THE EFFECT OF A CABBAGE - CARROT INTERCROPPING SYSTEM ON THE INCIDENCE OF CABBAGE PESTS.

W.J. WEEKS

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Supervisor:

Prof. J. van den Berg

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Dedicated to:

My wife and children,

and the late

Dr C. F. van Eeden

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ABSTRACT

Cruciferous crops comprise one of the major crop divisions and contribute significantly to global crop production. Insect pests associated with cruciferous crops have the potential to destroy harvests. The diamondback moth, Plutella xylostella (L.) (Lepidoptera: Plutellidae) and cabbage aphids, Brevicoryne brassicae (L.) and Lipaphis erysimi (Kaltenbach) (Homoptera: Aphididae) are considered the most important cabbage pests in South Africa. Pest control in cabbage is still heavily reliant on use of insecticides even though insecticide application usually result in increased pest status of P. xylostella. Use of integrated pest management (IPM) strategies may yet prove invaluable as a means of suppressing the more serious Global interest in cultural control strategies, that includes cabbage pests. intercropping of unrelated crop plants, has been rekindled because of problems experienced with pesticide use. A study that involved the planting of two field trials with cabbage and carrot plants in different ratios, as a substitutive intercropping system, was undertaken during the 2002/03 and 2003/04 planting seasons. Field trials had five treatments viz. control (cabbage monoculture sprayed with mercaptothion), cabbage monoculture (without chemical application), 1:1 intercropping (cabbage: carrots), 1:3 intercropping and 1:5 intercropping, replicated six times in a randomized block design. Insects were sampled weekly by removing the third-youngest open leaf, from one plant per plot (six plants per treatment). Feeding damage to cabbage leaves was assessed visually by rating 14 plants per plot according to a numeric scale based on damage severity. P. xylostella and aphid parasitism levels were determined. Prominence values were calculated for P. xylostella larvae and aphids for each treatment per sampling date. P. xylostella treatments. Intercropping ratio did not have a significant impact on pest infestations. P. xylostella infestations and parasitism on intercropping treatments did not differ significantly (P > 0.05) from that on monoculture plots (except for 1:5 intercropping during the 2003/04 season). Cotesia plutellae (Hymenoptera: Braconidae) was the dominant parasitoid and parasitism levels were significantly correlated with P. xylostella infestation levels. Prominence values showed a decline in P. xylostella infestations on intercropping treatments towards the last sampling date during both seasons. Feeding damage severity was lowest on the control treatment but similar for other treatments for both seasons. Aphid infestations were significantly ($P \le 0.05$)

lower on the control treatment, but did not differ significantly between intercropping treatments. Aphid prominence values indicated possible suppression of infestations at low population levels during the early part of the season. Aphid parasitism was low during both seasons. It seems more likely that the reduction in insect infestation levels reported from the literature are related more to spatial arrangement of plants than cropping ratios. The observed suppression of aphid infestation levels on intercropped plots early in the season may be valuable in reducing the need for early chemical applications. The limiting of early insecticide application against aphids may result in a reduced pest status of *P. xylostella*, due to the conservation of *C. plutellae* populations.

Keywords: aphids, cabbage, carrot, diamondback moth, intercropping

OPSOMMING

TITEL: DIE EFFEK VAN 'n KOOL/ GEELWORTEL TUSSENVERBOUING - SISTEEM OP DIE VOORKOMS VAN KOOLPLAE

Koolgewasse is gesamentlik een van die belangrikste gewasgroepe en maak 'n merkbare bydrae tot wêreldwye gewasproduksie. Insekplae wat met koolgewasse geassosieër word besit die vermoeë om oeste te vernietig. Die diamantrugmot, Plutella xylostella (L.) (Lepidoptera: Plutellidae), en die koolplantluise, Brevicoryne brassicae (L.) en Lipaphis erysimi (Kaltenbach) (Homoptera: Aphididae), word gereken as die mees belangrike koolplae in Suid Afrika. Plaagbeheer in koolgewasse steun tans nog swaar op die toediening van insekdoders, ten spyte daarvan dat die gebruik van insekdoders aanleiding gee tot 'n verhoging in die plaagstatus van P. xylostella. Die gebruik van geïntegreerde plaagbeheerstrategië kan 'n waardevolle bydrae lewer in die onderdrukking van populasiegroei van belangrike koolplae. Wêreldwye belangstelling in die gebruik van kulturele plaagbeheerstrategië, waaronder tussenverbouing van onverwante gewasse, het onlangs toegeneem as gevolg van probleme wat deur die gebruik van plaagbeheermiddels geskep is. Hierdie Studie is gedoen tydens die 2002/03 en 2003/04 plantseisoene waartydens kool en geelwortels in verskillende verhoudings verbou is volgens 'n substituwe tussenverbouingspatroon. Die veldproewe het uit die volgende behandelings bestaan: behandelde-kontrole (kool monokultuur met toediening van merkaptotion), koolmonokultuur (met geen chemiese toediening), 1:1 tussenverbouing (kool: geelwortels), 1:3 tussenverbouing en 1:5 tussenverbouing. Behandelings is in ses herhalings gedupliseer binne 'n gerandomiseerde blokontwerp. Insekmonsters is weekliks geneem deur die derde-jongste oop blaar vanaf een kool plant per perseel (ses plante per behandeling) te verwyder. Vreetskade op koolplante is visueel geassesseer deur 14 plante per perseel te takseer volgens 'n numeriese skaal (gebaseer op die graad van plantbeskadiging). Parasitismevlakke is vir P. xylostella larwes en plantluise bepaal. Prominensie-waardes vir P. xylostella larwes en plantluise is vir elke behandeling bepaal met gereelde intervalle gedurende die groeiseisoen. Resultate het aangedui dat P. xylostella infestasie en parasitismevlakke statisties (P \le 0.05) betekenisvol laer was op kontrole-behandelings. Tussenverbouingverhoudings het nie 'n betekenisvolle impak op plaaginfestasievlakke gehad nie. P.

xylostella infestasie- en parasitismevlakke op tussenverbouing-behandelings het nie betekenisvol (P > 0.05) verskil van die op die monokultuurpersele nie (behalwe vir 1:5 tussenverbouing tydens die 2003/04 seisoen). Cotesia plutellae (Hymenoptera: Braconidae) was die dominante parasitoïedspesie en parasitismevlakke het betekenisvol gekorreleer met P. xylostella infestasievlakke. P. xylostella prominensie het afgeneem op alle tussenverbouing-behandelings tydens die laaste monsterdatum van beide seisoene, wat dui op 'n afname in infestasies. Vreetskadevlakke was die laagste op die kontrolebehandeling en het nie baie verskil van ander behandelings nie. Plantluisinfestasies was betekenisvol (P < 0.05) laer op die kontrolebehandeling maar het nie betekenisvol verskil ander behandelings nie. tussen Plantluisprominensiewaardes dui op 'n moontlike verlaging in vroeë infestasies onder lae infestasiedruk vroeg in die seisoen. Plantluis-parasitismevlakke was laag tydens elk van die twee seisoene. Verlaging in insekinfestasievlakke, soos in die literatuur vermeld, kan moontlik eerder toegeskryf word aan die spasiëring van plante binne tussenverbouing-stelsels as aan die relatiewe verhouding van verskillende plante tot mekaar. Die verlaging in vroeë plantluisbesmettings wat op tussenverbouing-persele waargeneem is mag belangrik wees vir die vermindering van vroeë toediening van insekdoders. Die beperking van vroeë insekmiddeltoedienings teen plantluise kan daartoe aanleiding gee dat die plaagstatus van P. xylostella weer verlaag word weens die beskerming van C. plutellae populasies.

Sleutelwoorde: diamantrugmot, geelwortels, kool, plantluise, tussenverbouing

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CHAPTER 1

Introduction and literature review

1 Introduction on cruciferous crop pests and integrated pest management

Cultivated Cruciferae are considered high value crops that, as a group, comprise one of the major divisions among cultivated plants and contributes significantly to world crop production (Hooks & Johnson, 2003). The seriousness and cosmopolitan nature of certain cruciferous insect pests necessitated the development of integrated pest management (IPM) strategies. In spite of global efforts to develop IPM strategies, control of serious pests such as diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), still relies heavily on the use of synthetic chemicals. The global cost of chemical control of *P. xylostella* is estimated at US\$ 1 billion per annum (Talekar 1992, quoted by Kfir, 2003).

The IPM concept incorporates a wide range of strategies that are constantly evolving because of the development of new technology. Kogan (1998) probably came as close as anyone could when he defined the concept as follows: IPM is a decision support system for the selection and use of pest control tactics, singly or harmoniously coordinated into a management strategy, based on cost/ benefit analyses that take into account the interests of and impacts on producers, society and the environment. In essence the IPM approach utilises all available strategies that, for a given situation, can be employed to maintain pest populations below economic threshold levels. Included within the armada of IPM strategies a group of strategies can be loosely grouped under cultural control. The value of cultural control strategies lies in the fact that by nature they allow the modification of the environment within which a particular plant is grown (Maloy, 1993). In a sense cultural control strategies allow for the stage to be set on which many different but complementary IPM strategies may be introduced.

1.1 The nature of cruciferous crop pests

A total of 16 insect and one mite species have been listed as important pests of cruciferous crops in South Africa (Annecke & Moran, 1982). Cruciferous crops are typically attacked by a variety of "specialist" and "generalist" insect pests (Hooks &

Johnson, 2003). A good definition for what is termed a specialist pest is an oligophagous insect that has the ability to overcome, and to a large extent utilise plant chemicals that are otherwise responsible for antixenosis and/or antibiosis among less well adapted insect species. The majority of insect species that have been recorded as cruciferous crop pests are polyphagous generalists. The most injurious species however are oligophagous specialists that either mainly, or exclusively attack plants within the family Cruciferae.

1.1.1 The importance of diamondback moth as a pest

P. xylostella is an oligophagous pest (Verkerk & Wright, 1994) that only feeds on plants in the family Cruciferae and is regarded as the most important global cruciferous crop pest (Talekar & Shelton, 1993). The most serious crop losses caused by P. xylostella are in tropical vegetable production areas and can be related to high fecundity, short generation time, ability to develop resistance to insecticides and lack of effective biological control (Verkerk & Wright, 1994). The global pest status of this insect is however influenced most by its inherent ability to develop resistance to all the synthetic and biological insecticides used against it (Shelton, Robertson, Tang, Perez, Eigenbrode, Preisler, Wilsey & Cooley, 1993; Shelton, Wyman, Cushing, Apfelbeck, Dennehy, Mahr & Eigenbrode, 1993). P. xylostella was the first insect pest to develop resistance to DDT (Talekar & Shelton, 1993). Isolated populations have recently and alarmingly also developed resistance to spinosad, which is considered one of the latest introductions to the insecticide arsenal with a unique chemistry and mode of action. Spinosad is comprised of two macrocyclic lactones viz. spinosyn A and spinosyn D, which are secondary metabolites derived from Saccharopolyspora spinosa Mertz & Yao under natural fermentation conditions (Zhao, Li, Collins, Minuto, Mau, Thompson & Shelton, 2002). Ironically the global pest status of P. xylostella only increased after the widespread use of synthetic insecticides that started during the mid 1950s (Talekar & Shelton, 1993).

According to Pivinick, Jarvis, Gillott, Slater & Underhill (1990) two distinct phases viz. migratory and reproductive, govern adult activity in P. xylostella. The occurrence of these phases may hold considerable and as yet largely unexplored significance as far as the pest status of P. xylostella is concerned. P. xylostella adults partake in long-

distance migrations during their migratory phase (Chapman, Reynolds, Smith, Riley, Pedgley & Woiwod, 2002). Long distance migrations are typically associated with P. xylostella populations that occur in temperate areas and are responsible for recolonisation of areas where survival during winter months is not possible. Migrations typically take place during summer months when moth flights are concentrated in upper atmospheric temperature inversion layers that offer suitable conditions for sustained flight (Chapman et al., 2002). According to Pivinick et al. (1990) the longest recorded non stop oceanic flight is estimated to have covered a distance of 3218 km, and may have lasted four or five days. Flight patterns during the reproductive phase are typically shorter in duration and closer to ground level where host plants may be found. According to Mo, Baker, Keller & Roush (2001) dispersal flights between healthy host crops are limited, with less than 5% of released adults expected to disperse over more than 110 m and less than 1% over more than 200 m. P. xylostella has the ability to survive winter conditions in most parts of South Africa (Annecke & Moran, 1982). Talekar & Shelton (1993) speculated that along with other southern hemisphere countries similar migrations might also take place in South Africa. According to Goodwin & Danthanarayana (1984) movement of P. xylostella populations into southern regions of Australia do occur during springtime. Whether or not similar long distance migrations do take place in South Africa should however still be formally investigated.

The migratory phase that lasts from adult emergence until reproductive maturity is reached during the third or fourth night after moth emergence (Pivinick et al., 1990), and probably occurs within each new generation. The extraordinary dispersal ability of *P. xylostella* should subsequently serve as fair warning of the potential that exists within insecticide resistant populations to spread to new areas. Shelton (2001) also demonstrated the importance of *P. xylostella* distribution by means of contaminated cabbage seedlings and the risk of spreading resistant populations, such as those resulting in outbreaks in the USA. It is therefore vital that *P. xylostella* control be approached on a regional rather than local level, which can only be accomplished successfully through the implementation of various IPM strategies.

1.1.2 Diamondback moth within the southern African context

The origin of P. xylostella is believed to lie within Mediterranean parts of Europe and to be linked with the development and spreading of cabbage related crops (Brassica oleracea L.) throughout the world (Annecke & Moran, 1982). This viewpoint however, in spite of its apparent logic, that seems to be based on the origins of cabbage crops has been contested on ecologically based arguments. Kfir (1998) presented a number of interesting arguments that might be sufficient to consider a revision of the traditional viewpoints on this pest. He firstly mentioned the fact that the pest status of P. xylostella is lower in South Africa than in any other country with similar climatic conditions. In addition, the total number of P. xylostella parasitoid and hyperparasitoid species within the southern African region is exceptionally high (Kfir, 1997; Kfir, 2003). When considered along with the large number of wild Cruciferae species (175 species of which only 32 are exotic), evidence seems to point towards the Cape floral kingdom of South Africa as a likely place of origin for P. xylostella (Kfir, 1998). An interesting observation by Kfir (1998) relates to the fact that Diadromus collaris Gravenhorst (Hymenoptera: Ichneumonidae), one of the parasitoids of P. xylostella, reproduces sexually in South Africa whereas its reproduction in Europe is asexual. The fact that asexual reproduction is almost exclusively a secondary phenomenon also points towards a southern African origin for this parasitoid (Kfir, 1998).

Kfir (2001) emphasized the fact that the last comprehensive study that was done on *P. xylostella* in South Africa (by Ullyett, 1947), was followed by a 60 year "drought" during which virtually no interest was shown in this pest. The potential injuriousness of *P. xylostella* was however recognised locally when recurring outbreaks, which coincided with increased failure of chemical control became a problem during the 1990s (Kfir, 2003). Dennill & Pretorius (1995) illustrated that epidemic outbreaks of *P. xylostella* in South Africa are also closely linked to the misuse of insecticides. Excessive use of chemical control causes *P. xylostella* outbreaks by firstly eliminating natural enemies that are vulnerable to insecticides and secondly contributing to the development of resistance to the particular chemicals that are being misused.

Expansion of cruciferous crop production during recent years in South Africa could also have contributed to the recent elevation of the pest status of *P. xylostella*. The

availability of cabbage, *Brassica oleracea* L. var. *capitata*, (Cruciferae), cultivars capable of tolerating the high summer temperatures in South Africa enables continuous and uninterrupted production of this crop throughout the year (Kfir 2003). The introduction of canola (*Brassica napus* L.) into South Africa during 1994 and the rapid expansion of cultivation since then (Mosiane, Kfir & Villet, 2003) could have contributed to the area available for colonisation by *P. xylostella*. The comparatively low pest status of *P. xylostella* in South Africa that can be related to the diverse parasitoid population makes the region ideally suited for the development of IPM strategies against this pest.

1.1.3 Aphids as cabbage pests in South Africa

According to Moran (1983) who ranked insect pest families in South Africa based on relative pest status, the Aphididae (Homoptera) was the second most important after the lepidopteran family Noctuidae (out of 25 families listed). The fact that aphids are important vectors of diseases, which, according to Moran (1983) is the type of plant damage contributing most to pest status, further enhances the pest status of aphids as a group. The prowess of aphids as vectors can to a large extent be related to their restless nature. According to Davies (1932) a total of 73% of residential populations of *M. persicae* for instance would shift from their original feeding sites within a 24-hour period. Aphids are also prone to undertaking regular dispersal flights that, according to Carter (1961), can be seen as movement within a natural breeding area and necessary for completing a breeding cycle. The fact that aphid feeding damage is not always clearly discernable (unless they occur in high enough numbers to cause leaf deformities) may lead to a tendency where their potential for causing crop damage is under estimated.

Three aphid species viz. Brevicoryne brassicae (L.), Lipaphis erysimi (Kaltenbach) and Myzus persicae (Sulzer) (Homoptera: Aphididae) attack cruciferous crops in South Africa (Annecke & Moran, 1982). B. brassicae and L. erysimi are considered to be the most important species and are dominant during winter and summer months respectively. M. persicae, even though present during both seasons never attain high populations (Annecke & Moran, 1982). Both B. brassicae and L. erysimi are oligophagous with each species having a limited number of host plant records of 12

and 11 species respectively (Millar & Drürr, 1985). Among host plants recorded for *B. brassicae* and *L. erysimi* a large percentage *viz.* 83% and 91% respectively are within the family Cruciferae. This can be contrasted with the host plant tally of 139 species, of which only 25 species are classified as crops and only 10.8% of the grand total are within the family Cruciferae, that have been recorded for the highly polyphagous *M. persicae* (Millar & Drürr, 1985; Millar, 1991).

Reproduction of both *B. brassicae* and *L. erysimi* in South Africa is through viviparous parthenogenesis (Annecke & Moran, 1982) and extremely high populations may occur on crop plants. According to Annecke & Moran (1982) a population of *L. erysimi* containing 17 000 individuals was found on a single cabbage plant in a production area close to Pretoria.

1.2 Implementation of cultural control strategies as part of IPM against diamondback moth and aphids

As already mentioned, distinction can be made between culturally oriented strategies and most other IPM strategies. Cultural control typically includes those strategies that can be determined or influenced by producers. Maloy (1993) mentioned practices such as cultivation, site selection, tillage, selection of crop varieties, cropping sequence, method of crop establishment, planting layout, weed control, fertilisation and water management as typical cultural practices.

According to Talekar & Shelton (1993) interest in cultural control strategies for pest management in cruciferous crop production has been rekindled specifically because of difficulties experienced with *P. xylostella* control. The shift towards cultural control can also be linked to a broader IPM research shift towards recognising the importance of biological interactions and questioning of the value of high intensity monoculture production (Andow, 1991). The high arthropod diversity on, and variable responses of associated arthropods to cruciferous crops makes these crops ideally suited for crop diversity evaluations (Hooks & Johnson, 2003). Cultural control strategies that have had some degree of success against *P. xylostella* include intercropping, overhead irrigation, trap cropping, crop rotation and clean cultivation (Talekar & Shelton, 1993). Cultural control strategies on their own will however not be sufficient for pest

control in commercial production systems and will have to be combined with other strategies in more comprehensive IPM systems.

1.2.1 Use of intercropping strategies

According to Andow (1991) vegetational diversity can vary in terms of plant types, spatial array and temporal overlap of different plant species. Different plant species included in mixtures might be crop species in intercropping, a crop and a beneficial non-crop in nursery crops or a crop and a weed in weedy cultures. In the developing world the use of multiple cropping systems has been common practice over many centuries, and has proven to be of special importance in the tropics where the move to monocultures often met with disaster (Dover, 1986).

There are not many examples of instances where intercropping has reduced the significance of *P. xylostella*. In many cases intercropping had no impact or, worse still, caused higher pest infestations. This is illustrated by the fact that the testing of 54 non-host crops in Taiwan yielded none that had any significant impact on *P. xylostella* infestations (Talekar & Shelton, 1993). Andow (1991) stressed the fact that plant mixtures that are spatially intimate and that have a maximal temporal overlap are the most complex ecological systems classified under vegetational diversity. This can be ascribed mainly to the fact that inter and intra plant competition takes place within these systems at the same time as herbivory. It is however accepted as a general rule that oviposition patterns may be altered in instances where non-host plants are planted close to cruciferous crop plants (Hooks & Johnson, 2003). An important observation by Dover (1986) that should be stressed here is that behavioural alterations may be because non-host crops inter-planted with host crops extend the search area of pest insects.

According to Bukovinszky, Tréfás, van Lenteren, Vet & Fremont (2004) intercropping of Brussels sprouts (*Brassica oleracea gemmifera* L. cv. Maximus) with malting barley (*Hordeum vulgare* L. cv. Video) resulted in significantly reduced *P. xylostella* and *B. brassicae* infestations. This example however serves well as an illustration of the complexity of such systems when other observations made by Bukovinszky *et al.* (2004) are taken into consideration. *P. xylostella* densities were

higher on intercropped plants in spite of lower infestations because of reduced plant growth. Similarly *B. brassicae* infestations remained consistently higher on monoculture plants until the end of the growing season when the situation was reversed. This can be ascribed to delayed onset of senescence in intercropped plants because of slower plant growth.

1.2.2 Diamondback moth control through irrigation

Dennill & Pretorius (1995) recorded distinct periodicity of nocturnal activity of *P. xylostella* adults. Moth activity peaked between 21:30 and 23:30 and this phenomenon was used by McHugh & Foster (1995) to demonstrate the disruptive effect that intermittent overhead irrigation after sunset has on *P. xylostella* activity. According to McHugh & Foster (1995) *P. xylostella* infestation reductions of between 60,8% and 86,9% (as compared to drip irrigation) can be achieved if overhead irrigation is correctly scheduled. Rain and water drops from sprinkler irrigation systems are also believed to drown or physically dislodge all but first instar *P. xylostella* larvae, the latter of which feed as leaf miners (Talekar & Shelton, 1993).

1.3 Importance of parasitoids in diamondback moth and aphid IPM programmes in South Africa

A total number of 33 parasitoid and hyper parasitoid species have been recorded for *P. xylostella* in South Africa (Kfir, 2003), which is exceptional even when compared to other parts of the continent. The extremely high parasitism rates of *P. xylostella* in South Africa that often peak above 90% has ensured that its local pest status remained lower than in any other country in the world (Kfir, 2001). Natural suppression of *P. xylostella* populations was so complete that interest in the pest was only rekindled during the 1990s after recurring outbreaks and progressive pesticide resistance was reported (Kfir, 2003). The observed increase in pest status can be ascribed to the elimination of natural enemies and development of pesticide resistance through poorly managed chemical applications.

Kfir (2001) illustrated the importance of parasitism after experimentally inducing reductions in parasitism levels, of between 52% and 61%, by partially removing

parasitoids from cropping systems. The removal of parasitoids resulted in an increase of between 79% and 80% in *P. xylostella* infestations at different localities and an increase in peak infestation periods from five weeks for plots with normal parasitism to 12 weeks for plots with suppressed parasitism. Larval infestations per plant in plots where parasitoids were excluded increased by between 69% and 83%.

According to Annecke & Moran (1982), aphid control via parasitoids is restricted because of the large number of hyper-parasitoid species that attack primary parasitoids. Primary parasitoid suppression is most severe during summer months, when primary parasitoids are outnumbered by hyper-parasitoids.

1.4 Chemically and physically mediated trophic interactions between hosts, herbivores and natural enemies

The impact of plant chemicals on herbivores is typically described as a "bottom-up" force within the context of a tritrophic system (Karimzadeh, Bonsall & Wright, 2004). Plant chemicals are also considered to have a greater regulatory effect than natural enemies in many terrestrial systems. Chemical interaction between herbivores and plants typically take place when herbivores are initially attracted to suitable hosts and also when herbivores are in contact with host plant surfaces. Physical characteristics of plants such as general morphology, colour and leaf surface characteristics will however play a crucial part as far as acceptance of host plants for oviposition or feeding is concerned.

1.4.1 Plant resistance against diamondback moth and aphids

Host plant resistance forms an integral part of IPM strategies and considerable effort has been spent on determining and understanding resistance mechanisms within cruciferous crops. Resistance in cabbage crops is found in both normal bloom (normal leaf surface wax bloom) and glossy leaved types (Talekar & Shelton, 1993) but are mediated by different mechanisms.

Leaf surface characteristics encountered by herbivorous insects after physical contact with host plants has been established are crucial in mediating further plant-herbivore

interaction (Spencer, 1996). Among cruciferous crops the physical and chemical properties conveyed by leaf surface wax layers are important elements in determining the outcome of host plant – herbivore interactions.

1.4.1.2 Resistance mechanisms in normal bloom type plants

Talekar & Shelton (1993) listed a total of 48 cruciferous host plants that are globally attacked by *P. xylostella*. Among this group are 15 crop and 35 weed species. They also reported that weed species are only attacked in the absence of crops, which are preferred hosts. Orientation towards crop host plants is however also influenced by crop type, with significant differences being recorded among different subspecies (Reddy & Smith, 2004) of *B. oleracea* as well as between cultivars (Verkerk & Wright, 1994).

Host plant suitability will however also vary according to plant age. Wakisada, Tsukuda and Nakasuji (1992), cited by Verkerk & Wright (1994) found a 50% reduction in mean fecundity among *P. xylostella* females that had developed on mature cabbage leaves when compared to those that had developed on young leaves. These findings are in agreement with those made by Dennill & Pretorius (1995) in which the highest infestation levels for *P. xylostella* were recorded on plants that were younger than six weeks (after transplanting).

The trend towards increased resistance along with increased plant age reported by Verkerk & Wright (1994) may be explained by factors such as reduced nutritional value, increased leaf hardness and a decline in glucosinolates and derivative chemicals with plant age (Verkerk & Wright, 1996). The abovementioned suggestions would imply physically mediated antibiosis (more effective against specialist feeders able to overcome glucosinolate defence chemicals) and chemically mediated antixenosis. Eigenbrode & Shelton (1990) reported increased mortality of *P. xylostella* larvae after ethanol extracted polar fractions from cabbage leaves were added to an artificial diet. According to Verkerk & Wright (1996) the presence of secondary plant chemicals involved in antibiosis (chemically mediated antibiosis) are as yet unproven. Antibiosis observed by Eigenbrode & Shelton (1990) can subsequently only be considered as indirect evidence of partial resistance resulting

from as yet unidentified polar extracts from cabbage leaves (Verkerk & Wright, 1996).

1.4.1.3 Resistance mediated by physical leaf wax characteristics

The main function of epicuticular lipids on plant surfaces is to retain water (Eigenbrode & Espelie, 1995). Climatic and other environmental factors also exert an influence on epicuticular wax load and properties. According to Baker (1974), the greatest increases in wax load occurred under conditions where high levels of radiant energy are combined with low humidity levels. The structure of wax layers is most profoundly influenced by temperature. Temperature also has an influence on the chemical composition of epicuticular waxes (Baker, 1974) but the effect of environmental factors on the mode of crystallisation has the greatest impact on leaf wax crystal structure.

The specific nature of chemical and morphologic characteristics that will often vary from one plant genotype to the next within a single plant species suggests a more specific function related to insect/ plant host interaction. According to Eigenbrode & Espelie (1995) plants with glossy leaf characteristics typically have reduced epicuticular lipid microstructure complexity along with reduced amounts of lipids and an altered chemical composition. The phenomenon of glossy or bloomless plant genotypes is widespread and may result in either a reduction or increase in susceptibility to insect damage (Eigenbrode & Espelie, 1995). The most visible impact of epicuticular lipids on insect herbivores becomes evident when the susceptibility of glossy (bloomless) plant genotypes is compared with susceptibility of normal wax genotypes (Eigenbrode & Espelie, 1995).

It is important to note that the impact of glossy genotypes will vary, depending on the type of insect associated with the plant. The survival of neonate *P. xylostella* larvae on glossy leaf *B. oleracea* genotypes is greatly reduced (Lin, Eckenrode & Dickson, 1983). The impact of glossy leaf characteristics on populations of *B. brassicae* and *P. xylostella* is sufficient to reduce their populations to below 10% and to approximately 10% respectively compared to those found on normal bloom plants (Eigenbrode & Espelie, 1995). The impact of glossy leafed varieties on populations of closely related insect species may however also vary. The negative impact of the

glossy leaf trait in Brussels sprouts on populations of *B. brassicae* was found to be greater than that on populations of *M. persicae* (Way & Murdie, 1965). Glossy-leafed genotypes may however be preferred by certain herbivore groups, as is the case with the flea beetle (Chrysomelidae: Alticinae) *Phyllotreta striolata* (Lin *et al.*, 1983; Eigenbrode & Espelie, 1995), *P. atra*, *P. cruciferae* and *P. undulata* (Way, & Murdie, 1965). This effect can be explained by the greater traction provided by the tarsal setae of these chrysomelid beetles on leaves of glossy genotypes (Eigenbrode & Espelie, 1995).

Lin et al. (1983) found that P. xylostella females preferred to oviposit on plants with dark green coloured foliage associated with glossy leaf traits. Heavy infestations on the Australian cauliflower plant introduction PI 234599, hailed as the most promising source of P. xylostella resistance (Eigenbrode, Stoner, Shelton & Kain, 1991), were subsequently reported under greenhouse conditions (Lin et al., 1983). The failure of glossy leaf traits to provide protection against P. xylostella infestations under greenhouse conditions (Lin et al., 1983; Eigenbrode, Moodie & Castagnola, 1995), compared to results in the field, may be attributed to the predisposition of neonate larvae on glossy leafed plants to predation and adverse climatic conditions in the field (Eigenbrode, Moodie & Castagnola, 1995).

A study conducted by Eigenbrode *et al.* (1995) on generalist predators in three insect orders revealed greater predation efficiency of predators on glossy leaf surfaces. The greater effect of predation by generalist predators alone does however not explain the total impact of glossy leaf surfaces on the survival of *P. xylostella* larvae (Eigenbrode *et al.*, 1995). According to Way & Murdie (1965), evidence suggests that natural enemies of *B. brassicae* and *M. persicae* prefer glossy leafed Brussels sprout plants. The coleopterous families Coccinellidae, Anthocoridae and Staphylinidae were more prominent on glossy bloom plants. Plants with glossy leaf characteristics have been shown not to be toxic to *P. xylostella* larvae but rather to have an impact on larval behaviour during the first instar (Eigenbrode *et al.*, 1991). According to Eigenbrode *et al.* (1991) feeding by neonate larvae as leaf miners (normal behaviour on plants with normal surface waxes) during the first 48 hours after emergence on glossy leafed plants will determine their survival to the fourth instar. Elicited foraging behaviour and reduced tunnelling would result in serious reductions of time spent feeding. It

would also deny first instar larvae refugia and ensure that they are well dispersed, which, along with greater predator mobility on glossy leaf surfaces, would enhance the efficiency of generalist predators (Eigenbrode *et al.*, 1995).

Plant morphology may also contribute to the effect of epicuticular wax layers where the angle at which leaves are presented to larvae can significantly influence their survival. Verkerk & Wright (1994) found a significant increase in the duration of the larval phase of *P. xylostella* on vertically suspended glossy leaved cultivars when compared to horizontally suspended leaves. It is believed that feeding efficiency is reduced because of greater energy expenditure required to maintain footing on a vertical leaf surface. Similarly, the angle of normal wax bloom leaves that provide reduced traction to larger insects such as beetles because of slipping of their tarsal adhesive setae on loose crystalline structures (Eigenbrode & Espelie, 1995), may affect preference by both herbivores (Lin *et al.*, 1983) and generalist predators (Eigenbrode *et al.*, 1995).

Glossy leaf characteristics are the single most promising avenue in plant defensive traits as far as resistance breeding against insect pests among cruciferous crops is concerned. The discovery that application of s-ethyldipropylthiocarbamate (EPTC) herbicide as a soil treatment alters leaf surface wax characteristics of normal wax bloom to match those of glossy leafed plants, has broadened the scope for the use of glossy leaf traits in IPM strategies (Eigenbrode & Shelton, 1992).

1.4.2 Establishing a theory for host plant finding by herbivores

A general theory that satisfactorily explains how insects locate host plants has been lacking in spite of the many hypotheses that had been put forward during numerous attempts made at explaining observations in poly-cultures. Finch & Collier (2000) highlighted and discussed the validity of seven recognised hypotheses *viz.* physical obstruction, visual camouflage, masking of host plant odours, repellent chemicals, altering of host plant odour profiles as well as the resource concentration and enemies hypotheses. At this point it should be stressed that insects must always be firstly attracted to host plants before they are subsequently stimulated to accept any particular plant as a host, and that these mechanisms involve different plant chemicals

and other related stimuli. Metcalf & Metcalf (1992) distinguished between volatile plant kairomones that mainly act over long distances through diffusion through air and non- volatile kairomones of relatively high molecular weight that remain in plant tissues and on plant surfaces. According to Metcalf & Metcalf (1992) volatile plant kairomones act as insect attractants over a distance, while non-volatile kairomones act as insect arrestants, feeding stimulants or oviposition stimulants once direct contact with host plants has been established.

Among the seven theories highlighted by Finch & Collier (2000) four relate to trophic interactions that function in multi cropping systems. These theories are: masking of host plant odours, repellent chemicals, altering of host plant odour profiles and the resource concentration theory.

The question as to how accurate/ effective chemical attraction really is should however be asked first, if the role it plays is to be assessed. Finch (1980) has made an attempt at calculating the movement of plant odour molecules and the detectable distances thereof to insects. Plants emit a continuous yet variable stream of odour that spreads through the surrounding atmosphere through diffusion and dispersion. Odour "clouds" are subsequently present with various gradients of concentration around particular plants and tend to be hemispherical in still air and semi-ellipsoidal (even though quite variable) in moving air (Finch, 1980). The evaporation and diffusion properties of particular chemicals, olfactory sensitivity of a particular insect and the amount of chemical released by a particular plant at a particular growth stage under specific environmental conditions will impact on the distance at which a plant may be detected. The amount of volatile chemicals released from plants will decrease with an increase in air movement (because stomata close under such conditions) as will the concentration of such chemicals in a given volume of air (Finch, 1980). According to Wright 1958 (cited by Finch, 1980) the absolute limit for detection by the insect olfactory system would probably be in the concentration range of 1 x 10⁻¹⁴ g of chemical/ litre of air. Finch (1980) calculated the maximum downwind detectable distance for a cruciferous plant that releases 7 l of volatile chemicals/day based on the assumption that the threshold concentration for cruciferous odour detection is g of chemical/ litre of air. Results indicated that a single cruciferous plant would be undetectable at a downwind distance of 64 m when air is moving at 0.45 m s⁻¹ and at a distance of 17 m when air is moving at 4.5 m s⁻¹.

Distances for host plant detection might however be considerably less when taking into account that flight activity for P. xylostella peaks when wind speed is ≤ 0.8 m s⁻¹ and that moths appear to lose control over their movement at wind speeds exceeding 2.2 m s⁻¹ (Goodwin & Danthanarayana, 1984). Abovementioned should also be considered along with the fact that it is highly unlikely that cruciferous pests would be able to detect volatile chemicals at levels as low as 10^{-14} g of chemical/ litre of air. Finch & Collier (2001) stressed the fact that the amount of volatile chemicals necessary to induce directed responses in insects are considerably greater than the amounts released by plants naturally. The maximum distance recorded for insect orientation towards plant volatiles under field conditions is limited to a few metres only.

Observations made by Finch & Collier (2000, 2001) regarding the four hypotheses linked to chemical attraction has either dispelled or placed a serious question mark on each. The theory that host plants can be 'masked' by odours released by non-host plants has very little data to support it. The argument put forward by Finch & Collier (2000), that non-host plants' different chemical profiles compared to those of host plants cannot have an impact on insects not adapted to detect them, makes sense especially when specialist feeders are considered. To add to this, they also mention results obtained in other studies where similar 'disruptive' effects were obtained when host plants were surrounded by plant models or sheets of green paper. This evidence points towards a different repelling mechanism than that suggested by the theory. Similarly they argue that the mechanism of deterrence by means of volatile chemicals (on which the theory of repellent chemicals is based) still needs to be proven. Currently no real experimental evidence, other than circumstantial evidence obtained through artificial presentation of crushed aromatic plants under laboratory conditions, exists. The possibility of root exudates from non-host plants being taken up by host plants and then not being metabolised and subsequently impacting on the physiology of the host plant is a real possibility for some plant combinations. It can however be argued that the theory does not apply in instances where effects are noticed almost immediately after non-host introduction, such as the intercropping of cruciferous

crops with clover on which arguments put forward by Finch & Collier (2000) are based.

Finally the resource concentration hypothesis, which, along with the enemies hypothesis, is most often used (Finch & Collier, 2000) states that plant pests will be better capable to find and more inclined to remain in denser or purer host plant stands. According to Andow (1991) the generalized opinion that this hypothesis accounts best for herbivore responses to poly-cultures has little application value as far as specific pest reactions to specific poly-cultures are concerned. As already mentioned under intercropping, many exceptions to the rule exist where pests (especially monophagous species) are more abundant in poly-cultures than in monocultures. Greater predator efficiency is the reason most often given for lower pest numbers in poly-cultures. The argument for this is that predators and parasitoids are more effective in complex environments. This argument might hold true for some polyphagous predators but would be difficult to uphold for highly specialized monophagous or oligophagous parasitoids that depend on specific hosts as units of reproduction. The impact of parasitoids is dominant in South Africa as far as populations of *P. xylostella* are concerned (Kfir, 2001).

1.4.3 Host plant acquisition by diamondback moth

P. xylostella females depend on a wide range of compounds to stimulate oviposition (Renwick & Raadke, 1990). Green leaf volatiles released from cabbage leaves will on their own elicit behavioural changes in P. xylostella (Reddy & Guerrero, 2000) but may also act in synergism with sex pheromones (Reddy & Guerrero, 2000; Reddy & Guerrero, 2004). According to Reddy & Guerrero (2000) a number of volatile chemicals viz. 1-hexanol, (Z)-3-hexen-1-ol, hexen-3-ol, hexanal, (E)-2-hexenal, hexyl acetate and (Z)-3-hexenyl acetate are produced by cabbage plants. These green leaf volatiles on their own only had an impact on mated females in which arresting behaviour and upwind flight patterns were elicited (Reddy & Guerrero, 2000).

Oviposition patterns are also influenced by leaf damage, with significantly greater oviposition rates and an oviposition pattern shift for injured plants towards a preference for leaf tissue rather than stems (Reddy, Tabone & Smith, 2004).

According to Mithen & Campos-de Quiroz (1998) it is believed that glucosinolates are restricted to vacuoles in plant tissue and are brought into contact with thioglucosidases enzymes that are found in cytoplasm when tissues are damaged. Observations on plants with feeding damage may be explained by the fact that glucosinolates are hydrolysed by the enzyme thioglucosidase to produce volatile isothiocyanates along with glucose, sulphate ions and thiocyanates (Sang, Minchinton, Johnstone & Truscott, 1984). Another important factor is the great variation in glucosinolate profiles from different tissues on the same plant and between plant species (Sang *et al.*, 1984). These differences may also explain the significantly greater oviposition on cabbage and cauliflower plants when compared with broccoli and kohlrabi plants observed by Reddy *et al.* (2004).

1.4.3.1 Leaf waxes mediating host plant recognition by diamondback moth

According to Spencer (1996), sinigrin, a glucosinolate that is known to stimulate oviposition by *P. xylostella* females is found in a range of host plants. Paraffin waxes (a combination of branched and unbranched alkanes) are chemically similar to epicuticular waxes (mainly n-alkane compounds) that are found on plant surfaces (Eigenbrode & Espelie, 1995) and are increasingly used in artificial host plant studies (Spencer, 1996). Significant interactions in terms of elicited oviposition stimulus exist between paraffin wax applied in combination with sinigrin or cabbage homogenate substances when compared to primary oviposition and feeding stimulants and epicuticular waxes on their own. Spencer (1996) reported a threefold increase in oviposition on sinigrin-alkane mixtures along with more pronounced arrestment behaviour that included extended periods of antennating (with peculiar side-to-side movement of antennae) and probing with the ovipositor among *P. xylostella* females.

The exact interaction between waxes and primary stimulants is not clearly understood yet. Spencer (1996) proposed a combination of physical (tactile) stimuli provided by wax surfaces acting along with chemical stimuli to trigger leaf surface examination that leads to oviposition.

1.4.4 Host plant acquisition by aphids

Banks & Stark (2004) found that the type of margin surrounding plots that contained Broccoli (*Brassica oleracea* L. var. *italica*) plants had a significant effect on aphid density with more aphids close to bare ground than to weedy margins. These findings might be explained by the visual acuity of aphids and the way in which they recognise host plants and concurs with results obtained by Finch & Collier (2001). According to Kennedy, Booth & Kershaw (1959) no evidence exists for olfactory attraction of low-flying aphids towards plants. Yellow sensitive aphids that include species like *B. brassicae* and *M. persicae*, are however attracted to long wave energy emitted by plants and soil. Aphid colour vision is primarily geared towards discriminating between sky and ground, while allowing for subsidiary discrimination between plant and soil contrast (Kennedy, Booth & Kershaw, 1961). Visual acuity is subsequently designed to guide aphids towards plants of the correct physiological type rather than taxonomic type.

1.4.5 Semiochemicals and host location by the most important parasitoid of diamondback moth

A point stressed by Vet & Dicke (1992) centres on the fact that chemicals produced by herbivores are the most reliable for host detection, but that chemical stimuli produced by infested plants are more detectable. The nature of chemical stimuli required for host location depends on whether predation is of a generalist or specialized (as is the case with parasitoids) nature. Foraging by predators is governed by food requirements whereas foraging by parasitoids is governed by egg load (Vet & Dicke, 1992). The fact that predation among parasitoids has a reproductive impact implies that it involves a specific host at a specific developmental stage (Dicke, 1999) and that host acquisition must be facilitated by specific chemical queues.

Various sources of semiochemicals may be used by *C. plutellae*, which is the dominant *P. xylostella* parasitoid in South Africa (Kfir, 2001), to locate host larvae. Chemical stimuli, as in the case with *P. xylostella*, may act as attractants over a distance or at close range once contact with host larvae has been established. Reddy, Holopainen & Guerrero (2002) investigated the impact of semiochemicals originating from sources as diverse as green leaf volatiles released from cabbage leaves, sex

pheromones released by *P. xylostella* females and larval frass. According to Reddy *et al.* (2002) *C. plutellae* responded strongly to green leaf volatiles and also to *P. xylostella* sex pheromones. The attraction response was greatly enhanced when sex pheromones were combined with green leaf volatiles. *C. plutellae* females were also attracted to components *viz.* dipropyl disulfide, dimethyl disulfide, dimethyl trisulfide and allyl-isothiocyanate contained in larval frass.

The importance of chemical cues resulting from specific plant-host complexes in the case of host acquisition by C. plutellae has also been illustrated by Shiojiri, Takabayashi, Yano & Takafuji (2000). According to Shiojiri et al. (2000) C. plutellae, a solitary endo-parasite of P. xylostella, showed no attraction to larvae or their associated products in the absence of a host plant. Attraction towards herbivoreinduced volatiles was however highly specific with plant damage caused by P. xylostella larvae only, eliciting response reactions. The importance of multiple host-predator interactions mediated through plant volatiles generated through multiple plant-herbivore interactions can also be illustrated through this example. A less specialized host-predator interaction between Cotesia glomerata (a gregarious endoparasite of Pieris brassicae), in which parasitoid attraction is based on the extent of plant damage rather than the cause thereof, impacted negatively on C. plutellae efficiency. The negative impact results partly because of a greater attraction among foraging C. plutellae towards plants infested by P. xylostella larvae only when compared to plants infested by P. xylostella and P. brassicae (Shiojiri et al., 2000). This effect is compounded even further by the fact that both parasitoid species cannot distinguish between each other's hosts once contact has been established, but that only C. plutellae is capable of successfully ovipositing in non-host larvae. This apparent greater attraction to P. xylostella infested leaves may be misleading. Potting, Poppy & Schuler (1999) demonstrated that leaves damaged by larvae, but from which larvae were removed (with frass and silk retained on the leaf) were just as attractive to C. plutellae females as leaves with larvae still feeding on them. This indicates that the source of mechanical damage to leaf tissue is not important. It does however indicate the important role that frass and silk, which on its own is unattractive to C. plutellae (Poppy et al., 1999) may play when encountered in combination with damaged leaves.

Preference by *C. plutellae* females for volatiles from specific *Brassica* subspecies and, as shown by Bogahawatte & van Emden (1996), even towards specific cultivars will also be determined by whether or not they were part of the population that had developed in hosts feeding on that specific cultivar. Olfactometer tests conducted by Bogahawatte & van Emden (1996) revealed the ability among *C. plutellae* females to distinguish between and show preference towards the cultivar on which their generation had been reared. According to Bogahawatte & van Emden (1996) the preference for undamaged cabbage plants of the cultivar on which *C. plutella* females were reared was significantly greater than for *P. xylostella* damaged cauliflower plants also presented to them. It must however be stressed that similar levels of attraction towards most plants within the genus *Brassica* will result when the specific plant type on which *C. plutellae* females was reared is not present.

1.5 Crop design centred on crop characteristics and the functionality of intercropping systems

The selection of crop plant types considered for inclusion into intercropping systems should be done with care since not all plant species will be compatible. From a pest control perspective plants chosen should not be prone to attack by similar pests and diseases. This subsequently necessitates the planting together of unrelated plant species of which the known pest complex overlap is as little as possible. Oviposition patterns as mentioned by Hooks & Johnson (2003) as well as feeding patterns are ultimately determined by the recognition of leaf surface chemicals (Chapman & Bernays, 1989).

1.5.1 Cabbage and carrot pest spectra and the feasibility of their inclusion into an intercropping system

According to Chapman & Bernays (1989) ample evidence exists that secondary chemicals are probably in all cases responsible for preventing phytophagous insects from feeding on non-host plants. As already mentioned attraction to and recognition of host plants by *P. xylostella* females is to a large extent governed by the presence of various glucosinolates and their breakdown products. Glucosinolates, which are found in cruciferous plants act as feeding deterrents for most other insect species that

are not adapted to them. A parallel can be drawn with defensive chemicals acting as feeding deterrents in umbelliferous plants. Städler & Buser (1984) identified six active compounds acting in synergism viz. trans-methylisoeugenol, trans-asarone, osthol, bergapten, xanthotoxin and falcarindiol from carrot leaf surface extracts. Of the identified compounds, trans-asarone has been detected in the air space directly above carrot leaf canopies and falcarindiol is found among members of the family Umbelliferae only. Umbelliferous plants are subsequently also attacked by specialised oligophagous insects among which, the carrot fly, Psila rosa (Diptera: Psilidae) and the papilionid butterfly *Papilio polyxenes* (Lepidoptera: Papilionidae). This pattern shows great similarity to that of the insect complex attacking cruciferous plants. Because of this, the pest complex for carrot plants, Daucus carota L (Umbelliferae), in South Africa is very limited. Two polyphagous aphid species: M. persicae and Aphis fabae Scopoli (Homoptera: Aphididae) have been recorded on along with Tetranychus cinnabarinus carrot plants, (Boisduval) (Acari: Tetranychidae), but are all considered to be of minor importance (Annecke & Moran, 1982). None of the abovementioned pests are considered to be among the important cabbage pests even though M. persicae and T. cinnabarinus may occur on cabbage plants.

In terms of morphology, the leaf canopy of both plant types grows to approximately the same height, which should limit competition for sunlight. According to Hooks & Johnson (2003), cruciferous plants in general are considered weak competitors when growing among other crops. Competition between cabbage and carrot plants for water and nutrients might however be reduced because the root zone of the taproot system of carrot plants is restricted along a vertical plain (Janick, 1997).

1.6 Establishment of a cabbage and carrot intercropping system

The timing of companion plant establishment is of crucial importance and is viewed by Hooks & Johnson (2003) as one of the most challenging aspects related to crop diversification. According to Benjamin & Aikman (1995) the weights of cabbage and carrot seed used in trials to test growth prediction models were 4,15 mg and 2,50 mg respectively. This gave cabbage plants a distinct advantage in terms of overall growth rate. Trial evidence subsequently proved that cabbage and carrot plants were most

evenly matched when early sown carrots were grown together with late sown cabbage (Benjamin & Aikman, 1995). According to studies conducted on cruciferous crops by Finch & Kienegger (cited by Hooks & Johnson, 2003) the under-sown crop has to cover at least 50% of the vertical profile of the main crop before it will reduce colonization by insect pests. Hooks & Johnson (2003) also further stressed the fact that a treatment cannot be considered separate from a monoculture unless the undersown crop has expanded its canopy sufficiently to exert its influence. The final conclusion by Hooks & Johnson (2003) that relative early planting of companion crops contributes most to target pest species control agrees with findings made by Benjamin & Aikman (1995). A further point of consideration for this trial was that carrot seed had to be sown directly on the field while cabbage seedlings were produced under controlled greenhouse conditions. This would most likely have enhanced the benefit factor already experienced by cabbage seedlings and necessitated a further delay in their transplanting, in order to ensure a fully functional intercropping system during the trial period.

An effective crop diversification system layout should allow for sufficient alteration of the planting system to ensure its impact on pest populations without compromising the agronomic value thereof. According to Bukovinszky, Tréfás, Van Lenteren, Vet & Fremont (2004) most studies conducted to evaluate the impact of intercropping systems on pest populations do not take the impact of plant density as such into consideration. Leaving planting densities of the main crop (monoculture) unaltered to avoid any negative impact on arthropod response may however prove to be unacceptable from a crop production point of view. Plant competition often results when companion crops are added to existing monocultures without altering the planting density of the main crop (original monoculture). Bukovinszky et al. (2004) for this reason draws clear distinction between additive and substitutive intercropping systems (Figure 1 A-C). Plant density subsequently has an impact on arthropod response as well as on plant performance. As far as plant performance is concerned Bukovinszky et al. (2004) stressed that both, growth and developmental rates of intercropped plants are delayed by inter specific plant competition. This is due to the increased effect that factors such as overtopping and constriction of leaf canopies have on crops growing in mixed age and mixed species stands (Benjamin & Aikman, 1995). The point of departure for the proposed study would subsequently be to

establish multi crop planting systems and then to evaluate their impact on arthropod populations. If however the focus is placed solely on the manipulation of arthropod populations the outcome in terms of plant production would undoubtedly be of no practical value to the industry.

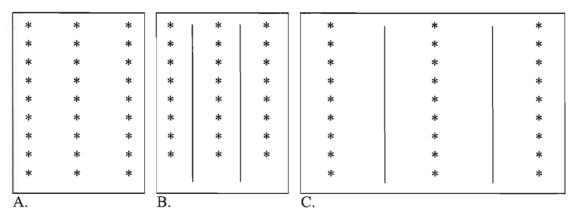


Figure 1. Schematic presentation of: a monoculture planting (A), an additive intercropping (B) and a substitutive intercropping system (Bukovinszky *et al.*, 2004) (Star represents main crop and line represents secondary crop).

1.7 Objectives of this study

General objectives were to study the effect of a substitutive intercropping system consisting of different ratios of cabbage and carrot plants on cabbage insect pests.

1.7.1 Specific objectives of this study were:

- To determine the impact of different cabbage-carrot intercropping ratios on *P. xylostella* and aphid infestation levels.
- To determine the impact of different intercropping ratios on *P. xylostella* parasitism, parasitoid dominance and parasitoid diversity.
- To determine the impact of different cabbage-carrot intercropping ratios on *P. xylostella* feeding damage to cabbage leaves.

Results of this study are presented in the form of chapters with the following titles:

• Impact of different cabbage-carrot intercropping ratios on diamondback moth (Lepidoptera: Plutellidae) infestation patterns, parasitoids and parasitism.

• Impact of different cabbage-carrot intercropping ratios on infestation of cabbage by aphids (Homoptera: Aphididae).

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CHAPTER 2

Impact of different cabbage/ carrot intercropping ratios on diamondback moth (Lepidoptera: Plutellidae) infestation patterns, parasitoids and parasitism

2.1 Introduction

Diamondback moth, Plutella xylostella (L.) (Lepidoptera: Plutellidae), is regarded as the most serious cruciferous crop pest and occurs in all parts of the world where these crops are cultivated (Talekar & Shelton, 1993). The high pest status of this insect can largely be ascribed to its ability to develop resistance to synthetic and organic insecticides (Shelton, Robertson, Tang, Perez, Eigenbrode, Preisler, Wilsey & Cooley, 1993; Shelton, Sances, Hawley, Tang, Bourne, Jungers, Collins & Farias, 2000). It should however be noted that the pest status of P. xylostella varies in different parts of the world, which can be ascribed to insufficient natural control in certain areas. Parasitoids are paramount to P. xylostella suppression and the high pest status of P. xylostella in most parts of the world can be linked to a shortage of effective natural enemies (Lim, 1986 cited by Kfir, 1998). The pest status of P. xylostella, is lower in South Africa than in any other country with comparable climatic conditions (Kfir, 1996). According to Waladde, Leuthe & Villet (2001) Cotesia plutellae (Kurdjumov) (Hymenoptera: Braconidae) parasitism levels in South Africa may peak at 90-95% for at least eight months of the year. The impact of parasitism on P. xylostella infestations in South Africa is such that annual infestation cycles occur that maintain a similar pattern regardless of localities (Smith & Villet, 2001). The pest status of P. xylostella has however increased in South Africa since the 1990s because of insecticide misuse that eliminated natural enemies and led to the build up of resistance (Kfir, 2003).

A feature among *P. xylostella* parasitoids is the tendency for certain genera to be dominant in terms of their impact. Currently *Cotesia* and *Diadegma* are considered to be globally the most important primary parasitoid genera (Verkerk & Wright 1996a). *Diadegma* spp. (Hymenoptera: Ichneumonidae) and *Apanteles halfordi* Ullyett (Hymenoptera: Braconidae) that were the most and second most important parasitoids

(Annecke & Moran, 1982) seem to have been dislaced by *C. plutellae* in South Africa. In more recent times however *A. halfordi* was recorded again as the dominant and only parasitoid species in certain production areas (Dennill & Pretorius, 1995). Temporal replacement of particular parasitoid species by other parasitoid species is possible (personal communications Dr. G.L. Prinsloo) and abovementioned observations might indicate species dominance alterations in both directions. *C. plutellae* is currently considered to be the most dominant parasitoid species in South Africa (Kfir, 2001; Kfir, 2003; Mosiane, Kfir & Villet, 2003; Waladde, Leuthe & Villet, 2001).

No research work has been done in South Africa on pest suppression via the use of intercropping systems that contain cabbage and carrot plants. In other countries studies involving cruciferous crops intercropped with different other crops as diverse as malting barley (Bukovinszky, Tréfás, van Lenteren, Vet & Fremont, 2004) and subterranean clover (Finch & Kienegger, 1997) reported reductions in *P. xylostella* infestations. Intercropping of host and non-host plants is most commonly done under resource-poor conditions in tropical countries where the value thereof has been proven (Dover, 1986). Cultural control strategies such as intercropping ultimately impact on all trophic interactions, which is ideal when a pest complex with diverse species has to be dealt with.

The aim of this study was to determine the impact of different cabbage/ carrot intercropping ratios on *P. xylostella* infestation patterns as well as on feeding damage to cabbage leaves. Given the crucial role parasitoids play in suppression of *P. xylostella* numbers the impact of intercropping on *P. xylostella* parasitism, parasitoid dominance and overall parasitoid diversity was also determined.

2.2 Material and methods

Two field trials were conducted in which different ratios of under-sown cabbage and carrot plants were planted. Trials were planted at the Scientific and Technical Support Services research station of the North-West Department of Agriculture at Potchefstroom. The first planting was done during the 2002/03 season, and the second during the 2003/04 planting season. Sowing of carrots was done during the

first two weeks of September during the 2002/03 season and had (for technical reasons) to be delayed until the end of November during the 2003/04 planting season. Sowing of carrots was done in dry soil to ensure that germination only took place over the entire trial surface area after irrigation had commenced.



Figure 1. Trial layout and plot distribution of the cabbage-carrot intercropping trial.



Figure 2. Intercropping plots at a 1:1 (foreground) and 1:3 (background) cabbage/ carrot ratio.

The cabbage cultivar Star 3301 was planted during the 2002/03 planting season and had to be replaced with Green Star during the 2003/04 planting season because seed became temporarily unavailable. The carrot cultivar Star 3006 was planted during both seasons. Thirty-day-old cabbage seedlings were transplanted into plots with well-established carrot plants that were 60 days old. The trial consisted of five treatments that were replicated six times in a randomised block design (Figure 1). The treatments were: control (cabbage monoculture with chemical insect control), cabbage monoculture (without insecticide application), 1:1 intercropping (ratio of cabbage and carrot rows), 1:3 intercropping and 1:5 intercropping. Plot size was 27 m² and measured 5.4 m by 5 m. All plots were spaced 2 m apart to ensure that individual treatments did not interfere with each other and that each plot was contrasted against bare soil. Cabbage plants were spaced 40 cm within rows and cabbage rows were spaced 60 cm in monoculture plots (control plots included). All intercropping was done according to a substitutive planting system to ensure that inter-row spacing on mixed plots, as far as the main and under-sown crops were concerned, were maintained at similar distances compared to those of monocultures.

The treated control was included to serve as a control for yield data. Yield data were however omitted from this dissertation because this study focused on insect-plant interactions and further research is currently conducted to explain possible plant-plant interactions and competition effects on yield. Planting density of carrots was increased by planting double rows, to correspond to a plant population increase of 37.5 %, compared to plant spacing recommendations made by Joubert, Boelema & Daiber (1994), in the 1:3 and 1:5 ratio intercropping treatments. This was done firstly to ensure that leaf canopy density and volume was as evenly spread and large as possible, especially in the 1:1 intercropping treatment. All irrigation was done with pressure compensated Netafim button drippers with a 2 l hour⁻¹ delivery rate. It was important to make use of drip irrigation to ensure that insects were not washed from leaves or drowned. It was important to prevent P. xylostella flight pattern disruption since infestation reductions of between 61 % and 87 % are possible when making use of overhead irrigation (McHugh & Foster, 1995). Fertilizers were applied according to recommendations based on soil analysis. Application of phosphates was done per plot by broadcasting before seedbed preparation, which was done with a rotovator to ensure thorough mixing and even spreading. Cabbage plants were fertilized individually and inorganic fertilisers were placed at a depth of 5 cm and a distance of 10 cm from each plant's stem. The first inorganic fertiliser application was made during planting and was followed with nitrogen topdressing that was applied in two instalments during the leaf initiation growth period prior to head initiation. Control plots were sprayed weekly with mercaptothion at the recommended dosage rate of 25 ml/10 l of water to prevent insect infestations. Insecticides were applied with a hollow cone nozzle at sufficient pressure to ensure that the application spray pattern was normal and droplets were fine enough to penetrate among leaves. All applications were done with a knapsack sprayer, which allowed individual cabbage plants to be sprayed and the nozzle to be held quite close to individual plants during spraying. Care was taken to avoid drift to neighbouring plots by not applying insecticides while the wind was blowing and by never spraying with the nozzle held high above canopy level.

P. xylostella infestation levels were determined weekly by sampling the third youngest open leaf (third fully opened leaf when plant is viewed from above) from one randomly selected plant per plot and counting the number of larvae per leaf. This was continued during each season for as long as it was possible to distinguish leaves of similar physiological maturity on different plants. Sampling was done seven times during the 2002/03 planting season (earlier planting date) and five times during the 2003/04 planting season. Visual ratings to assess the degree of feeding damage were done on two rows per plot, each consisting of seven plants per row. Plants were rated according to a numeric scale based on the severity of feeding damage. Undamaged plants were allocated a value of 1; plants with below average damage a value of 2; plants with average damage a value of 3 and plants with above average damage a value of 4. A mean score was calculated for each plot and used to calculate the Reciprocal Index of Attack (RIA) as described by Hanuss, Stelzer, Wietzke, Stendal, Warmbrunn & Weigand (1968).

The RIA was calculated according to the equation:

$$RIA = \underline{f1 + (0.8 \times f2) + (0.5 \times f3) + (0.2 \times f4)}$$
$$f1 + f2 + f3 + f4$$

where f1 to f4 is the frequency of plants in classes one to four respectively.

In order to determine parasitism levels, the P. xylostella larvae that were collected weekly from the six randomly selected leaves per treatment (one per plot) were reared on cabbage leaves at room temperature until moths or parasitoids appeared. The sex ratio was determined for all C. plutellae individuals reared from P. xylostella larvae. Abundance of the most important parasitoid species was calculated as a percentage of the total number of parasitoids that emerged. Data on P. xylostella larval counts was P0 log (P1) transformed and subjected to one-way analyses of variance at P100 confidence limit (Least Significant Difference). Untransformed data on P2 parasitism are however provided in the tables. The Statraphics P3 for Windows (2003) package was used to perform data analyses.

Prominence values (PV) (De Waele & Jordaan, 1988) were calculated for *P. xylostella* larvae for each treatment and sampling date according to the equation:

where population density represents the mean number of larvae per leaf, and frequency of occurrence represents the mean number of infested cabbage leaves per treatment calculated for each sampling date.

Specimens of all parasitoid species were sent to the ARC- Biosystematics Division in Pretoria for identification.

2.3 Results and discussion

Prominence values of *P. xylostella* infestations during both seasons are provided in Figures 3 and 4. At the first sampling dates prominence values differed only slightly between the mono crop and intercropping treatments, except for the 1:5 intercropping ratio during the 2002/03 season (Figure 3). The prominence values for *P. xylostella* populations varied largely during seasons. However, towards the end of the season

Table 1 Mean number of *Plutella xylostella* larvae per leaf at different cabbage-carrot intercropping ratios during the 2002/03 and 2003/04 growing seasons.

Treatment	Mean number of larvae per leaf	
	2002/03 season	2003/04 season
Control	0.24 a	0.07 a
Ionoculture	0.67 b	0.67 c
ntercropping 1:1	0.60 ab	0.50 c
ntercropping 1:3	0.88 b	0.33 bc
ntercropping 1:5	0.98 b	0.17 ab

Means within columns followed by the same letter do not differ significantly at P = 0.05 (LSD). Data were log (x + 1) transformed. All intercropping ratios indicate cabbage/ carrots.

Table 2 Mean percentage *Plutella xylostella* larvae parasitised per leaf at different cabbage-carrot intercropping ratios during the 2002/03 and 2003/04 planting seasons.

Treatment	Mean % parasitised larvae per leaf	
	2002/03 season	2003/04 season
Control	11.9 a	0.0 a
Monoculture	29.7 b	30.5 c
Intercropping 1:1	17.1 ab	20.5 bc
Intercropping 1:3	31.7 b	18.3 bc
Intercropping 1:5	28.9 b	10.0 ab

Means within columns followed by the same letter do not differ significantly at P = 0.05 (LSD). All intercropping ratios indicate cabbage/ carrots.

prominence values on all treatments in both seasons were always lower in intercropped than monoculture plots. No trend was observed for *P. xylostella* prominence in relation to increased intercropping ratios (Figure 3) during the 2002/03 planting season. *P. xylostella* prominence during the 2003/04 planting season (Figure

4) had a generally similar temporal pattern, when comparing the monoculture and 1:1 intercropping treatments. The tendencies over time were not similar for monoculture compared to higher intercropping ratio treatments.

P. xylostella infestation levels and parasitism levels were significantly lower for control treatments during both seasons (Tables 1 and 2). Parasitism was significantly correlated with infestation levels during the 2002/03 (r = 0.98) and 2003/04 (r = 0.98) growing seasons (Figures 5 & 6).

Table 3 Parasitoids (Hymenoptera) reared from *Plutella xylostella* larvae.

Family	Species	Туре
Pteromalidae	Pteromalus sp.	Primary parasitoid
Eulophidae	Oomyzus sokolowskii (Kurdjumov)	Primary parasitoid
Braconidae	Cotesia plutellae (Kurdjumov)	Primary parasitoid
	Diaeretiella sp.	Primary parasitoid
	? Apanteles halfordi	Primary parasitoid
Ichneumonidae	Unknown genus and species	Primary parasitoid
Cynipidae	Alloxysta sp.	Hyper parasitoid
		through Braconidae

Feeding damage on cabbage plants expressed in terms of RIA values showed that the control treatment had the lowest level of feeding damage while the severity of damage in other treatments were similar during both seasons (Figures 7 & 8). Cabbage transplanted during November 2002 also suffered more feeding damage, as indicated by the lower RIA averages for all treatments (lower RIA values indicate higher damage) (Figure 7), than cabbage transplanted during February 2004 (Figure 8). Lower *P. xylostella* infestation levels and lower feeding damage indices on control treatments can be attributed to the impact of regular spraying of insecticides.

Six hymenopteran parasitoid species belonging to four families were reared from parasitized *P. xylostella* larvae (Table 3). *C. plutellae* was the most abundant parasitoid and was responsible for 84 % and 96 % of parasitism during the 2002/03 and 2003/04 planting seasons respectively. Few individuals of other parasitoid

species were recorded. The sex ratio of *C. plutellae* adults was 1:1.4 (male: female) during the 2002/03 planting season and 1: 0.85 during the 2003/04 planting season.

The lack of a gradual decrease in prominence value in relation to decreased host plant concentrations in the intercropping treatments suggested that the ability of P. xylostella to infest host plants was not greatly influenced by this intercropping system. P. xylostella prominence values in intercropping treatments did however decline sharply towards the last sampling date during both seasons. This decrease in prominence was more pronounced during the 2002/03 season when all intercropping treatments had a prominence value of zero at the final sampling date (during the onset of cabbage head formation). According to Dennill & Pretorius (1995), cabbage plants are most attractive for oviposition during the growing period prior to head initiation, which might offer a partial explanation for the observations made during this study. The likelihood that cabbage plant growth and/or physiology in intercropping plots might have been affected during head initiation because of competition with carrots should also not be ruled out. If evidence can be found that interplant competition impacted on the onset of the head initiation growth stage of cabbage plants in intercropping treatments, it may explain the fact that monocultures were not affected similarly than intercropping treatments in terms of infestation patterns. The erratic prominence value patterns observed during both seasons might also indicate that infestation patterns could have been influenced by green leaf volatile (GLV) releases triggered by plant damage that may alter oviposition patterns of P. xylostella (Reddy, Tabone & Smith, 2004).

In terms of visual detection by *P. xylostella* moths, under-sown cabbage seedlings in the substitutive intercropping plantings used in this study would still have contrasted with bare soil, in spite of efforts to maximise main crop (carrot) foliage density and volume. Results obtained by Finch & Kienegger (1997) for eight insect species on cruciferous plants presented in a background of green clover, indicated reduced oviposition for all species. Their observations indicated that visual stimuli to a greater or lesser extent played an important part in host plant location with all species tested. Results obtained by Finch & Kienegger (1997) were more dependent on the spatial arrangement of crop plants than on the ratio of host and non-host plants. The fact that intercropping was done according to a substitutive pattern (described by Bukovinszky,

Tréfás, Van Lenteren, Vet & Fremont, 2004) may explain the lack of clear *P. xylostella* infestation patterns on plants in different cabbage and carrot-planting ratios (Figures 3 and 4).

C. plutellae was the most abundant parasitoid species on all treatments. The importance of chemical cues for host acquisition by C. plutellae was illustrated by Potting, Poppy & Schuler (1999). According to Potting et al. (1999) plant derived olfactory stimuli are the main source of attraction towards infested plants, with previous exposure to herbivore-damaged plants playing a major role in response enhancement. C. plutellae attraction to plant volatiles is based on quantity rather than quality, with no distinction being made between plants damaged by larvae or any other agent. Potting et al. (1999) also noted that neither visual stimuli nor larvae or their by-products had any impact on long distance detection of infested plants by C. plutellae. The significant correlation between parasitism and larval infestation levels (Figures 5 and 6), along with the fact that parasitoid attraction is based on plant kairomones, suggest that feeding damage to plants and associated volatiles were most likely the dominant factor governing parasitoid attraction.

The relative densities of cabbage plants in the different treatments may have influenced parasitoid attraction since *C. plutellae* females were also attracted to uninfested (undamaged) leaves. *C. plutellae* females can however distinguish between undamaged and damaged leaves while in flight (Potting *et al.*, 1999) in which case damaged leaves would be preferred. This mechanism of host location is confirmed by behavioural adaptations of host larvae. *P. xylostella* larvae have short duration feeding periods on particular leaf loci and will also feed on several widely spaced loci on a specific leaf to reduce time spent close to freshly damaged leaf tissue (Wang & Keller, 2002).

The dominance of *C. plutellae* agrees with observations made by Kfir (2001) and Mosiane *et al.* (2003). The success of this species relative to others in South Africa is attributed to its ability to remain active during winter months when most other parasitoids are inactive (Mosiane *et al.*, 2003). Records on *C. plutellae* parasitism of a few other Lepidoptera species do exist (Potting *et al.*, 1999; Fitton & Walker, 1992, cited by Wang & Keller, 2002) in spite of *C. plutellae* still being regarded as a host

specific parasitoid (Verkerk & Wright, 1996). These observations which possibly indicate oligophagous habits would suggest that *C. plutellae* is less efficient than monophagous parasitoids in terms of host location. This was shown to be true by direct behavioral comparisons that were made between *C. plutellae*, and the more specialized *Diadegma clausum* by Wang & Keller (2002). It does however help to explain the greater success of *C. plutellae* in a broader ecological sense and its apparent ability to maintain viable populations in the absence of *P. xylostella* infestations.

The observed shift in *C. plutellae* sex ratios from female dominated during the 2002/03 season (spring transplanting) to male dominated during the 2003/04 planting season (late summer transplanting) might indicate reduced host fitness due to less favourable environmental conditions late in the growing season. According to Waage & Hassell (1982) hymenopteran parasitoid success is also linked to their sex ratio, because it is only females that are responsible for parasitising hosts. A parasitoid evolutionary model cited by Waage & Hassell (1982) predicts that in any situation, wasps should allocate female offspring to the relatively larger individuals of available hosts.

2.4 Conclusions

Different planting ratios of cabbage and carrot plants did not impact significantly on population density and frequency of occurrence of *P. xylostella* larvae. Results indicated that attraction of parasitoids to *P. xylostella* larvae was probably dominated by factors such as distribution of damaged plants and the extent of damage rather than planting ratios of crops. The dominance of *C. plutellae* in relation to parasitism by other parasitoid species is in agreement with results obtained with other studies for cruciferous monocultures. This suggested that factors related to *C. plutellae* ecology, rather than the impact of different intercropping treatments largely determined its success as the main parasitoid species.

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2.6 Figures

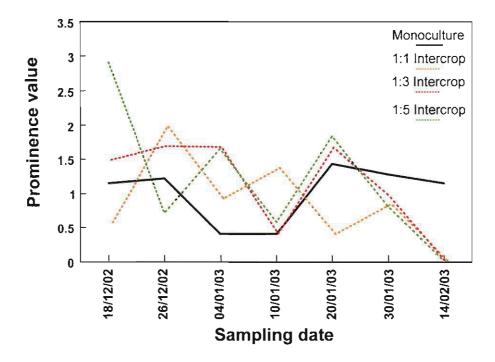


Figure 3. *Plutella xylostella* prominence on the 1:1, 1:3 and 1:5 intercropping treatments, as compared to the monoculture treatment during the 2002/03 planting season.

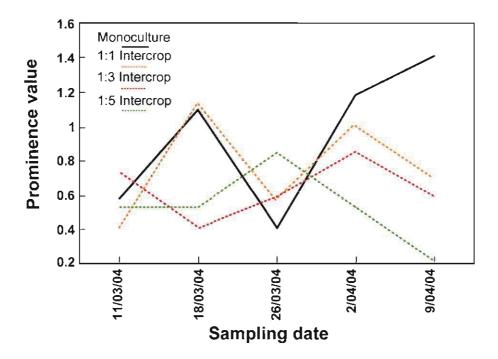


Figure 4. *Plutella xylostella* prominence on the 1:1, 1:3 and 1:5 intercropping treatments, as compared to the monoculture treatment during the 2003/04 planting season.

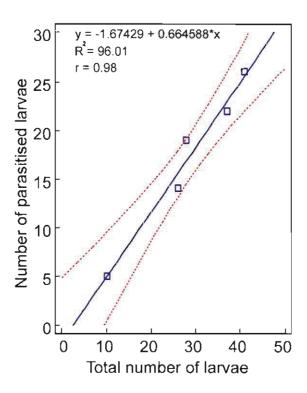


Figure 5. The relationship between *Plutella xylostella* infestation levels and parasitism on all five treatments during the 2002/03 planting season (dotted lines indicate 95% confidence intervals).

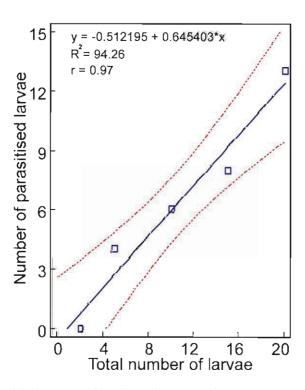


Figure 6. The relationship between *Plutella xylostella* infestation levels and parasitism on all five treatments during the 2003/04 planting season (dotted lines indicate 95% confidence intervals).

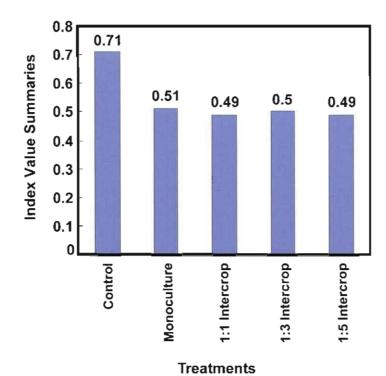


Figure 7. Reciprocal Index of Attack (RIA) values indicating the severity of *Plutella xylostella* damaged leaves during the 2002/03 planting season (highest index value indicates lowest leaf feeding damage).

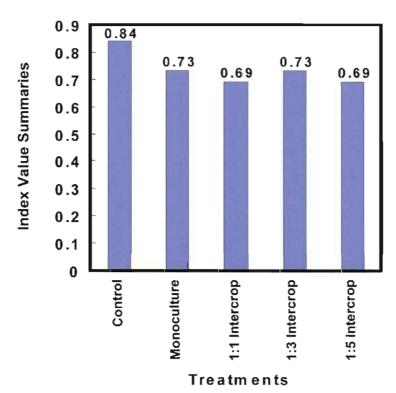


Figure 8. Reciprocal Index of Attack (RIA) values indicating the severity of *Plutella xylostella* damaged to cabbage leaves during the 2003/04 planting season (highest index value indicates lowest leaf feeding damage).

CHAPTER 3

Impact of different cabbage/ carrot intercropping ratios on infestations of cabbage by aphids (Homoptera: Aphididae)

3.1 Introduction

Cabbage plants grown in South Africa are attacked by the cabbage aphid, *Brevicoryne brassicae*(L.), turnip aphid *Lipaphis erysimi* (Kaltenbach) and green peach aphid *Myzus persicae* (Sulzer) (Homoptera: Aphididae). *Brevicoryne brassicae* populations dominates during winter months while *L. erysimi* is the dominant species during summer (Annecke & Moran, 1982). According to Annecke & Moran (1982) *M. persicae* is capable of infesting cabbage plants throughout the year but is unable to achieve the high populations of the other two species. Aphid feeding causes distortion and bleaching of leaves and prevents the development of marketable cabbage heads on plants where large populations have developed (Ellis, Pink, Phelps, Jukes, Breeds & Pinnegar, 1998). The importance of aphids is largely due to their habit of selecting sheltered feeding sites, high mobility and ability to reproduce rapidly through parthenogenesis (Coll & Hopper, 2001).

The high pest status of *B. brassicae* and *L. erysimi* on cruciferous crops can also be ascribed to the inability of parasitoids to control their populations effectively (Annecke & Moran, 1982; Coll & Hopper, 2001). According to Annecke & Moran (1982) parasitoid inefficiency is directly linked to high levels of hyper-parasitism, with two to seven hyper-parasitoids emerging for every primary parasitoid during summer months.

The suppression of cruciferous crop pests through intercropping is practiced widely even though the underlying mechanisms are not yet fully understood (Vidal, 1997). Intercropping has been employed successfully on a number of occasions to reduce populations of *B. brassicae* and *L. erysimi*. Intercropping systems including cruciferous crops along with crops as diverse as fennel (Foeniculum vulgare Mill.) (Singh & Kothari, 1997), ryegrass (Lolium perenne L.) (Vidal, 1997) and

subterranean clover (*Trifolium subterraneum* L.) (Finch & Kienegger, 1997) successfully reduced aphid populations.

The aim of this study was to determine the impact of a substitutive intercropping system, containing different cabbage and carrot intercropping ratios, on aphid infestation levels and parasitism.

3.2 Material and methods

Aphid sampling was done from the same six leaves that diamondback moth larvae were collected from (see chapter 2 for complete description of material and methods). All aphids were removed from these leaves and killed to prevent population increase after leaf removal. Dead aphids were stored in propylene glycol contained in glass bottles until counting could commence. The number of individuals collected from each leaf was determined. Parasitism levels were determined by counting parasitized aphids (mummies) on leaves after removal of all living aphids. The total number of aphids collected from all treatments per season was then divided by the number of sampling dates in that particular season to determine the seasonal average for aphids counted per sampling. This was done to provide a means of comparison of infestation levels between seasons, because transplanting of cabbage seedlings during the second season was delayed compared to transplanting during the first season.

Prominence values (PV) (De Waele & Jordaan, 1988) were calculated for aphids collected on each treatment and were calculated according to the equation:

$$PV = population density \sqrt{frequency of occurrence} / 10$$

where population density represents the mean number of aphids per leaf and frequency of occurrence represents the mean number of infested cabbage leaves per treatment calculated for each sampling date.

Aphid counts were log(x + 1) transformed before being subjected to one-way analyses of variance at P=0.05 confidence limit (Least Significant Difference). Parasitism was

expressed as a percentage of the total number of aphids collected per week. The Statgraphics + (5.1) for Windows (2003) package was used to perform data analyses.

3.3 Results and discussion

Aphid infestation levels were higher during the second (2003/04) planting season when the transplanting of cabbage seedlings was done later during the season. The average number of aphids removed from leaves (average per sampling date over all treatments) during the first 45 days after transplanting was 75 % higher during the 2003/04 planting season. The average frequency of occurrence of aphid infested cabbage plants over this 45 day period was three out of six for the 2002/03 season and five out of six for the 2003/04 season. These results support the notion that the greater number of leaves that were colonised during the second season might have been in direct relation to greater numbers of winged females, as was observed by The impact of intercropping treatments on aphid populations differed Vidal, 1997. between seasons. Data gathered during the two seasons will subsequently be presented separately (Table 1 and Figures 1 & 2). The monoculture and control (mercaptothion sprayed) treatments had the highest and lowest infestation levels respectively during the 2002/03 season and also differed significantly from the 1:1, 1:3 and 1:5 intercropping treatments, which did not differ significantly from each other (Table 1). An opposite pattern was observed during the 2003/04 planting season when the 1:3 and 1:5 intercropping treatments had significantly higher infestation levels than the control and 1:1 intercropping treatments.

Prominence values during the 2002/03 planting season for the monoculture treatment were high on the first sampling date (Figure 1). Prominence values on monoculture plots declined rapidly during the following two weeks followed by an increase towards the head initiation growth stage after which the sampling period ended. Prominence values of all intercropping treatments during 2002/03 were low at the beginning of the sampling period and increased moderately towards the end of the sampling period (Figure 1). Prominence values for intercropping treatments did however, with a few exceptions, remain below those of monoculture treatments for the duration of the sampling period.

During the 2003/04 planting season prominence values for 1:1 and 1:5 intercropping treatments were all lower than those for the monoculture treatment during the first two sampling dates (Figure 2). Aphid prominence was higher on the first sampling date and similar on the second sampling date for the 1:3 intercropping treatment. Aphid prominence in all intercropping treatments however never declined to below aphid prominence in the monoculture treatment after the second sampling date (Figure 2).

Parasitism levels were low during both seasons and could not have played a significant role in reducing aphid numbers. Aphid parasitism was highest on the 1:5 intercropping treatment during both seasons but was significantly higher only during the 2002/03 season (Table 2).

Table 1 Mean number of aphids per cabbage leaf at different cabbage-carrot intercropping ratios during the 2002/03 and 2003/04 planting seasons.

Treatment	Mean number of aphids per leaf	
	2002/03 season	2003/04 season
Control	2.1 a	0.6 a
Monoculture	22.1 c	11.0 bc
Intercropping 1:1	9.3 abc	7.8 в
Intercropping 1:3	8.4 ab	31.5 c
Intercropping 1:5	9.8 ab	104.7 c

Means within columns followed by the same letter do not differ significantly at P = 0.05 (LSD). Data were log (x + 1) transformed. All intercropping ratios indicate cabbage/ carrots.

Aphids have a tendency not to move on after alighting on suitable host plants. It was suggested by Finch & Edmonds (1996) (cited by Finch & Kienegger, 1997) that differential colonisation during the initial colonisation process was the main driving force behind infestation differences observed between different intercropping treatments. Vidal (1997), after investigating *B. brassicae* population dynamics in under-sown Brussels sprouts also observed that higher infestation levels on control

plots (compared with under-sown plots) were the result of higher colonisation by winged females.

Table 2 Mean percentage parasitized aphids per cabbage leaf in different cabbage-carrot intercropping ratios during the 2002/03 and 2003/04 planting seasons.

Treatment	Mean % parasitism of aphids per leaf	
	2002/03 season	2003/04 season
Control	0.0 a	0.0 a
Monoculture	0.1 a	3.3 a
ntercropping 1:1	0.0 a	3.6 a
ntercropping 1:3	0.0 a	0.0 a
Intercropping 1:5	4.4 b	4.4 a

Means within columns followed by the same letter do not differ significantly at P = 0.05 (LSD). All intercropping ratios indicate cabbage/ carrots.

Aphid populations were higher during the 2003/04 than the 2002/03 planting season when cabbage seedlings were transplanted earlier during the season. This observation agrees with Annecke & Moran (1982) who noted that all aphids are comparatively scarce during spring before their numbers begin to increase as a result of seasonal effects.

Prominence values were on average lower on intercropped plots than on monoculture plots during the first season (Figure 1) indicating that, at least at lower population levels, the presence of non-host crops may have had a disruptive influence on aphid colonisation.

Since aphids form part of a complex of cabbage pests, the evaluation of the success of intercropping systems should also consider other pests, especially diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae). It is important to note that where aphid numbers are low during spring (Annecke & Moran, 1982), *P. xylostella* infestations are usually at their highest (Smith & Villet, 2001). According to Smith &

Villet (2001), *P. xylostella* infestations decrease during November and December and remain relatively low, with exception of some smaller peaks from March to May, until the onset of the following spring. It is also important to note that, in contrast to aphids, *P. xylostella* infestations are largely affected by parasitism (Kfir, 2001). The typical seasonal infestation pattern of *P. xylostella*, reported by Smith & Villet (2002), is largely determined by parasitism levels.

From the above contrast between aphid and *P. xylostella* population dynamics the potentially important role that chemical aphid control may have in disrupting *P. xylostella* parasitism becomes apparent. The possibility exists that what has been deemed misuse of chemicals by Kfir (2003), while describing the reasons for increased *P. xylostella* pest status, might have its roots in the necessity for chemical aphid control. This might have been largely overlooked because of the heavy focus being placed on *P. xylostella*. The likelihood of excessive insecticide applications is increased by the inefficiency of aphid parasitoids because of high levels of hyperparasitism, especially during summer months (Annecke & Moran, 1982). The observed reduction of aphid infestations in intercropped plots, even though it may only be for a short period of time or only at the beginning of the season, can play a significant role within the larger picture of cabbage IPM, and may yet prove invaluable by reducing the need for insecticide applications.

3.4 Conclusions

The effect of different intercropping ratios on cabbage aphid infestations differed over seasons and seems to be influenced by aphid population pressure. Early infestation of cabbage plants by aphids necessitates chemical control under normal farming conditions. These chemical applications and their effect on parasitoids in general could be the primary reason for outbreaks of *P. xylostella*. This needs further investigation.

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3.6 Figures

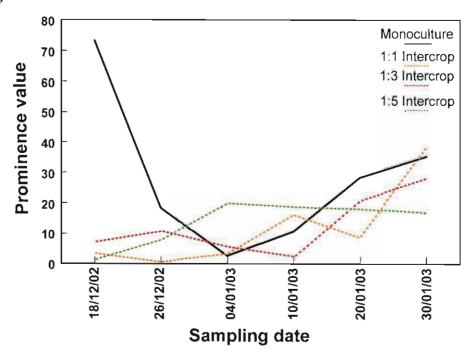


Figure 1. Aphid prominence on the 1:1, 1:3 and 1:5 intercropping treatments, as compared to the monoculture treatment during the 2002/03 planting season.

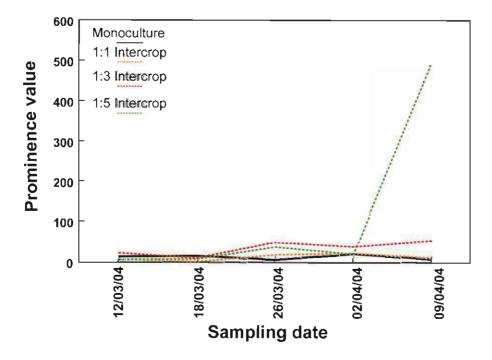


Figure 2. Aphid prominence on the 1:1, 1:3 and 1:5 intercropping treatments, as compared to the monoculture treatment during the 2003/04 planting season.

CHAPTER 4

Conclusions

4.1 Conclusions made from study

The unique character of the cruciferous crop pest complex, which includes a combination of 'generalist' and 'specialist' pest species (Hooks & Johnson, 2003), present a unique challenge to IPM practitioners. The most serious threat to production comes from pests classified as oligophagous 'specialists' that, even though loosely classified together do not attack cabbage plants in the same way or react to control strategies in a similar way. *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) and the cabbage aphids, *Brevicoryne brassicae* (L.) and *Lipaphis erysimi* (Kaltenbach) (Homoptera: Aphididae) are the most important species in the cabbage pest complex and can be considered to be 'specialist' species. For this reason intercropping could play a role in the management of pest populations.

The main factors contributing to the pest status of *P. xylostella* are destruction of natural enemies (Kfir, 2001) and developing of insecticide resistance. A peculiar feature of this pest is that its global pest status only increased after the introduction of widespread use of synthetic insecticides, which affected natural enemies and induced resistance (Talekar & Shelton, 1993).

The absence of parasitoids of *P. xylostella* because of the necessity to control aphids is probably responsible for the increased pest status of *P. xylostella* in recent years. The abovementioned situation calls for a more holistic approach towards cruciferous crop pest management. The inclusion of cabbage as an under-sown crop in an intercropping system where carrots were planted as main crop was subsequently used to determine the impact of and possible use of such a system on infestation patterns of the most important 'specialist' cabbage insect pests.

Research conducted over two growing seasons showed that aphid infestation levels were higher later in the season, which is similar to the situation normally encountered under monoculture production conditions. This can largely be ascribed to high aphid

reproduction rates and low parasitism levels. These results also indicate that the most effective outcome for cabbage pest control that could possibly be hoped for through intercropping would be suppression of aphid populations, which otherwise might necessitate the application of an increased number of insecticide applications. A reduction in aphid infestation levels were observed on intercropping treatments under lower aphid population pressure during the first season, which was encouraging and warrants further investigation.

Intercropping ratios did not have an impact on *P. xylostella* infestation patterns or parasitism levels. The parasitoid complex was dominated by *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae) and their occurrence was also not altered by different intercropping ratios. Positive results obtained with intercropping systems by other authors were probably due to spatial arrangements of plants rather than to relative sowing ratios of individual crops. Planting of crops in a sufficiently close configuration to induce visual disruption through 'hiding' of host plants will undoubtedly result in severe interplant competition. Planting of substitutive intercropping systems is more appropriate in terms of their possible practical application. The impact of such systems on inter-plant competition as well as their efficiency in terms of agronomy will however have to be further investigated.

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