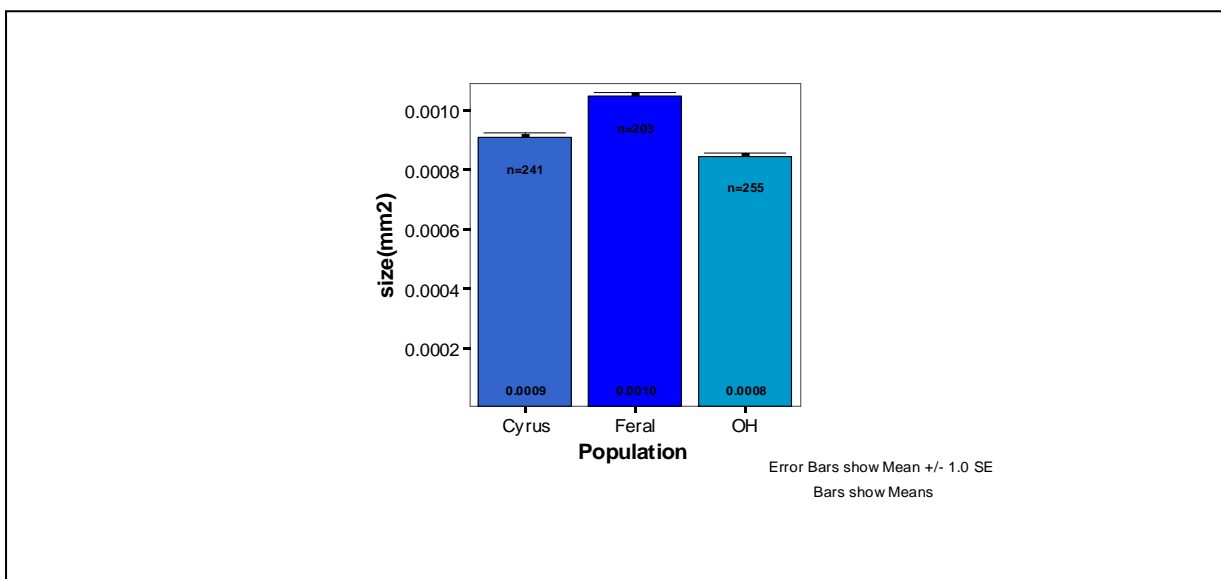


Figure 15. Averages of mummies sizes during week 5 and 7.

6. EFFECTS OF PLANT POPULATION-SPATIAL ARRANGEMENT ON MUMMY SIZE

The effect of cabbage population on mummy hosting *D. rapae* was significant ($F_{2,291} = 22.5$; $P < 0.05$). However, males and females emerged from mummies of comparable sizes. ($F_{1,295} = 2.27$; $P > 0.05$). Spatial arrangement did not have significant effects on *D. rapae* size (Fig 16).

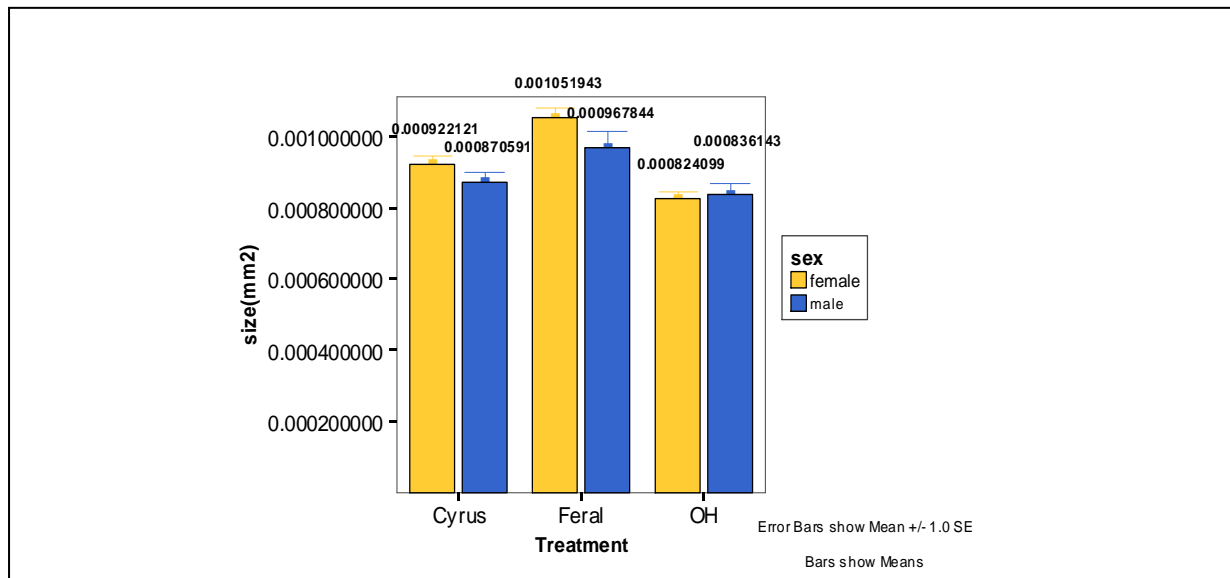


Figure 16. Host sizes for *Diaeretiella* spp. in three cabbage populations (males and females)

The effect of cabbage population was significant ($F_{2,230} = 22.10$; $P < 0.05$) on mummies hosting *Alloxysta* spp. Moreover, the differences in mummy sizes depending on the sex of the parasitoid are significant ($F_{1,230} = 4.28$; $P < 0.05$). Spatial arrangement did not have significant effects on *Alloxysta* spp. size (Fig 17).

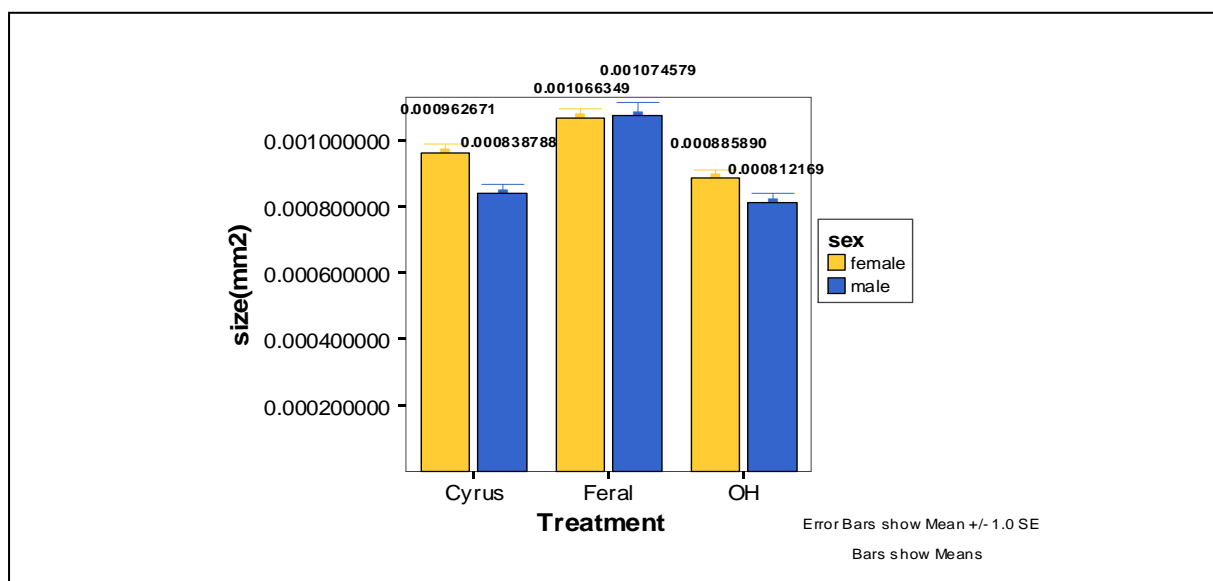


Figure 17. Host sizes for *Alloxysta* spp. in three cabbage populations (males and females)

The influence of cabbage population on mummy hosting *A. suspensus* was significant ($F_{2,124} = 13.58$; $P < 0.05$) as well as the sex of mummy parasitoid ($F_{1,124} = 4.62$; $P < 0.05$). Spatial arrangement did not have significant effects on *A. suspensus* size (Fig 18).

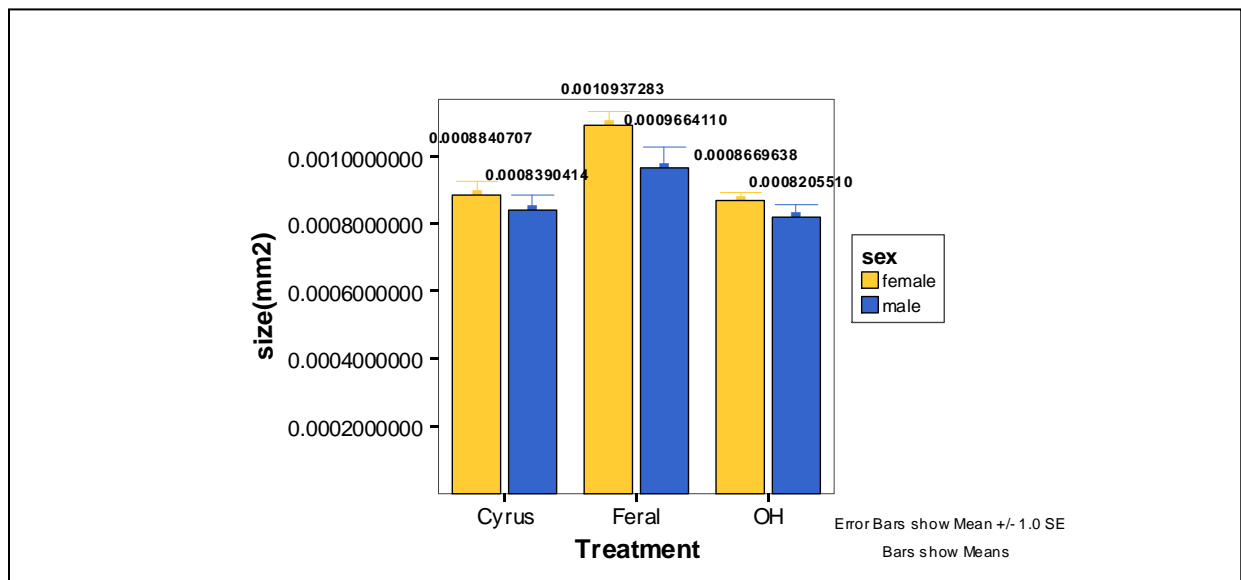


Figure 18. Host sizes for *A. suspensus*. in three cabbage populations (males and females)

The effects of cabbage population on mummy size hosting *A. vulgaris* were not significant ($F_{2,31} = 2.84$; $P > 0.05$). The effects of sex were also not significant ($F_{1,31} = 3.34$; $P > 0.05$). Spatial arrangement did not have significant effects on *A. vulgaris* size (Figure 19).

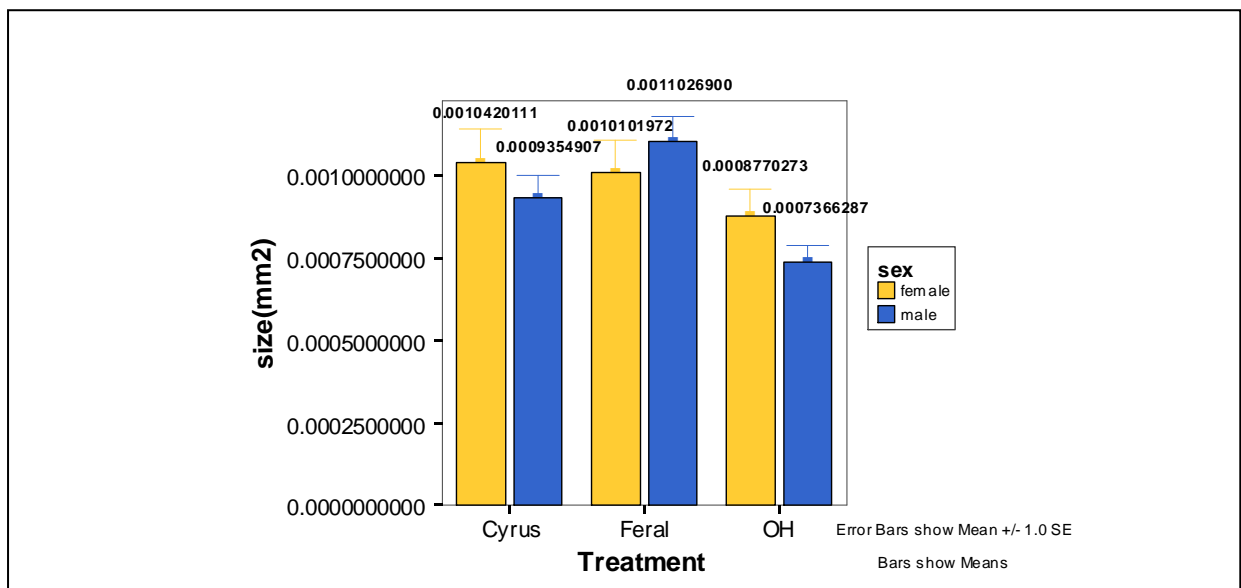


Figure 19. Host sizes for *A. vulgaris*. in three cabbage populations (males and females)

6. EFFECTS OF PLANT POPULATION -PARASITOID SEX ON PARASITOID SIZE

Cabbage population ($F_{2,668} = 5.87$; $P < 0.05$) and the sex of the parasitoid ($F_{1,668} = 28.56$; $P < 0.05$) affected significantly parasitoid size in the overall analysis.

The effects of cabbage population on hind tibia length of *D. rapae* were translated on effects of mummy size ($F_{1,289} = 195.06$; $P < 0.05$). However, the sex of the primary parasitoid was not related with the size of the mummy from which it emerged ($F_{1,289} = 2.69$; $P > 0.05$) (Fig 20).

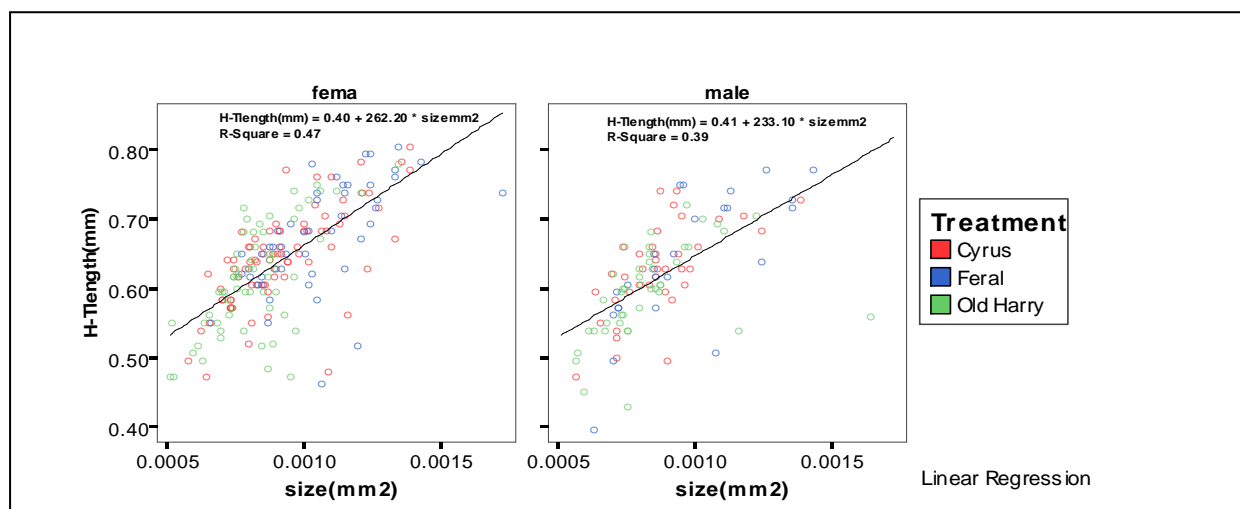


Figure 20. Mummy size-hind tibia relationship in *D. rapae*

The effect of cabbage population on hind tibia length of *Alloxysta* spp. was significant and it was translated in the effect of mummy size ($F_{1,224} = 170.82$; $P < 0.05$). Similarly the sex of the emerging parasitoid had an significant effect on hind tibia length ($F_{1,224} = 7.26$; $P < 0.05$) (Fig 21).

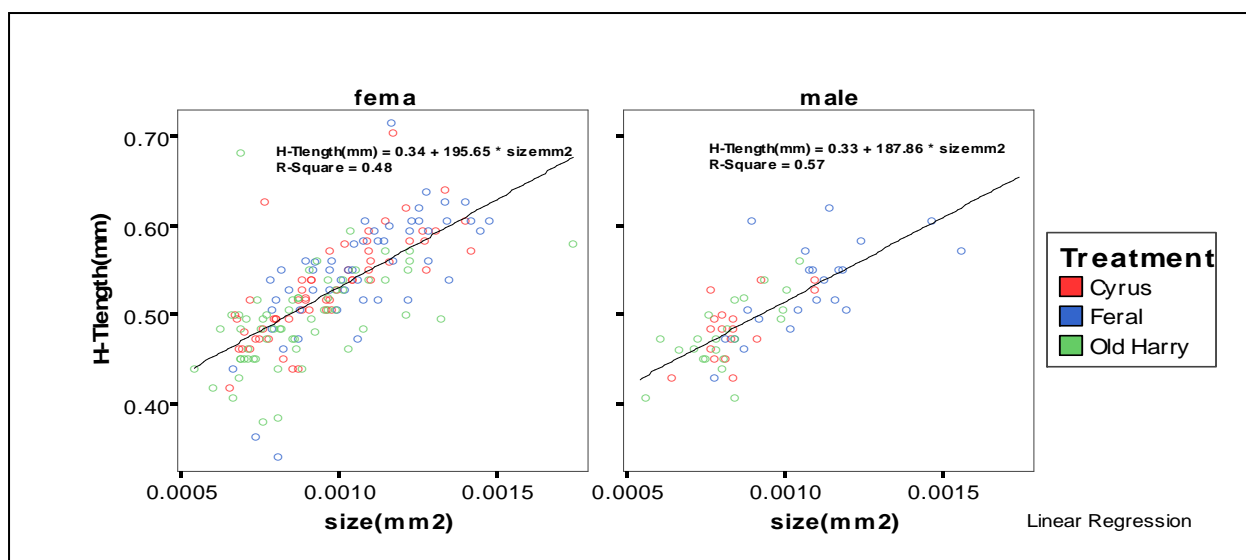


Figure 21. Mummy size- hind tibia length relationship in *Alloxysta* spp.

There was a significant effect for cabbage genotype ($F_{2,122} = 3.88$; $P < 0.05$) and for sex of the emerging parasitoid ($F_{2,122} = 25.98$; $P < 0.05$) on hind tibia length in *A. suspensus* (Fig 22).

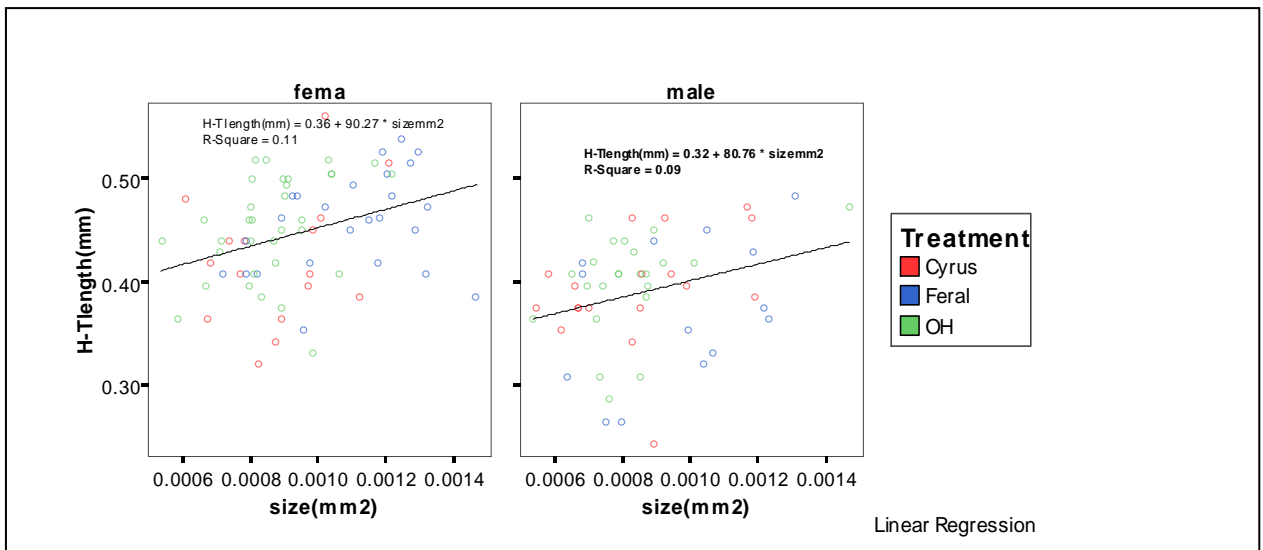


Figure 22. Mummy size- hind tibia length relationship in *A. suspensus*

The effects of cabbage population ($F_{2,29} = 3.50$; $P < 0.05$) on hind tibia length was significant, but the sex of the emerging parasitoid ($F_{1,29} = 3.48$; $P > 0.05$) did not have influence on the hind-tibia length in *A. vulgaris* (Fig 23).

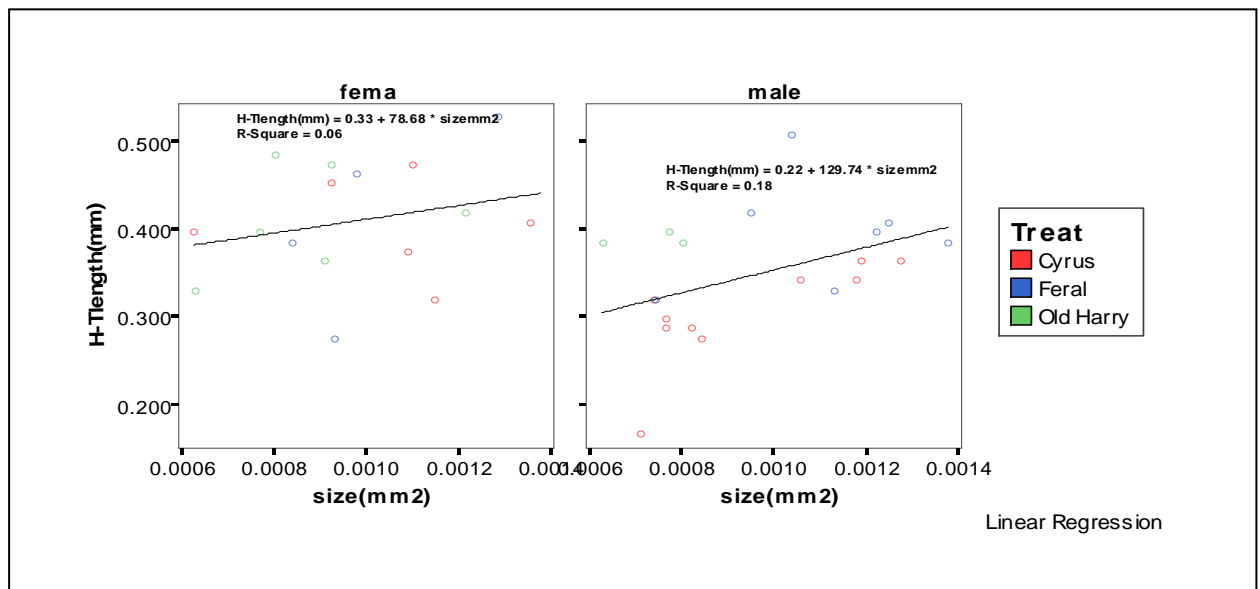


Figure 23. Mummy size- hind tibia length relationship in *A. vulgaris* .

IV. DISCUSSION

1. EFFECTS OF VARIATION IN PLANT QUALITY AND SPATIAL HETEROGENEITY ON APHIDS DENSITIES

Scarce densities of the cabbage aphid *B. brassicae* were found on the three *Brassica* populations during the first five weeks of monitoring in both pure and mix stands, and outbreaks of the aphid population were recorded at the end of the season especially in feral *Brassica*. However, in pure stands densities of *B. brassicae* were low along seven consecutive weeks of monitoring, what probably caused the contrast with *B. brassicae* densities found in previous field studies (Bukovinszky, 2008) was selective pigeon grazing on feral plants. The high density recorded in feral *Brassica* in pure stands compared with other genotypes at the end of the season may be attributable to differences in host quality. Indeed, host plant quality is determined not only by primary chemistry but also by secondary chemistry of the plant (Gols, 2008; Schoonhoven, 2005), and plant chemistry is also modulated by insect attack, light conditions and nutrient availability among other factors (Schoonhoven, 2005). In the case of Cyrus and Old Harry, it seems that these cabbage populations are less suitable for feeding than feral *Brassica* for *B. brassicae*. Furthermore, the low densities found in the former cabbage populations at the end of the season very probably are due to lack of floral stem, where most of the aphids were found feeding in feral. There were found differences on densities of *B. brassicae* between pure and mix stands, may be speculated that these differences are due to differences in host plant quality between feral *Brassica* plants in each type of stand or to low apparency of feral plants on mix stands.

On the other hand, similar trends in densities of *M. persicae* were found on the three genotypes. However, numbers of individuals per field were much lower than numbers of *B. brassicae* mainly because it is not a specialized aphid on brassicaceas. In the same way, densities reached on pure stands in feral *Brassica* were higher than in mix arrangement, suggesting again probable differences in host quality among plant populations or effects of low apparency. These, results confirm that feral *Brassica* is a host of high quality for aphids. Moreover, it has been shown that effects of plant quality are affecting population dynamics of aphid species.

2. EFFECTS OF VARIATION IN PLANT QUALITY AND SPATIAL HETEROGENEITY ON LEPIDOPTERAN DENSITIES

Pieris brassicae did not respond differently on any of the cabbage genotypes or spatial arrangements. Furthermore, it did not reach high nor stable densities may be because of unfavorable climatic conditions for developing of the population.

Mamestra brassicae presented different densities on each cabbage genotype and the highest were recorded in Cyrus. The laboratory study of Gols (2008) showed that *M. brassicae* perform better in Cyrus than in feral *Brassica* and Old Harry. Her data has been supported by our findings in the field. Also, early in season *Mamestra* densities were not different on the three *Brassica* populations and divergence in *Mamestra* densities occurred with a time-lapse. Also, Gols *et al.* (2008) showed, that *M. brassicae* performance did not differ between *Brassica* populations, when feeding on excised leaves, which seriously limited any possibilities for induced responses in the plant to herbivory. Together with these earlier findings, our data suggest that induced plant defences to *Mamestra* feeding probably contributed to the observed differences in the field. However, an additional effect of differential phenological (i.e. age-related) changes in

palatability of plant tissue in the three *Brassica* populations cannot be excluded. These results corroborate that domesticated plants contain lower concentrations of defensive compounds than their wild relatives and consequently are more palatable for herbivores (Benrey et al, 1998; Harvey *et al*, 2003). Furthermore, in the study of Gols *et al* (2008) it was shown that glucosinolates (sinigrin, gluconapin and total glucosinolates) play a role in reducing performance of *M. brassicae* in Old Harry plants.

The largest populations of *P. rapae* and *P. xylostella* were supported by Cyrus plants. Densities of *P. xylostella* were generally lower on feral *Brassica* than on Old Harry during the season. Also densities of *P. rapae* recorded in feral *Brassica* and Old Harry were lower. In fact, a similar effect as above was observed in *P. rapae* densities, they were higher in Cyrus than in the other genotypes. Indeed, results from laboratory experiments demonstrated that *P. rapae* performed better in feral *Brassica* and Cyrus than in Old Harry (Harvey *et al*, 2003). Densities of the specialist *P. xylostella* were higher in Cyrus than in feral *Brassica* and higher in feral than in Old Harry, suggesting that the latter plant population is not suitable for *P. xylostella*. Indeed, results of Harvey *et al* (2008) demonstrated that *P. xylostella* did perform better in Cyrus than in the wild cabbage Old Harry. As stated by these authors, specific glucosinolates may be responsible for reduced performance of *P. rapae* and *P. xylostella* in Old Harry. Even *M. brassicae* is a generalist herbivore its performance is being affected in Old Harry and feral *Brassica* plants. Generalist herbivores are usually more sensitive to high levels of specific allelochemicals compared to specialists (Gols, 2008).

Similar to earlier studies, *Autographa gamma*, an extreme generalist adapted to feed in many species of plants, was found in very low numbers on *Brassicacae* (too low for statistical analysis), suggesting that this is not the preferred food plant of this lepidopteran species. These results acknowledge the differences between domesticated and wild cabbage populations in terms of plant chemistry and; physiological differences between generalist that can detoxify a wide range of toxins (e.g. *M. brassicae*) and generalists well adapted to feed in certain type of brassicaceae (e.g. *P. rapae* and *P. xylostella* in Cyrus) (Gols, *et al* 2008). Furthermore, the results suggest that bottom-up effects are more likely influencing the lepidopteran densities in this system.

3. EFFECTS OF VARIATION IN PLANT QUALITY AND SPATIAL HETEROGENEITY ON NATURAL ENEMIES

3.1. Predators

The populations of predators were affected differently by plant population and spatial arrangement. In first instance, syrphids were distributed differently on the three *Brassica* populations, when cropped in mix and pure stands. Syrphids were more abundant on Cyrus and Old Harry in mix spatial arrangement than on feral *Brassica*. However, more syrphid larvae were found on feral *Brassica* in pure arrangement probably because this plant provides a better sheltering for them. Indeed, temperature and humidity favor egg laying behavior in syrphids (Bukovinszky, 2004). Furthermore, the abundance of *B. brassica* on feral in pure arrangement represents an important source of food for syrphid larvae. On the other hand, coccinelidae larvae were also more abundant on feral *Brassica* in both spatial arrangements. Plant architecture may also be playing a role in sheltering these predators, then it can be suggested that Cyrus and Old Harry are not attractive for coccinelidae females as a place to lay eggs. It means that the presence of predators on is being determined by physical characteristics of the habitat and availability of food as well. Thus, spatial arrangement is influencing physical characteristics of the habitat leading to high densities of predators.

3.2. Parasitoids

Parasitism on *B. brassicae* reached its maximum rate late in the season in the three plant populations in both spatial arrangements. The highest rate of parasitism was recorded in feral *Brassica* (30%) in both spatial arrangements, and lower rates of parasitism were recorded in Cyrus (20%) and in Old Harry (21%). These low rates of parasitism suggests what Hafez (1961) reported, that mortality due to parasitism constituted a small fraction of the total mortality and is not a main factor affecting population change of *B. brassicae*. Because the population of *M. persicae* was smaller than the one of *B. brassicae* the rate of parasitism of *M. persicae* was higher than the rate of parasitism of *B. brassicae*. Moreover, a high rate of parasitism registered in pure arrangement at the end of the season apparently is responsible of the decline of *M. persicae* population. Both aphid species can be parasitized by *D. rapae*, however; apparent competition may be occurring, judging by the low rates of parasitism in *B. brassicae*, even though the latter is the preferred aphid by *D. rapae* (Gols, 2008).

Parasitoid wasps of lepidopteran species were not found regularly through the period of monitoring and did not cause high rates of mortality. Parasitism by *C. glomerata* was not important in regulating the populations of *P. brassicae* during the season. However, an increment in parasitism was registered at the end of the season mainly in Cyrus and Old Harry. Parasitized larvae of *P. brassicae* were not found in feral *Brassica* in mix arrangement but some parasitism did occur in pure spatial arrangement. The attractiveness of the three genotypes to *C. glomerata* has not been studied so far, then is still unknown if *C. glomerata* respond differently to each of these cabbage genotypes when infested by *P. brassicae*. On the other hand, proportion of parasitism in *M. brassicae* declined across the season for the three genotypes. This result suggests that parasitism is not involved as a mortality factor of *M. brassicae* in the field. In the case of *P. rapae*, some parasitized larvae were found at the end of the season; however the rates of parasitism in this lepidopteran did not reach levels to reduce its population. Finally, even though it can be predicted that parasitoids species of *P. xylostella* are highly attracted to Cyrus because the latter is a suitable host plant for this herbivore, low rates of parasitism were recorded in Cyrus in mix spatial arrangement. It may explain the high densities reached by *P. xylostella* in Cyrus in this spatial arrangement. The rates of parasitism were higher than 50% between week 5 and 8 which may explain the low densities of *P. xylostella* at the end of the season. The low rates of parasitism in lepidopteran can suggest that indirect defenses induced by herbivory are not being emitted by plants of any cabbage population. Moreover, given the low densities of *P. rapae* and *P. xylostella*, especially in Old Harry and feral *Brassica*, it can be inferred that differences in plant chemistry between cabbage populations are shaping *P. rapae* and *P. xylostella* communities in this system.

4. EFFECTS OF PLANT POPULATION-SPATIAL ARRANGEMENT ON MUMMY SIZE

It was found, as in previous studies (Bukovinszky, 2008; Teder & Tammaru, 2002), that host plant influences herbivore size. Specifically, host plant genotype did influence aphid body size, and in turn mummy size. Then, the three plant populations are different in suitability as host foodplant for the cabbage aphid *B. brassicae*. As found by Bukovinszky *et al* (2008), in *D. rapae* the size of the mummy from which males and females emerge are comparable. However, the size of the mummies from which females emerge differ from the size from which males emerge in *Alloxysta* spp. and *A. suspensus*. In *A. vulgaris* no differences were found between mummy sizes from which males and females emerged. Females emerged from larger mummies.

In addition, the effect of spatial arrangement did not have any influence on aphid size, and in turn on mummy size.

5. EFFECTS OF MUMMY SIZE-SEX ON PARASITOID SIZE

The size of the primary, hyper and mummy-parasitoids was directly influenced by mummy size as in the study of Cohen *et al* (2005), and mummy size was influenced by cabbage population, in turn. These results show that cascading effects did occur in the cabbage–aphid system, influencing the second, the third and even the fourth trophic level, as demonstrated in previous investigations (Teder and Tammaru, 2002; Harvey et al, 2003; Bukovinszky, 2008). On the other hand, the hind tibia length of the *D. rapae* did not depend on its sex, which indicates that not sexual dimorphism is occurring in this primary parasitoid. Some other studies have also shown minimal sexual dimorphism or even male biased (Teder *et al*, 1999) However, body sizes in the hyperparasitoids and mummy parasitoids depend on its own sex. Generally, females presented larger hind tibia length than males.

V. CONCLUSIONS

There were effects of plant quality on herbivore densities. For aphid species *B. brassica* and *M. persicae* the host plant with highest quality was feral *Brassica*. Even statistically significant differences were not found for densities, feral *Brassica* supported the highest densities and formed the largest mummies. The effects of plant quality on lepidopteran densities were different, for *M. brassicae* (generalist) *P. rapae* and *P. xylostella* (specialists) *Cyrus* is the host plant with the highest quality. Differences in plant chemistry between *Cyrus* (domesticated population) and feral *Brassica* and Old Harry (wild population) are playing a role in this effect. Glucaninolates are known to impede a good performance of lepidopteran specially in Old Harry. Effects of spatial arrangement on densities of aphids were not significant but such effects on lepidoteran could be neglected. Possible effect of phenological variation in host plant-food quality between the three cabbage populations can be occurring when *M. brassicae*, *P. xylostella* or *P. rapae*.

The highest parasitism by *D. rapae* was recorded in feral *Brassica* and the lowest in Old Harry and *Cyrus* analogously with aphid densities, but differences were not significant. The effect of spatial heterogeneity on parasitism by *D. rapae* was significant. Parasitism on lepidopteran was not influenced by cabbage population nor by spatial heterogeneity. Differences in predators populations are being produced by differences in the physical characteristics of the habitat that promote a better shelter and places for oviposition.

The effects of host plant quality were transmitted to the second, third and fourth trophic levels as variation in body sizes. Mummies were the largest in the host food-plant of highest quality, and in turn parasitoids and hyperparasitoids were also the largest. Differences in body sizes between males and females were found in *Alloxysta* spp. and *A. suspensus* but not for *D. rapae* and *A. vulgaris*.

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