Natural enemy ecology in apple orchards: spider colonization of orchards and effects of kaolin on the apple pest *Choristoneura rosaceana* and its natural enemies

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Abstract

Integrated pest management (IPM) uses multiple approaches to keep pest levels below economic injury levels. Integrated pest management combines preventative methods such as biocontrol with curative methods; this synthesis requires an understanding of the ecology of natural enemies in the agroecosystem.

Arthropod natural enemy communities in apple orchards are diverse, and spiders (Araneae) are particularly abundant and species rich. Orchard arthropods are affected by multiple factors, both external (e.g. immigration) and internal (e.g. pesticides) to the orchard environment. In this thesis I explored the influence of these factors on natural enemy communities in apple orchards. I investigated which natural habitats adjacent to orchards are potential sources of spiders, and the influence of distance from a source habitat on the composition of colonizing spider assemblages. I tested how kaolin clay, a pest management technique, affects orchard generalist predator communities and the parasitoids of a pest species and prey item of spiders, *Choristoneura rosaceana* (Harris) (Lepidoptera: Tortricidae). I also examined how applications of kaolin to apple foliage affect the behaviour of *C. rosaceana* larvae and whether this alters the predation on larvae by spiders.

Comparisons of spider assemblages in natural habitats adjacent to apple orchards in southern Québec indicated that deciduous forest had spider assemblages similar in to those in the orchard foliage. The composition of the spiders that colonized the apple orchards changed over a small spatial scale (10-50 m). The relative abundance of individuals among spider species in older orchards was more evenly distributed than in assemblages of recently colonized spiders, suggesting that local dynamics also shape the composition of the spider assemblages over time.

Kaolin on apple leaves changed *C. rosaceana* larval behaviour: third and fourth instar larvae and neonates took longer to build leaf shelters, and neonate larvae moved off kaolin-covered foliage more frequently than off unsprayed

i

foliage. However, kaolin did not affect the predatory ability of a common family of spiders found in the orchards, jumping spiders (Salticidae). In orchards kaolin reduced the densities of wandering generalist predators such as ants, assassin bugs, and hunting spiders. Kaolin did not affect the overall parasitism of *C. rosaceana* larvae.

Résumé

La lutte intégrée combine plusieurs méthodes de lutte pour maintenir les populations de ravageurs sous des seuils d'intervention. Ces méthodes incluent des mesures préventives, comme l'augmention des agents de lutte biologique, et des mesures curatives. Cette synthèse nécessite des connaissances sur l'écologie des vergers et ses espèces.

Les communautés d'espèces utiles dans les vergers sont diverses, et les assemblages d'araignées (Araneae) sont notamment abondants et riches en espèces. Plusieurs facteurs affectent les organismes dans les vergers, incluant les facteurs externes (ex. immigration) et internes (ex. l'application d'insecticides). Dans cette thèse, j'ai étudié l'influence de ces facteurs sur les communautés d'araignées et d'autres espèces utiles. J'ai déterminé quels habitats adjacents au verger ont le potentiel d'être des sources d'araignées, et comment la distance de la source change les dynamiques de colonisation des vergers par les araignées. J'ai déterminé les effets du kaolin (un pesticide à base d'argile) sur les assemblages de prédateurs arthropodes et parasites du ravageur *Choristoneura rosaceana* (Harris) (Lepidoptera: Tortricidae) dans les vergers.

Les forêts adjacentes au verger ont des assemblages d'araignées similaires à ceux des vergers, vraisemblablement parce que leur structure végétale et leur niveau de dérangement temporel sont semblables. La composition des assemblages d'araignées change à petite échelle spatiale (10-50 m). La répartition des individus parmi les espèces des assemblages d'araignées dans les vergers établis était plus homogène que celle des vergers récemment colonisés. Ceci suggère que les dynamiques locales façonnent aussi la composition des assemblages d'araignées.

Le kaolin a changé le comportement des larves de *C. rosaceana*: les larves ont requis plus de temps pour se faire un abri sur les tiges traitées avec le kaolin. Les larves néonates se sont dispersées plus fréquemment que les larves sur les tiges témoin. Malgré ce dérangement du comportement de *C. rosaceana* par le

iii

kaolin, la prédation sur les larves par les araignées sauteuses (Salticidae) n'a pas été affectée. En verger, des applications de kaolin ont réduit les densités des prédateurs, notamment les prédateurs chasseurs comme les fourmis, les araignées cursoriales, et les hémiptères. Le kaolin n'a pas affecté le taux de parasitisme des larves de *C. rosaceana*.

	page
Abstract	i
Résumé	iii
Table of Contents	v
List of Tables	viii
List of Figures	ix
Thesis Format and Contributions of Co-authors	xi
Contributions to Knowledge	xii
Acknowledgements	xiv
Chapter 1: Introduction, literature review, and objectives	1
1.1. Introduction	1
1.2. Literature Review	3
1.2.1. Orchard IPM	3
1.2.2. Spiders in biocontrol	4
1.2.3. Habitat manipulations	6
1.2.4. Spider dispersal and colonization	9
1.2.5. Effects of pest management on spiders	10
1.2.6. Kaolin	11
1.2.7. Choristoneura rosaceana	13
1.3. Research Approach, Objectives and Hypotheses	14
Chapter 2: Comparisons of the composition of foliage dwelling spider	
assemblages in apple orchards and adjacent natural habitats	17
2.1. Abstract	17
2.2. Introduction	17
2.3. Materials and Methods	19
2.3.1. Study sites	19
2.3.2. Adjacent habitats	20
2.3.3. Spider sampling.	20
2.3.4. Data analyses	22
2.4. Results.	
2.5. Discussion	
2.6 Connecting Statement	30
Chapter 3: Spider colonization of apple orchards: distance from the source a	affects
abundance and species composition	31
3.1 Abstract	31
3.2 Introduction	31
3.3 Materials and Methods	33
3 3 1 Micro-orchards	33
3 3 2 Experimental design	34
3 3 3 Snider sampling	34
3 3 4 Data analyses	35
3 4 Results	30
3.5 Discussion	<i>59</i> 44
3.6. Connecting Statement	۲ ۰۰۰۰ ، ۱۶
5.0. Connecting Statement	40

Table of Contents

Chapter 4: Relevance of collected juveniles to the analysis of spider commun	ity
studies	49
4.1. Abstract.	49
4.2. Short Communication	49
4.3. Connecting Statement	57
Chapter 5: Effect of kaolin on the fitness and behaviour of <i>Choristoneura</i>	
rosaceana (obliquebanded leafroller) (Lepidoptera: Tortricidae) larvae	58
5.1. Abstract	58
5.2. Introduction	58
5.3. Materials and Methods	60
5.3.1. Laboratory rearing of C. rosaceana	60
5.3.2. Experiment 1: Kaolin in artificial diet	61
5.3.3. Experiment 2: Kaolin applied to apple leaves	61
5.3.4. Experiment 3: Kaolin and neonate dispersal	61
5.3.5. Experiment 4: Kaolin and rolling behaviour of larvae	62
5.3.6. Statistical Analyses	63
5.4. Results and Discussion	64
5.4.1. Kaolin feeding experiments	64
5.4.2. Effects of kaolin on larval behaviour	66
5.5 Connecting Statement	00 71
Chapter 6. Predation of salticid spiders on neonate <i>Charistoneura rosaceana</i>	/ 1
(I epidontera: Tortricidae) and a test for indirect effects of a kaolin particle sn	rav
(Lepidopiera. Tortreidae) and a test for indirect effects of a kaonin particle sp	72
6.1 Abstract	72 72
6.2 Short Communication	72 72
6.3 Connecting Statement	72 70
Chapter 7: Effects of kaolin on the composition of generalist predator	/)
assemblages and parasitism of <i>Charistoneura rosacana</i> (Lepidoptera: Tortri	aidaa)
in apple orchards	
7 1 Abstract	80 80
7.2 Introduction	00
7.2. Matarials and Matheda	01
7.2.1. Outputs and Methods	83
7.3.1. Orchards and kaolin treatments	83
7.3.2. Effect of kaolin on generalist predators	84
7.3.3. Effects of kaolin on C. <i>rosaceana</i> parasitism	85
7.3.4. Statistical analyses	85
7.4. Results	87
7.4.1. Effect of kaolin on generalist predators	87
7.4.2. <i>Choristoneura rosaceana</i> parasitism and density	92
7.5. Discussion	94
Chapter 8: Research summary, synthesis, and future work	97
8.1. Introduction	97
8.2. Research Summary	97
8.2.1. Spider assemblages in orchards and adjacent habitats	97
	> /
8.2.2. Spider colonization of apple orchards	98
8.2.2. Spider colonization of apple orchards8.2.3. Relevance of juvenile spiders to community studies	98 99

8.2.4. Kaolin and orchard arthropods	100
8.2.5. Effects of kaolin on <i>C. rosaceana</i> larval behaviour	101
8.2.6. Predation on C. rosaceana by salticid spiders and interactio	ns with
kaolin	102
8.2.7. Effects of kaolin on generalist predator assemblages in orcha	ards and on
parasitism of C. rosaceana larvae	103
8.3. Synthesis and Suggested Future Directions	103
References	
Appendix I. Data from Chapter 2	121
Appendix II. Data from Chapter 3	124

List of Tables

page
 Table 2-1: Site characteristics: distance of orchards from forest and landscape composition, in southern Québec, Canada
Table 3-1: Mean number of spiders (± SE) (n=6) and results from analyses of variance between micro-orchard locations (10 and 50 m from the forest) in southern Québec, Canada, for the ten most commonly collected spider species and genera. 40
Table 3-2: Significance and effect size (agreement statistic, A) of multi-response permutation procedure (MRPP) comparisons of spider assemblages sampled from micro-orchards (10 and 50 m from forest), and adjacent deciduous forest in southern Québec, Canada
Table 5-1. Number of third and fourth <i>C. rosaceana</i> larvae with (rolled) or without (nonrolled) shelters (control $n=27$ kaolin $n=28$) 69
 Table 7-1: Relative abundances (mean ± SE) (n=6) and total number of generalist predators collected immediately after (July) and 1 month after (August) the final kaolin application in orchards F1 (2004) and F2 (2005) in southern Québec, Canada
Table 7-3: Effect size (agreement statistic, A) from multi-response permutation procedure (MRPP) comparisons of generalist predator assemblages sampled from Frelighsburg (Québec, Can.) orchards from control and kaolin plots in July and August of 2004 and 2005
Table AI-1: Counts of spiders, and life-stage when collected, of spiders from sites (A, B, C, and D) and habitats (orchard (orc.), forest (for.), field (fie.), and ecotone (eco.)) in 2004 in apple agroecosystems in Québec. Sample dates were pooled
Table AII-1: Counts of spiders collected from habitats (micro-orchards 10 and 50 m from forest, forest, and field) in apple agroecosystems in Québec in 2006.Sample dates were pooled.124

List of Figures

page
Figure 2-1: Individual-based rarefaction curves depicting estimated spider species
richness (SR) (\pm 95% confidence intervals) for orchards and their adjacent
habitats in southern Québec. Arrow indicates number of individuals at
which species richness of forest and orchard were compared
Figure 2-2. Sample unit (site habitat and sampling event) non-metric
multidimensional scaling (NMDS) of spider collections from southern
Outhon Logand describes sample site (A to D) and habitat (arehard (are)
Quebec. Legend describes sample site (A to D) and habitat (orchard (orc)) $A = A = A = A = A = A = A = A = A = A $
or forest (for)). Numbers following symbols indicate sampling event (1-5).
Figure 2-3: Relative abundance (\log_{10}) of spider species in four habitats in
southern Québec. Species are ordered along the x-axis from most to least
common in orchards, thereafter ordered in decreasing abundance for forest,
low vegetation (ecotone), and field habitats
Figure 3-1: Spiders collected per m ³ of foliage in micro-orchards 10 m or 50 m
from deciduous forest (sum for $n=6$ at each distance) over 15 weeks from
June 6 until September 15 2006 in southern Ouébec Canada 39
Figure 3-2: Individual-based rarefaction curves depicting estimated spider species
richness (SR) (\pm 95% confidence intervals) for the forest and the micro-
archards 10 and 50 m from deciduous forest in Southern Ouébec. Arrow
indicates number of individuals at which spacies richness comparisons were
mulcales number of mulviduals at which species fieldess comparisons were
$\mathbf{H}_{\mathbf{H}} = \mathbf{H}_{\mathbf{H}} = $
Figure 3-3: Sample unit (by location) non-metric multidimensional scaling
(NMDS) of spider collections from deciduous forest and micro-orchards 10
m and 50 m from deciduous forest in southern Quebec. Numbers following
symbols refer to site number
Figure 3-4: Relative abundance (% of collection) in micro-orchards and older
orchards (2004 collection) of the ten most common spider species from
micro-orchard collections in southern Québec
Figure 3-5: Rank abundance (Whittaker) plot of spider species (excluding
singletons) from micro-orchards 10 and 50 m from deciduous forest, and
collections from established orchards in 2004, in southern Ouébec,
Figure 4-1: Individual-based rarefaction curves depicting estimated spider species
richness (SR) (+ 95% confidence intervals) for orchard and forest habitats in
southern Québec using complete and mature-only ("mat only") datasets
Arrows indicated species richness at which orchard and forest were
approved for complete detect (A) and meture only detect (D) 52
Eigure 4.2: Don't obundance (Whittelter) nlet of relative obundance of spider
Figure 4-2: Rank-abundance (winttaker) plot of relative abundance of spider
species (\log_{10} abundance, expressed as percent of total) in orchard and
deciduous forest in Southern Quebec, and from complete and mature only
("mat.only") datasets
Figure 4-3: Sample unit (orchard or forest for each site, collection dates pooled)
non-metric multidimensional scaling (NMDS) analysis of southern Québec
spider collections from complete and mature-only ("mat.only") datasets.

Labels following symbols indicate habitat (orchard: "orc", forest: "for") and
site (A to D) of sample
Figure 5-1. Mortality (A), pupal mass (B), and time to pupation (C) of C.
rosaceana larvae reared on apple leaves sprayed with kaolin. For B and C,
bars represent mean values \pm SE. Means were compared within sexes and
bars beneath different letters are significantly different at p=0.05 (n=60) 66
Figure 5-2. Neonates hanging from the branches (A) and total number of neonates
on branches (including larvae hanging from the branches) (B). Means \pm SE
are presented, and within each time period bars with different letters are
significantly different at p=0.05 (n=20)
Figure 6-1: Number (A) and proportion (B) of <i>C. rosaceana</i> neonates eaten by
salticid spiders at different densities of neonates (n=5 for each density) 75
Figure 6-2: Mean number of remaining <i>C. rosaceana</i> larvae on apple seedlings
sprayed with kaolin (K) or with water (C), and with the addition of a salticid
spider (+S). Different lower case letters above the bars indicate
significantly different means (Tukey test) (p<0.05) (n=11 for each
treatment)77
Figure 7-1: Relative abundance of all spiders collected from orchard F1 in 2004 in
control and kaolin plots (n=6) after each of four kaolin applications, and one
month after the fourth application. Different letters above bars within one
sampling event indicate significantly different means ($p < 0.05$)
Figure 7-2: Sample unit (treatment block and date) non-metric multidimensional
scaling (NMDS) of the final two spider collections from orchard F1 in
Frelighsburg (Québec, Canada) in 2004. Symbols represent spider samples
from control (C) and kaolin (K) blocks (n=6) in July and August
Figure 7-3: Sample unit (treatment block and date) non-metric multidimensional
scaling (NMDS) of arthropod (spider and insect) collections from orchard
F2 in Frelighsburg (Québec, Canada) in 2005. Symbols represent arthropod
samples from control (C) and kaolin (K) blocks (n=6) in July and August. 93

Thesis Format and Contributions of Co-authors

This thesis is written as a collection of publishable manuscripts, with the exception of the introduction (chapter 1) and conclusion (chapter 8) which introduce the topics and hypotheses, review the relevant published literature, summarize the thesis, and provide recommendations for future research. Chapters 5 and 7 have been already published or accepted for publication in peer-reviewed journals as original research articles. The remaining chapters also will be submitted to peer-reviewed journals: chapters 2 and 3 as original research papers, and chapters 4 and 6 as short communications. The acknowledgements from each manuscript have been combined into one section, appearing at the beginning of the thesis, and the references from each manuscript have been combined into a single bibliography.

My co-supervisors, Dr. Chris Buddle (NRS, McGill University) and Dr. Charles Vincent (Agriculture et Agroalimentaire Canada, Saint-Jean-sur-Richelieu and adjunct professor, NRS, McGill University) are co-authors on all of the manuscripts (both published and those to be submitted). Dr. Buddle and Dr. Vincent participated in the conceptualization and design of the experiments, the choice of analytical techniques, and the editing of the manuscripts.

Contributions to Knowledge

Chapter 2:

This survey included the first statistical comparison of the composition of foliage-dwelling orchard spider assemblages to assemblages in adjacent habitats. The results indicated that agricultural crops do not necessarily have unique agrobiont assemblages, but rather that spider assemblage composition is comparable in habitats (crop and natural) with similar vegetation structure and frequency of structural disturbance.

Chapter 3:

This was the first experiment to study the effects of distance on the composition of spider assemblages colonizing a particular habitat, and the results showed that the composition of spiders colonizing apple orchards significantly changed over a distance of 50 m from the source habitat. Previous studies have only documented effects of distance on species richness and abundance of spider assemblages. This experiment quantified the rate and phenology of spiders colonizing the foliage of apple orchards. The composition of the assemblages in older orchards was different from that of the colonizing fauna, indicating that local interactions modulate the relative abundances of the colonizing species.

Chapter 4:

Spider community studies routinely exclude immature specimens from analyses that require species or generic level identifications. This study was the first to test whether or not the exclusion of these specimens changes the results of analyses.

Chapter 5:

Kaolin particle sprays reduce populations of and damage by a great number of pests in a variety of crops. To optimize the use of kaolin and predict

xii

indirect effects, it is necessary to know the mechanisms through which kaolin affects arthropods. Leafrollers are common pests in orchards and the leaf-rolling behaviour is a main factor in their defence against natural enemies and the full effect of insecticides. This study was the first to determine the effects of kaolin on the rolling and establishment behaviour of a leafrolling species, *Choristoneura rosaceana*.

Chapter 6:

Indirect effects of insecticides can often be as strong as the direct effects. This was the first study to test for indirect effects of kaolin on the interaction between a generalist predator and its prey, in this case a salticid spider and neonate *C. rosaceana*. This study also determined the functional response of salticids to changing densities of neonate *C. rosaceana*.

Chapter 7:

The success of kaolin formulations in controlling various pests in a variety of crops has led to its widespread use. However, studies of the effects of kaolin on natural enemies are rare. Spiders are the most numerous generalist predators in Québec apple orchards. This was the first study to look at the effects of kaolin on different guilds and families of spiders found in apple orchards, and also was the first study to investigate the effect of kaolin on the rate of parasitism of the leafroller, *C. rosaceana*.

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I was extremely fortunate to have the advice and guidance of two terrific supervisors, Dr. Chris Buddle and Dr. Charles Vincent. Their knowledgeable advice, prompt feedback, and support through my entire degree were constant.

Chris Buddle has an exceptional and contagious passion for ecology, ideas, (and spiders!), and I have learned an enormous amount working with him, not only academically, but also about how to be a good collaborator and a good teacher. As a supervisor he achieves that fine balance between providing advice and letting students pursue their own ideas. He has provided financial support for me to attend several conferences per year during my degree, allowing me to make connections with other scientists and present my work at these forums.

Not long after I met Charles Vincent he remarked that, as agricultural entomologists, "we aren't in the business of killing insects". With this perceptive and thoughtful approach he has encouraged me to think creatively about pest management, but has also always emphasized the importance of having well designed experiments and significant and robust results before drawing conclusions.

Along with my supervisors, the third member of my academic committee was Dr. Sylvie de Blois. Although we only met a few times a year, over the years she has always come to my committee meetings well prepared, and with pertinent and useful suggestions, especially when I have been unsure of the direction of my project.

I am grateful to the organizations that have provided me with consistent funding during my research project. In 2003 and 2004, I was financially supported by the Canadian Federal Student Work Exchange Program (FSWEP/PFETÉ) through Agriculture and Agri-food Canada to work in the lab of Dr. Vincent. I also was supported by a McGill Graduate Studies fellowship in 2003-2004, and the Margaret A. Duporte fellowship in 2004-2005. From 2005-2007 I was fully supported by an NSERC (National Science and Engineering Research Council) post-graduate scholarship. A Matching Fund Initiative Project co-funded by the Québec Apple Growers' Association and Agriculture and Agri-Food Canada also supported the experiments with kaolin, and D. Sekutowski (Engelhard Corp., Iselin, N.J.) provided the Surround WP for the experiments.

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I thank the Journal of Economic Entomology for their permission to include the published article "Effect of kaolin on the fitness and behaviour of *Choristoneura rosaceana* (obliquebanded leafroller) (Lepidoptera: Tortricidae) larvae" as chapter 5, and the Journal of Applied Entomology for their permission to include the published article "Effects of kaolin on the composition of generalist predator assemblages and parasitism of *Choristoneura rosaceana* (Lepidoptera: Tortricidae) in apple orchards" as chapter 7.

While working in the Buddle lab I've met, talked, discussed, debated, skied, and laughed with a fantastic group of fellow students: Kathleen Aikens, Elise Bolduc, Joey Bowden, Andrea Déchêne, Val Evans, Carol Frost, Annie Hibbert, Max Larrivée, Yao Hua Law, J-P Lessard, Alida Mercado, Tania Motchula, Michel Saint-Germain, Briana Schroeder, Charles Stephen, Zach Sylvain, Hirondelle Varady-Szabo, and Annie Webb. They have also been invaluable in providing feedback on ideas and on written drafts of the manuscripts. Max Larrivée was a great help with the copy-editing of the résumé.

Finally, my friends and family, both in Montreal and via telephone and email, have been encouraging, patient, and understanding of how much my work means to me, and how much time and energy it requires. I especially thank my friends in Montreal and my family, including Mélanie St. Onge, Liz Meyer, Lis Marks, Katie Gibson, Nancy and Jim Wright, Andrew, Dad and Margot, and Mum and Alan. I owe special thanks to my mum for her thorough copy-editing of the entire final thesis.

Chapter 1: Introduction, literature review, and objectives

1.1. Introduction

Integrated pest management (IPM) uses multiple approaches to keep pest levels below economic injury levels (Kogan 1998). Accomplishing this requires an understanding of ecological processes in agroecosystems and how they are modified by disturbances such as the application of pesticides or harvesting (Kogan 1998; Brown 1999). Although agroecosystems are more disturbed than natural habitats, the interactions between organisms, the characteristics of the habitat, and immigration and emigration of species at local and regional scales are common factors structuring any community. Perennial crops such as orchards are more stable temporally and spatially than annual crops; this will be reflected in the community dynamics (Brown 1999).

Integrated pest management strategies must consist of both preventative and curative methods (Kogan 1998). Preventative methods include conservation biological control: manipulation of the agroecosystem environment to favour the immigration, establishment, survival and reproduction of biocontrol agents such as parasitoids and generalist predators (insects and spiders) (Landis *et al.* 2000). For preventative biological control to work, we need to understand the ecology of natural enemies in the agroecosystem to increase and sustain natural enemy populations. Curative (i.e. active, immediate) pest control methods should minimally disrupt these natural enemy assemblages.

In this thesis I focused on issues relevant to arthropod natural enemy ecology in apple orchards, especially spiders, which are the most diverse taxa of generalist predators in Québec apple orchards. Specifically, my main objectives were to determine (1) the potential of natural habitats adjacent to orchards to be sources of colonizing spiders, (2) how kaolin, a clay particle spray, affects the behaviour of *Choristoneura rosaceana* larvae and whether these behavioural changes affect spider predation on larvae, and (3) the effects of disturbance through the application of kaolin on orchard natural enemies: spiders, insect

generalist predators, and parasitoids of a pest species *Choristoneura rosaceana* (Harris) (Lepidoptera: Tortricidae). In the remainder of this first chapter I review the literature relevant to these objectives. In the first part of the thesis (chapters 2-4) I considered the relationship between spiders assemblages in orchards and their adjacent habitats: in chapter 2, I investigated whether or not natural habitats surrounding an orchard are potential sources for spiders to recolonize orchards, and if so, what characteristics of the habitat are important. Following from these findings, in chapter 3 I measured the dynamics (rate, phenology) of this colonization and determined how distance from the source affected the composition and rate of colonizing spiders. In chapter 4, I explored a methodological issue in spider community studies: whether excluding unidentified immature spiders from the dataset yields results that inaccurately reflect the composition of the spider assemblages.

In the second part of the thesis (chapters 5-7) I addressed the relationship between spider and natural enemy assemblages, their prey, and the clay particle spray, kaolin clay. Although kaolin is a curative pest management technique, it differs from conventional pesticides in that by forming a physical barrier, it affects the behaviour of arthropods rather than acting as a toxin (Glenn *et al.* 1999). I used a case study approach to investigate the effects of kaolin on arthropod behaviour and interactions: how kaolin affects the behaviour of a pest species and potential prey item of spiders, larvae of *Choristoneura rosaceana* (chapter 5), and how kaolin affects interactions between spiders and their prey, such as the predation of spiders on *C. rosaceana* larvae (chapter 6). Finally, in field experiments I examined the direct effects of kaolin application on the spider and insect predator communities in apple orchards and the parasitism of *C. rosaceana* larvae (chapter 7).

In choosing these topics, I wanted to address questions within the two branches of IPM mentioned previously: agroecosystem management that considers the ecology of the organisms involved and how to encourage natural enemy populations that help prevent pest outbreaks, and the investigation of

curatives that can potentially solve acute pest problems without disrupting the longer term, preventative strategies.

1.2. Literature Review

1.2.1. Orchard IPM

A complex suite of pests and diseases is found in apple orchards, and as a result (and due to the market's demand for unblemished fruit), orchards in Canada require more pesticide treatments per year than many other crops (Vincent and Roy 1992; MacHardy 2000). Integrated pest management in apple, as in other crops, is classified by levels that increasingly incorporate non-pesticide methods into the production system; higher levels integrate tactics across multiple classes of pests (e.g. both diseases and insects) and broaden the ecological focus from the species/population level up to the community and ecosystem levels (Prokopy 1993; Kogan 1998). Québec apple orchards have a remarkable number of pest species; Chouinard et al. (2001) classifies 5 insects and mites as major pests (i.e. cause at least 10% of losses on average) and 20 as minor pests (i.e. cause losses occasionally or in particular locations). Because of this, and also because of the complexity of the orchard habitat compared to an annual crop, the interactions between arthropods (pests, natural enemies and neutral) are complex and difficult to predict and control. Although controlling certain pests still requires the use of chemical pesticides, advances in IPM have greatly reduced the quantity of pesticides used in orchards by combining a variety of alternative methods, many of which are founded on ecological knowledge of the agroecosystem and its fauna (MacHardy 2000; Chouinard et al. 2001; Prokopy 2003). These include mating disruption, trapping (e.g. red spheres to trap apple maggot), pruning and thinning, selective insecticides (e.g. Bacillus thuringiensis formulations or insect growth regulators), ground cover management, and habitat diversification to encourage natural enemy populations (Chouinard et al. 2001). Assemblages of parasitoids have been identified for many orchard pests (Cross et al. 1999), and generalist insect predators such as mirid, anthocorid, and reduviid bugs (Hemiptera), coccinellids (Coleoptera), chrysopids (Neuroptera), cecidomyiids (Diptera), and ants (Hymenoptera) consume orchard pests such as

phytophagous mites, psylla, and aphids (Paulson and Akre 1992; Wyss *et al.* 1999; Chouinard *et al.* 2001; Brown 2004; Ragkou *et al.* 2004; Chouinard *et al.* 2006). In Québec orchards, as in apple orchards worldwide, spiders (Araneae) are one of the most abundant and species rich group of foliage-dwelling predators (Dondale 1956; McCaffrey and Horsburgh 1977; Dondale *et al.* 1979; McCaffrey and Horsburgh 1980; Olszak *et al.* 1992a; Samu *et al.* 1997; Bogya *et al.* 1999; Brown *et al.* 2003). Although spider assemblages have been well characterized, only a few studies have explored their biocontrol potential in orchards (Mansour *et al.* 1980; Haddad *et al.* 2004; Rodriguez *et al.* 2005; Sarvary *et al.* 2007). However, considerable theoretical and empirical advances on the role of spiders in biocontrol have been made in other crop systems.

1.2.2. Spiders in biocontrol

There is theoretical and empirical support that generalist predators, including spiders, can contribute to pest control, in contradiction to the long-held assumption that only natural enemies that exhibit density dependent tracking and prey specificity are relevant (Riechert and Lockley 1984; Symondson et al. 2002; Snyder and Ives 2003; Stiling and Cornelissen 2005). Spiders can prevent the early increase in pest populations by acting as a buffer on pest populations rather than reacting to pest outbreaks in a density dependent fashion (Riechert and Lockley 1984; Riechert et al. 1999). This potential to buffer pest populations at low levels requires particular characteristics, many of which spiders exhibit: polyphagy, self-limiting populations (Wise 1993), the ability to exploit changes in temporal availability of prey (Riechert et al. 1999), and being part of a diverse assemblage of species; multi-species generalist predator assemblages may consume prey at a higher level and with more temporal stability than one species alone (Riechert and Lawrence 1997; Riechert et al. 1999; Stiling and Cornelissen 2005; Tscharntke et al. 2005), but see Rosenheim (1998). Additionally, spiders can respond quickly to changes in pest densities as they are among the first predators to colonize a crop (Gut et al. 1988; Rathman and Brunner 1988; Bishop and Riechert 1990; Ehmann 1994) and are not dependent upon the presence of particular prey to maintain their populations within crops (Symondson *et al.* 2002). Spiders also kill more prey than they consume, through both wasteful killing (Wise 1993) and indirect effects on prey (e.g. inducing prey to leave the plant) (Mansour *et al.* 1981; Gastreich 1999; Cronin *et al.* 2004).

Spiders exhibit a variety of hunting behaviours and, as such, occupy a diversity of microhabitats. Uetz *et al.* (1999) classify agricultural spiders into guilds that reflect similarities in hunting strategy. The primary division is between webspinners and hunting spiders (the latter hunt without webs). Within the hunting spider guild, there are the running spiders (actively wander searching for prey), stalkers (wandering followed by stalking prey), and ambushers (remain still and ambush prey). Web-spinners are classified into guilds depending on the type of web they build. These include space-web builders (three-dimensional web occupying a defined space), tangle-web weavers (a looser, less defined web) and the orb-web weavers (the archetypal, two-dimensional orb web). Due to their different foraging modes the diet of the spiders in different guilds varies: web-spinners eat almost entirely insects, while hunting spiders have a wider diet breadth, including up to 25% other spiders (Nyffeler 1999).

Spider predation on pests has been studied extensively in field crops, where they can reduce pest populations (Nyffeler and Sunderland 2003), cascading down to a reduction in plant damage (Riechert and Bishop 1990; Carter and Rypstra 1995; Halaj *et al.* 2000; Lang 2003). Few studies have manipulated spider populations in orchards to investigate their biocontrol potential. However, Mansour *et al.* (1980; 1981) found spiders, primarily the hunting spider *Cheiracanthium mildei* L. Koch (Miturgidae), controlled populations of *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae) in apple orchards. More recently, Sarvary *et al.* (2007) found that the predation rate (by all predators) on *C. rosaceana* larvae in orchard plots ranged from 20-35% and did not differ between conventionally treated plots and those treated with reduced-risk insecticides.

The impact of spiders and other generalist predators on pest populations is often unpredictable as they also feed on economically unimportant arthropods and other natural enemies within the crop (i.e. intra-guild predation, IGP), which can dampen the top-down influence on herbivores or even cause increased herbivore

populations (Rosenheim 1998; Hodge 1999; Symondson *et al.* 2002). In some cases, even with documented IGP, the activity of generalist predators still cascades down to decreases in pest numbers (Snyder and Ives 2001; Denno *et al.* 2004) and increases in plant yield or quality (Lang 2003). Whether or not IGP dampens biocontrol of pests is difficult to predict as it depends on a variety of factors, such as natural enemy characteristics (e.g. foraging mode) (Rosenheim and Corbett 2003), habitat complexity (Finke and Denno 2002), and the community composition and phenology of the arthropods within the crop over the season (Snyder and Wise 2001). Despite the complexities inherent in predicting the success of biocontrol with IGP as a factor, a review of manipulative field experiments showed that natural enemy assemblages, including generalist predators, caused a significant reduction in the pest population in 77% (n=181) of the reviewed cases (Symondson *et al.* 2002).

1.2.3. Habitat manipulations

Generalist predators work most efficiently as assemblages of multiple species (Riechert and Lawrence 1997; Stiling and Cornelissen 2005), but because the inundative release of generalist predators is largely impractical, other methods to increase and stabilize generalist predator populations (and other natural enemies) are important. Diversification of the agroecosystem is an effective way of increasing natural enemy populations, as these alternative habitats are a source of natural enemies for periodic recolonization and provide extra microhabitats, protected microclimates, overwintering sites, and alternative resources (Landis et al. 2000; Sunderland and Samu 2000). Habitat manipulations include changes within the agroecosystem, surrounding the agroecosystem, or at a landscape scale (Symondson et al. 2002). Habitat manipulations within the agroecosystem such as reduced tillage, mulching, and the addition of straw bales increase the densities and species richness of predators like spiders and carabids (Halaj et al. 2000; Landis et al. 2000). Noncrop plants planted in rows through the crop or surrounding the crop provide alternative resources (i.e. nectar, pollen, shelter) for parasitoids (Bostanian et al. 2004; Norris and Kogan 2005) and predators (Lemke and Poehling 2002; Prasifka et al. 2006). Natural habitats surrounding the crop, such as woodland and fields, may

be sources of natural enemies to recolonize the crop after disturbance (i.e. harvesting or pesticide application) (Landis *et al.* 2000). The regional landscape can affect species richness and density of natural enemies in agroecosystems, as higher landscape diversity has been correlated with higher abundance and species richness of generalist predators and parasitoids (Landis *et al.* 2000; Sunderland and Samu 2000; Bianchi *et al.* 2006). There are problems associated with increased diversification of the agroecosystem, including providing refuges and source populations of pests (MacHardy 2000; Vakenti *et al.* 2001; Prokopy 2003; Norris and Kogan 2005) and keeping land out of production (Landis *et al.* 2000).

For epigeic spiders in arable crops, increased density and species richness of spider populations, through mulching or the addition of crates or straw bales between the rows, reduces pest populations and plant damage (Riechert and Bishop 1990; Carter and Rypstra 1995; Halaj *et al.* 2000). In perennial crops such as orchards, the planting of non-crop strips, usually flowering annuals, may augment the diversity of spiders inhabiting the foliage of the trees. In some cases, spider abundance increases in orchard plots containing flowering strips (Wyss 1995), but in other cases there is no significant effect, and the species overlap between spiders on the orchard foliage and herbaceous plants is low (Samu *et al.* 1997; Jenser *et al.* 1999). A potential disadvantage of intercropping is that spiders may not consistently move from the non-crop strips into the crops if the resources are superior in the non-crop strips (Riechert and Bishop 1990; Samu 2003).

A viable alternative to intercropping to increase the immigration of spiders into orchard foliage is to design agroecosystems to include natural habitats that harbour similar spider assemblages to the orchard (i.e. landscape approach). The amount of movement and establishment of arthropods between patches in a landscape will vary depending on relative population densities, species dispersal abilities and propensities, and habitat affinities (Hillebrand and Blenckner 2002). For many arthropods there is some overlap of species between the crop and adjacent fields and woodlands (Bedford and Usher 1994; Rieux *et al.* 1999; Tixier *et al.* 2000; Thomas *et al.* 2001; Varchola and Dunn 2001). However, for spiders, it is not clear if these adjacent habitats are a source of colonists to the crop, because the epigeic spider

assemblages as a whole are dissimilar in crops and their adjacent habitats (Bishop and Riechert 1990; Samu *et al.* 1997; Topping and Lovei 1997; Samu and Szinetár 2002), suggesting that long-distance dispersal, rather than local, plays a major role in the colonization of crops. Arable crops have a distinct "agrobiont" spider fauna; species that make up a large proportion of the spider community in crops, are less dominant in natural habitats, and are adapted for frequent dispersal between ephemeral habitats (Wissinger 1997; Samu and Szinetár 2002). However, the density of agrobiont species per unit area may actually be equivalent or higher in adjacent perennial grasslands, indicating that the dominance of these species in crops may be due to low densities of other species rather than numerical dominance of the agrobionts *per se* (Schmidt and Tscharntke 2005a).

Arable crops and their adjacent habitats often differ in several key factors that influence the composition of spider assemblages: vegetation structure (Greenstone 1984; Rypstra *et al.* 1999; Langellotto and Denno 2004) and frequency of structural disturbance (i.e. annual tilling of fields) (Topping and Lovei 1997; Wissinger 1997; Samu and Szinetár 2002; Schmidt and Tscharntke 2005a). To have similar spider assemblages in a crop and its adjacent habitat, both vegetation structure and the frequency of structural disturbance (through harvesting) should be similar (Bishop and Riechert 1990; Samu and Szinetár 2002).

Perennial crops are structurally more stable than annual crops, and, as such, the spider assemblages may be similar to the assemblages in perennial habitats such as deciduous forest, which may also have a similar vegetation structure. Studies have shown that there is species overlap between orchards and adjacent trees and shrubs (Olszak *et al.* 1992a; Olszak *et al.* 1992b; Miliczky and Horton 2005), and that there is a negative correlation between the relative abundance of spiders in orchard foliage and distance of the orchard to the adjacent habitat (Miliczky and Horton 2005). These studies suggest that habitats that are similar to the orchard in both vegetation structure and temporal stability may be sources of colonists to the orchard.

1.2.4. Spider dispersal and colonization

Spiders can potentially move from patch to patch in a landscape via two modes of dispersal: cursorial (walking) and ballooning. The main mode of colonization for both epigeic and foliage-dwelling spiders is ballooning (Bishop and Riechert 1990; Weyman 1993; Ehmann 1994; Weyman et al. 2002). For ballooning, strands of silk from the spinnerets create drag with which spiders are pulled aloft, and they drift passively with the wind. Spiders can theoretically balloon up to tens of kilometers per day (Thomas *et al.* 2003). The total distance travelled is probably less and varies with the propensity of the spider to re-balloon after alighting, related to species, environmental conditions (e.g. air flow), population density, and prey availability (Morse 1993; Weyman and Jepson 1994; Weyman et al. 1995; Weyman et al. 2002). The ability of spiders to balloon is limited by size; ballooning spiders are typically less than 2 mg in mass (Greenstone et al. 1987). Spiders in some families are small as adults and can balloon during all life stages (e.g. Linyphilds), which may be an adaptation to living in unpredictable, ephemeral habitats (Weyman et al. 2002). Linyphilds are often the most common spiders caught in aerial traps (Greenstone et al. 1987; Pearce et al. 2005). In most other families the spiders tend to be larger as adults and therefore balloon as juveniles (Duffey 1956), often during the spring and summer (Marc et al. 1999).

The ability of spiders to disperse long distances by ballooning indicates that the regional landscape, in addition to the habitats surrounding the agroecosystem, may influence spider populations within a crop. Early models demonstrated the importance of non-crop habitats as sources and refuges for spiders to recolonize agricultural habitat (Halley *et al.* 1996; Samu *et al.* 1999). Subsequent studies have confirmed the importance of landscape: the species richness of epigeic spiders in cereal is positively correlated with the percentage of non-crop area within radii of 500 m (Clough *et al.* 2005), and the abundance of Linyphiids in winter wheat also increases with higher percentages of non-crop habitats in a 1-to-3 km radius (Schmidt and Tscharntke 2005a). In winter wheat the abundance of epigeic spiders is higher in organic as compared to conventionally managed fields (Schmidt *et al.* 2005), but species richness of spider assemblages is not always related to the management regime (Clough *et al.* 2005; Schmidt *et al.* 2005). According to models, the landscape diversity (i.e. number of different types of non-crop habitats) is more important to epigeic spider diversity than the spatial arrangement of these habitats (Thorbek and Topping 2005).

Habitat diversification at all spatial scales clearly affects the species richness and abundance of spiders, but how dispersal at these various spatial scales affects species composition of assemblages is poorly understood. Additionally, most research into the dispersal and colonization of spiders into crops has focused on epigeic species, primarily the Linyphiidae. The colonization dynamics of foliage-dwelling spiders into perennial crops such as orchards are largely unexplored.

1.2.5. Effects of pest management on spiders

The species composition of a community results from the regional influences from dispersal and colonization and from factors within the habitat such as biotic interactions, environmental and habitat conditions, and disturbance to the assemblages through changes in habitat structure (such as seasonal growth or senescence of plants)(Ricklefs 1987). Agricultural crops differ from natural habitats in that there are also periodic disturbances to the system from the application of pesticides, which have varying effects on the arthropod community (Hu et al. 1996; Prokopy et al. 1996; Desneux et al. 2007). The abundance and diversity of spider populations are reduced by conventional (broad-spectrum) insecticide application to orchard foliage (Croft and Whalon 1982; Hull and Starner 1983; Bostanian et al. 1984; Olszak et al. 1992a; Wisniewska and Prokopy 1997; Pekár 1999a; Pekár 1999b; Bogya et al. 2000). Insecticides used in conventional management also reduce the number of overwintering spiders in orchards (Pekár 1999c; Bogya et al. 2000; Horton et al. 2001). Spiders are sensitive to insecticides from multiple chemical families; broad-spectrum organophosphates, pyrethroids and carbamates decrease spider populations (Bajwa and Aliniazee 2001), although when applied at reduced frequencies the effects are not as pronounced (Wisniewska and Prokopy 1997; Bajwa and Aliniazee 2001). Some insecticides such as insect growth

regulators or *Bacillus thuringiensis* formulations do not affect spider populations (Gurr *et al.* 1999; Bajwa and Aliniazee 2001). Spider guilds differ in susceptibility to pesticides partially because their different foraging modes lead to different degrees of contact with the insecticide. In laboratory assays hunting spiders are more sensitive than web-spinners, as the latter are protected to a certain degree by their webs and are not in constant contact with the sprayed foliage (Pekár 1999b). In the field, the response of particular guilds and families to insecticide applications is not consistent, indicating that the vulnerability to the insecticide is not the only important factor, but that different rates of resistance development and competitive release may also contribute to observed patterns (Wisniewska and Prokopy 1997; Pekár and Kocourek 2004; Cardenas *et al.* 2006). Spiders can recognize and avoid insecticide residues within one day of application, but not after, leading to potentially harmful contact (Pekár and Haddad 2005).

Because of the negative impact of chemical insecticides on natural enemies, as well as on human health and the environment (Wilson and Tisdell 2001), alternatives to broad-spectrum insecticides are in increasing demand. Alternatives to chemical methods include physical methods, which use a variety of techniques to alter the physical environment of the pest and thereby reduce its threat to the crop (Vincent *et al.* 2003). Recently, a physical method, consisting of particle spray formulations of kaolin clay, has been developed for pest management (Glenn *et al.* 1999). This technique is unusual in that it is applied as a spray (much like a pesticide), but its mode of action is physical rather than chemical.

1.2.6. Kaolin

Kaolin is a non-abrasive, white, aluminosilicate clay used in a variety of industrial applications such as the production of paper, porcelain, paint, cosmetics, and pharmaceuticals. In agriculture, kaolin was initially used to reduce heat stress of crops: when applied to foliage the resulting reflective film reduces heat stress of crops, including apple, without negatively effecting yield (Glenn *et al.* 1999). Kaolin is now also used for pest management, either as hydrophobic or hydrophilic formulations (Puterka *et al.* 2000; Lalancette *et al.* 2005; Eigenbrode *et al.* 2006), and

is currently available on the market as a hydrophilic formulation, Surround WP Crop Protectant, from Engelhard Corporation (Iselin, New Jersey). Kaolin was regulated for use in Canada by the Pest Management Regulatory Agency in 2003. Kaolin formulations have been used on a variety of crops and reduce plant damage by, and populations of, arthropods from multiple taxa, including aphids (Puterka et al. 2000; Cottrell et al. 2002; Daniel et al. 2005; Liu and Trumble 2005; Puterka et al. 2005; Saour 2005; Karagounis et al. 2006), weevils (Lapointe 2000; Showler 2002; Lalancette et al. 2005), tephritid fruit flies (Saour and Makee 2004), plant bugs and stink bugs (Lalancette et al. 2005), and leafrollers and other caterpillars (Showler 2003; Sisterson et al. 2003; Lalancette et al. 2005; Barker et al. 2006). In apple orchards, kaolin formulations have been effective in reducing damage by or populations of codling moth (Cvdia pomonella (L.)) (Unruh et al. 2000), leafrollers such as the fruittree leafroller (Archips argyrospilus (Walker)), oblique-banded leafroller (Choristoneura rosaceana) and red-banded leafroller (Argyrotaenia velutinana (Walker)) (Knight et al. 2000; Knight et al. 2001; Thomas et al. 2004), rosy-apple aphid (Dysaphis plantaginea (Passerini)) (Wyss and Daniel 2004; Burgel et al. 2005); Mediterranean fruit fly (Ceratitis capitata (Wiedemann)) (Mazor and Erez 2004), and plum curculio (Conotrachelus nenuphar (Herbst)) (Thomas et al. 2004). Kaolin's main mode of action is to disrupt processes requiring physical contact with the plant, such as settling frequency, feeding, and ovipositing (Lapointe 2000; Unruh et al. 2000; Showler 2003; Sisterson et al. 2003; Burgel et al. 2005; Puterka et al. 2005). Kaolin is not always effective, as some arthropod populations increase when plants are sprayed with kaolin (Knight et al. 2001; Showler and Setamou 2004; Lombardini et al. 2005), and ovipositing of diamondback moth (Plutella xylostella L.) increases on calabrese leaves sprayed with kaolin (Barker et al. 2006). There are negative effects on natural enemies as well: kaolin reduced parasitism of western tentiform leafminer (Phyllonorycter elmaella Doganlaar & Mutuura) in apple (Knight et al. 2001) and of blueberry maggot (Rhagoletis mendax Curran) larvae in blueberry (Stelinski et al. 2006). The effect of kaolin on generalist predators is variable. Kaolin did not affect the populations of coccinellids or lacewings in pecan orchards (Lombardini et al. 2005) or reduviids and neuropterans

in cotton (Showler and Setamou 2004). Kaolin reduced densities of spiders in apple orchards (Knight *et al.* 2001), but only on some dates and years in pecan orchards (Lombardini *et al.* 2005), and did not reduce spider populations in cotton (Showler and Setamou 2004). Because kaolin coats the surface of the foliage, hunting spiders will have more contact with the substance than web-spinners, but whether there are differential impacts of kaolin on particular guilds or families of spiders, as with conventional pesticides (Pekár 1999b), is as yet unknown.

Because kaolin affects the behaviour of arthropods it may influence the interactions between predators, parasitoids, and their prey. For example, although kaolin did not affect the attraction of the parasitoid *Diachasma alloeum* (Muesebeck) (Braconidae) to fruit containing *Rhagoletis mendax* (Tephritidae), it prevented the wasps from ovipositing into the fruit (Stelinski *et al.* 2006). Therefore, the use of kaolin for pest control is best understood by observing kaolin's direct effects on the pest, the predators and parasitoids, and any indirect effects on interactions between these organisms.

1.2.7. Choristoneura rosaceana

The tortricid moth *C. rosaceana* is native to North America and is highly polyphagous, but prefers plants in the Rosaceae family (Chapman and Lienk 1971). In apple, *C. rosaceana* is classified as a secondary pest (Chouinard *et al.* 2001), but causes major problems in regions of Québec and other parts of North America (Reissig 1978; Smirle *et al.* 2002).

The insect is bivoltine in Québec. It overwinters as a second or third instar within hibernacula in the bark of the host and emerges in the spring to colonize the young foliage. In June, the females lay egg masses of several hundred eggs, from which the neonates disperse, and these summer generation larvae develop in July, coinciding with the development and maturation of apples. *Choristoneura rosaceana*, like many tortricid moths, builds leaf shelters, a behaviour that probably evolved as a defense against natural enemies (Powell 1980). This is one of the reasons that the insect is a challenge to manage as the leaf shelter may also protect the larvae from insecticides. *Choristoneura rosaceana* began to be a serious

problem in the late 1970s in New York State (Reissig 1978), and increasing populations and fruit damage have subsequently been correlated with resistance to insecticides, including the organophosphates, azinphosmethyl and phosmet, and more recently, carbamates and pyrethroids (Reissig et al. 1986; Pree et al. 2001). Crossresistance of azinphosmethyl-resistant populations to benzoylhydrazine insect-growth regulators also occurs (Smirle et al. 2002). Populations resistant to azinphosmethyl revert back to susceptibility after three or four generations suggesting insecticide treatments can be alternated with other treatments (Smirle et al. 1998). There has been extensive research on alternative methods of control of C. rosaceana populations and fruit damage, including pheromone-based mating disruption (Agnello et al. 1996; Knight et al. 1998), Bacillus thuringiensis Berliner var. kurstaki sprays (Li and Fitzpatrick 1996; Côté et al. 2001; Cossentine et al. 2003), inundative releases of Trichogramma spp. (Lawson et al. 1997a; McGregor et al. 2000) and the release of nematode-infected larvae (Bélair et al. 1999). Surveys have found C. rosaceana populations are attacked both by pathogens and parasitoids: nucleopolyhedroviruses have been isolated from larvae in Eastern Canada (Lucarotti and Morin 1997; Pronier et al. 2002), and over 40 species of parasitoids have been identified (Huber et al. 1996; Li et al. 1999; Vakenti et al. 2001).

Kaolin formulations reduce the density of the overwintering generation of *C. rosaceana* larvae when applied to the trees before bud break (Knight *et al.* 2000) and reduce the relative abundance of summer generation larvae when applied 7-10 times from March to August (Knight *et al.* 2001). Kaolin reduces ovipositing by female *C. rosaceana* although there is no effect on egg eclosion. Larvae prefer unsprayed leaves and kaolin lowers pupation rate and mean pupal weights (Knight *et al.* 2000).

1.3. Research Approach, Objectives and Hypotheses

The research papers in this thesis cover multiple issues relevant to IPM in apple orchards but centre around the ecology of spiders and other orchard natural enemies. The first objective of this thesis was to understand the dynamics of spider immigration from adjacent habitats into orchards, such as which habitats harbour source populations, and effects of distance from source habitat on colonization. The second objective was to understand how kaolin, by affecting arthropod behaviour, might affect the interactions between pest insects and their predators. To achieve this second goal I used a case study approach and tested the effects of kaolin on the behaviour of the pest species, *Choristoneura rosaceana*, and its interactions with a common predator, a salticid spider. The third objective was to determine, using field experiments, the effects of kaolin on orchard spider and insect natural enemy communities, including parasitoids of *C. rosaceana*. A fourth objective concerns the methodology of spider community studies: to determine if the exclusion of immature spiders from species level analyses, a common procedure as they cannot always be identified to species, significantly changes the results from analysis of the assemblage data and the conclusions we draw from these analyses.

In pursuit of these objectives, I investigated the following hypotheses:

Hypothesis 1: The composition of spider assemblages in orchard foliage is the same as found in natural adjacent habitats if these habitats have similar vegetation structure and degree of structural disturbance as the orchard (chapter 2).

Hypothesis 2: Spiders will colonize orchards from adjacent deciduous forest, and the distance from this source habitat at a small spatial scale (tens of metres) will not significantly affect the composition of the colonizing spider assemblages (chapter 3).

Hypothesis 3: The composition of the spider assemblages that have recently colonized apple orchards will differ from the spider assemblages in longer established orchards and largely consist of species with the greatest propensity to disperse (chapter 3).

Hypothesis 4: When immature spiders are included in datasets, there will be significant changes in the assemblage composition as compared to when they are excluded. This will affect subsequent analyses that compare assemblages (chapter 4).

Hypothesis 5: The mechanisms responsible for the negative effects of kaolin on *C. rosaceana* observed in previous field and laboratory experiments are due to changes in behaviour, not from the negative effects of ingestion. Changes in behaviour include negative effects on leaf shelter formation and establishment of the larvae (chapter 5).

Hypothesis 6 (a): Hunting spiders such as salticids (jumping spiders) will eat *C. rosaceana* neonates and, as neonate density increases, the proportion of larvae eaten will decrease (type II functional response). (b) At a constant prey density kaolin-induced changes in larval behaviour will increase the rate of predation on the larvae (chapter 6).

Hypothesis 7: Kaolin applications to apple foliage, designed for controlling populations of *C. rosaceana* summer generation larvae, will negatively affect the abundance and composition of spiders and insect generalist predator assemblages in the orchards, as well as the rate of parasitism on *C. rosaceana* larvae (chapter 7). Chapter 2: Comparisons of the composition of foliage dwelling spider assemblages in apple orchards and adjacent natural habitats

2.1. Abstract

Previous studies have shown that crops have different spider assemblages than adjacent natural habitats, suggesting that spider recolonization of crops is via long-distance ballooning. We propose that if two factors, habitat structure and frequency of structural disturbance, are similar between the crop and the adjacent habitat, then the spider assemblages also will be similar. Spiders were collected from four apple orchards in southern Québec, Canada, and their adjacent habitats (forest, field, and low-growing vegetation in the forest-field ecotone) from May until August 2004. The similarity of assemblages between the orchard and forest habitats was evaluated using non-metric multidimensional scaling (NMDS) and multi-response permutation procedures (MRPP), and the species richness of spiders in the habitats was compared using rarefaction. Although spider species richness was higher in the forest than orchards, the composition of spider assemblages in apple orchards was not significantly different from those found in adjacent deciduous forests at three of the four sites. Very few spiders were collected from field and low-growing vegetation. Thus adjacent deciduous forest, which is most similar to the orchard with respect to vegetation structure and frequency of structural disturbance, likely functions as the main source of spiders to apple orchards.

2.2. Introduction

Spiders (Araneae) are abundant and species-rich generalist predators in agroecosystems, especially in perennial crops such as apple orchards (Dondale *et al.* 1979; McCaffrey and Horsburgh 1980; Olszak *et al.* 1992a). Spiders are among the first arthropods to colonize disturbed agricultural areas, primarily arriving by ballooning rather than cursorial dispersal (Bishop and Riechert 1990; Ehmann 1994; Marc *et al.* 1999). Higher proportions of non-crop habitat and

greater heterogeneity of the landscape are correlated with the persistence of populations and higher ground-dwelling spider abundances and species richness in agricultural fields (Halley *et al.* 1996; Clough *et al.* 2005; Thorbek and Topping 2005; Schmidt and Tscharntke 2005b; Isaia *et al.* 2006). Spiders are negatively affected by insecticide applications (Bostanian *et al.* 1984; Wisniewska and Prokopy 1997; Pekár 1999a; Pekár 1999b; Bajwa and Aliniazee 2001), although populations are more stable in perennial crops (e.g. orchards) than annual crops because of the absence of physical disturbance through harvesting (Riechert and Lockley 1984). Enhancing spider recolonization after populations are reduced by disturbances such as harvesting or insecticide application requires a knowledge of which natural habitats are potential sources (Marc *et al.* 1999; Sunderland and Samu 2000).

Notwithstanding the positive correlation between regional habitat diversity and spider abundance and species richness, the source of spiders colonizing crops is not clear; many studies have found that habitats adjacent to crops have different spider assemblages than the crop, suggesting that most colonization is through long-distance dispersal (Bishop and Riechert 1990; Samu *et al.* 1997; Topping and Lovei 1997; Samu and Szinetár 2002). However, the adjacent habitats in previous studies may have been too dissimilar to the crop with respect to factors that determine spider assemblage composition, mainly habitat structure and degree of disturbance. Some spider species are specialized for habitats that have high frequencies of structural disturbance (Topping and Lovei 1997; Samu and Szinetár 2002; Schmidt and Tscharntke 2005a), and are sensitive to habitat structure (Greenstone 1984; Rypstra *et al.* 1999; Langellotto and Denno 2004).

To determine if natural habitats and crops that have similar vegetation structure and disturbance frequency also have similar spider assemblages, we surveyed the spider assemblages in the foliage of apple orchards and compared these assemblages to those from three natural habitats that varied in their vegetation structure and frequency of structural disturbance. These habitats were deciduous forest, fields, and the ecotone between the forest and fields, consisting of perennial and annual shrubs and vegetation. The broad-leafed foliage of
orchards is most similar to that of deciduous forest and ecotone vegetation, and least similar to fields (i.e. grasses). The orchards are also most similar to deciduous forests with respect to frequency of structural disturbance, as the woody framework of trees is retained from year to year but the non-woody shrubs and grasses collapse annually.

Although no comparisons of spider community composition have been done between orchards and adjacent habitats, spider species found in the foliage of apple trees have been collected from adjacent deciduous shrubs and trees (Olszak *et al.* 1992a; Olszak *et al.* 1992b; Miliczky and Horton 2005). The relative abundance of spiders in orchard trees decreases with increased distance of the orchard from the adjacent habitat (Miliczky and Horton 2005) and within the orchard on the distance of the tree to the edge of the orchard (Bogya *et al.* 2000). These studies suggest that spiders are colonizing orchards from adjacent vegetation. The objective of this study was to determine if the species composition of foliage-dwelling spider assemblages in four apple orchards was similar to assemblages in any of three adjacent natural habitats that varied in vegetation structure and frequency of structural disturbance: forest, forest-field ecotone vegetation, or field.

2.3. Materials and Methods

2.3.1. Study sites

We sampled four orchards and their adjacent habitats in southern Québec, Canada. Three sites (A, B, and C) were near Frelighsburg (45° 03' N, -72° 50' W), on an Agriculture and Agri-Food Canada experimental farm. All orchards at this location were 15 years old, and ranged in size from 0.5 ha (orchard A) to 0.8 ha (orchards B and C). The fourth site (D) was a commercial orchard located 55 km away near Mt. St. Hilaire (45° 31' N, -73° 09' W), was 1.5 ha in size and approximately 15 years old. No insecticides or acaricides had been applied in any of the four orchards for at least nine years. The landscape around the Frelighsburg and Mt. St. Hilaire sites consisted mainly of mixed deciduous forest, orchards, and arable fields, but at different compositions, and the orchards varied in distance from the closest forest fragment (Table 2-1).

Site	Distance from nearest forest (m)	Landscape composition in 1 km circumference	Landscape composition in 3 km circumference	
А	12	000/ 0 / 70/ 1 1	80% forest, 10% orchards, 10% fields	
В	40	90% forest, 5% orchards, 5% fields		
С	12	270 Hereb		
D	200	35% forest, 50% orchards, 10 % fields, 5% residential	25% forest, 10% orchards, 50% fields, 15% residential/golf course	

Table 2-1: Site characteristics: distance of orchards from forest and landscape composition, in southern Québec, Canada.

2.3.2. Adjacent habitats

We sampled three habitats adjacent to the orchards: deciduous forest foliage, low-growing vegetation beside the forest (included both annuals and perennials), and fields. The forests contained similar deciduous tree species, but the species composition was slightly different at each site, as was the amount of forest bordering the orchard (Table 2-2). The fields mainly contained grasses, but with some broadleaf annuals such as clover (*Trifolium repens* L.) and spotted knapweed (*Centaurea maculosa* Lamark). The low-growing vegetation forming the ecotone between forest and field consisted of flowering raspberry (*Rubus occidentalis* L.), red raspberry (*Rubus idaeus* L.), black raspberry (*Rubus occidentalis* L.), jewelweed (*Impatiens capensis* Meerburgh), wild flowers such as goldenrod (*Solidago* sp.), and ferns. Orchards B and C shared a field site, and there was no low-growing vegetation at the Mt. St. Hilaire site.

2.3.3. Spider sampling

Foliage-dwelling spiders in orchards and adjacent forest were collected by beating branches over a 1-m² white collecting sheet, and low-growing vegetation and field sites were sampled with a sweep net (diameter 30 cm). There were five sampling events over the season: 17-19 May, 7-8 June, 30 June–3 July, 19-22 July, and 9-11 August. In orchards, we collected spiders from trees in the two

Species	Α	В	С	D
Red maple (<i>Acer rubrum</i> L.)	1	8	16	
Sugar maple (Acer saccharum Marshall)		7	2	
Striped maple (Acer pensylvanicum L.)		1		
Red elm (Ulmus rubra Muhlenberg)	6			
White elm (Ulmus americana L.)		2		
White ash (Fraxinus americana L.)	36	2	2	
Grey birch (Betula populifolia Marshall)	4	12	39	
Yellow birch (Betula alleghaniensis Britton)		45		
Speckled alder (Alnus incana (L.) Moench)		3		
Black cherry (Prunus serotina Ehrhart)			18	
Choke cherry (Prunus virginiana L.)	2		2	
Hawthorn (Crataegus succulenta Link)	1			
Willow (Salix sp.)	9	1		47
Trembling aspen (Populus tremuloides Michaux)	2	5	13	
Large toothed aspen (Populus grandidentata Michaux)		2		
Staghorn sumac (Rhus typhina L.)	14	8	9	17
Alternate leaf dogwood (Cornus alternifolia L.f.)		3		
Virginia creeper (<i>Parthenocissus quinquefolia</i> (L.) Planchon)	17			
Wild grape (Vitis sp.)	8			27
Red pine (Pinus resinosa Sol. ex. Aiton)				9
Total	100	100	100	100
Forest sampled (m)	105	60	55	40

Table 2-2: Tree species composition (%) of forest adjacent to orchards at each site in Southern Québec, Canada.

rows at the edge of the orchard, and for each sampling event we collected from 16 trees, 5 randomly chosen branches per tree, between 0.5 and 2 m in height. In the forest, for each event we sampled a different 10-m length of forest and collected spiders from foliage between 0.5 to 2 m in height, and 1 m into the forest. Low-growing vegetation in the ecotone was sampled along the same 10 m length of forest, and in the field we swept a 25-m^2 area. Ecotone vegetation and fields were sampled only on the last three sampling dates, as vegetation was still growing

during the spring. Site D was included in the survey after the Frelighsburg sites and sampled only three times (last three dates), and only interior trees (200 m from the forest) were sampled due to constraints from other research projects in trees on the edge of the orchard.

Both immature and mature spiders were collected. Specimens were identified to species using primarily Dondale and Redner (1978; 1982), Dondale *et al.* (2003), Prozsynski (2003), and Paquin and Dupérré (2003). Nomenclature follows that of the World Spider Catalog (Platnick 2007), and vouchers were deposited in the Lyman Entomological Museum of McGill University (Ste-Annede-Bellevue, Québec).

2.3.4. Data analyses

To compare species richness between the four habitats, we calculated individual-based rarefaction curves (Magurran 2004) using Ecosim Version 7 and an independent sampling algorithm with 1000 iterations (Gotelli and Entsminger 2001).

To compare the composition of spider assemblages collected from orchards and forest foliage we used non-metric multidimensional scaling (NMDS). Non-metric multidimensional scaling is a non-parametric ordination technique that does not require linear or unimodal relationships among variables (McCune and Grace 2002). Only two habitats were compared using NMDS: orchard foliage and forest foliage, as a requirement for NMDS is that the same sampling method is used (i.e. beating). Abundances were log₁₀ (abundance+1) transformed to decrease the influence of common species. The sample units used for analysis grouped spider collections by habitat (adjacent forest or orchard), site (orchards A-D), and collection date to assess temporal changes as well as effects of location and habitat. We ran a preliminary six-dimensional analysis to determine the number of dimensions to minimize stress (parameters: Sorenson distance measure, random starting configuration based on time of day, 100 iterations, 50 runs with real data, and 100 runs with randomized data (Monte Carlo test)). We re-ran the NMDS using the same parameters as above, but altered the number of dimensions as recommended by the preliminary run and used the graph data from the initial run for starting coordinates (McCune and Grace 2002). For ordinations with three dimensions, we report the stress and total amount of variance explained by the 3-D ordination, but for clarity we present the data with charts showing only the two axes explaining the most variance.

To determine if differences in species composition between sites and habitats were statistically different, we used non-parametric multi-response permutation procedures (MRPP) (Zimmerman et al. 1985) on the log-transformed data, with a Sorenson distance measure to correspond with the NMDS metric (McCune and Grace 2002). Multi-response permutation procedures do not require that the data be distributed normally or with homogeneous variances. We defined eight groups based on site (4) and habitat (2), with each group containing five sampling events (except for site D, with three sampling events in each habitat, and forest C, where no spiders were collected during two sampling events). Using MRPP we compared all groups for significant differences in composition, followed by pair-wise comparisons between each group. We report the p-value of the MRPP test statistic as well as the agreement statistic, A, which describes the within-group homogeneity as compared to random expectations; when A<0, there is more heterogeneity within the groups than expected by chance, and the values of A indicate the relative effect size (McCune and Grace 2002).

We used indicator species analysis (Dufrêne and Legendre 1997) to determine if any species were associated with either orchard foliage or adjacent forest foliage. We calculated indicator values between 0 and 100, with a higher value meaning the species is associated with one habitat. Statistical significance of the indicator values was determined using a Monte Carlo test with 1000 runs. PC-Ord version 4 was used for NMDS, MRPP, and indicator species analysis (McCune and Mefford 1999).

2.4. Results

In total, 1767 spiders and 49 species were collected over the course of the study, and 890 (50%) of these were identified to species and subsequently analyzed. Raw data are presented in Appendix I. The orchards and forest foliage contained the most spiders; very few individuals were captured in the field or low-growing vegetation of the forest-field ecotone, only 21 and 60 individuals, respectively (Figure 2-1). Species richness was higher in forest foliage than orchard foliage, as the 95% confidence intervals of the rarefaction curves did not significantly overlap for a comparable number of individuals (n=280). Further statistical comparisons of community composition focused on the orchard and forest.



Figure 2-1: Individual-based rarefaction curves depicting estimated spider species richness (SR) (\pm 95% confidence intervals) for orchards and their adjacent habitats in southern Québec. Arrow indicates number of individuals at which species richness of forest and orchard were compared.

Non-metric multidimensional scaling produced a three-dimensional solution that minimized stress (final stress=12.6) and explained 88% of the variance. Samples primarily separate based on region: orchard D and forest D (Mt. St. Hilaire) are separated along the two axes from samples collected from the three orchards and adjacent forests in Frelighsburg (A, B and C) (Figure 2-2: axis 1: R^2 =0.455; axis 2: R^2 =0.326). There was little separation of the samples based on habitat within each site (Figure 2-2).



Figure 2-2: Sample unit (site, habitat and sampling event) non-metric multidimensional scaling (NMDS) of spider collections from southern Québec. Legend describes sample site (A to D) and habitat (orchard (orc) or forest (for)). Numbers following symbols indicate sampling event (1-5).

Pair-wise analyses using MRPP confirmed that for three sites, A, C, and D, the orchard samples were not significantly different from the samples from the immediately adjacent forest (Table 2-3). For site B, however, the orchard samples

were significantly different in composition than forest samples (Table 2-3; Figure 2-2). Although samples were taken throughout the summer, there were no clear temporal patterns to species composition (Figure 2-2).

Table 2-3: Significance and effect size (agreement statistic, A) of comparisons of spider assemblages, sampled from orchards (orc) and adjacent deciduous forest (for) in southern Québec, using multi-response permutation procedures (MRPP).

Groups ^a compared	Agreement statistic (A)	р
All groups	0.198	< 0.001
Orc A vs For A	-0.015	0.62
Orc B vs For B	0.070	0.019
Orc C vs For C	0.055	0.153
Orc D vs For D	-0.048	0.694

^a Groups consist of the pooled samples from 3 or 5 sampling events from each habitat.

Indicator species analysis showed that only one of the 49 species was associated with one habitat over another: *Philodromus praelustris* Keyserling had an indicator value of 61.9 (p=0.01) and was associated with orchards. When the species counts from the four habitats were summed from all sites, nine of the ten most common species in orchards were also the most common in the deciduous forest (Figure 2-3).

Out of the 809 individuals collected from orchards and forest, 771 (95%) belonged to species found in both of these habitats. The most common species were not dominated by any particular guild or family of spiders, but represented both web-spinners (Theridiidae, Dictynidae, and Araneidae) and the hunting and ambush spiders (Philodromidae, Salticidae, and Thomisidae). The low-growing vegetation of the ecotone contained many of the same species as the orchard and deciduous forest habitats, but in lower numbers (Figure 2-3). Very few spiders

were collected from the fields (Figure 2-3). Among these, the most common species were crab spiders (Thomisidae and Philodromidae).



Figure 2-3: Relative abundance (\log_{10}) of spider species in four habitats in southern Québec. Species are ordered along the x-axis from most to least common in orchards, thereafter ordered in decreasing abundance for forest, low vegetation (ecotone), and field habitats.

2.5. Discussion

The foliage-dwelling spider assemblages inhabiting the bottom 2 m of apple orchard foliage had a similar composition to the assemblages collected in adjacent deciduous forest, and in three out of four sites the composition of the assemblages was not significantly different in the two habitats. The orchard spider assemblages were less similar to assemblages in fields and low-growing vegetation in the forest-field ecotone. Between regions, the spider assemblages in orchards and adjacent deciduous forest were more similar to each other than to assemblages in the same habitat in another region.

Spiders in different families prefer particular densities and orientation of foliage (Robinson 1981; McNett and Rypstra 2000; Heikkinen and MacMahon 2004). Although orchards and deciduous forest contain different plant species, the spider assemblages were still similar. Multiple families of spiders were well represented in both habitats, suggesting that the foliage had enough structural variability to suit multiple species (Ysnel and Canard 2000). Bishop and Riechert (1990) found that 41-50% of the cursorial spiders in a garden system were different species than were found either in the bordering forest or field. In our study, there was low species overlap between habitats due to the large number of singletons, but 95% of individuals collected from either orchard or forest belonged to species found in both habitats.

Frequency of structural disturbance can also influence species assemblages. Annual field crops have different spider species assemblages than adjacent grasslands, despite the structural similarity between the habitats (Topping and Lovei 1997; Samu and Szinetár 2002). In ephemeral, frequently disturbed annual agroecosystems, agrobiont species tend to dominate the collections (Wissinger 1997). In our study only one species was an indicator of habitat, *Philodromus praelustris*, which was associated to a moderate degree (IndVal=61.9) with orchard habitats. We may not observe agrobiont species in orchard foliage because the trees are perennial, and insecticides, which are the main agent of disturbance in apple orchards, were not used.

Olszak *et al.* (1992a; 1992b) found spider species in shrubs planted around an apple orchard that were also in the orchard, suggesting that these spider species found both types of foliage suitable habitat. Apple orchards contain spider species collected from adjacent trees and shrubs in riparian habitat, mixed oakconifer woodland, and sagebrush steppe (Miliczky and Horton 2005). Our results

confirmed the species overlap between orchard and adjacent deciduous trees, and we also showed that the composition of assemblages in the lower branches of orchards and adjacent forest was statistically the same.

Few spiders were collected from the fields and low-growing vegetation beside the forest, indicating these habitats are not the primary source of spiders to orchards, although this type of habitat may be beneficial to parasitoids (Landis *et al.* 2000). The broad-leafed foliage of the low-growing vegetation harboured the same species as orchards and forest, albeit at lower abundances (Figure 2-3). We expect that the annual disturbance through collapse of the herbaceous structures prevents spiders from overwintering on these plants and that this foliage is recolonized annually from the more stable orchard and forest habitats.

There have been no studies documenting movement of foliage-dwelling spiders from forest into orchards, although studies have documented aerial movement of other arthropods, both insect natural enemies and pest species, between forest and orchard (Altieri and Schmidt 1986; Jeanneret and Charmillot 1995). The forest habitat surrounding orchards should be managed as certain plant species, especially in the Rosaceae, will also support pests and diseases to which apple is susceptible (Altieri and Schmidt 1986; Prokopy 2003). Our study shows that adjacent forest containing a variety of deciduous tree species, which has similar plant structure and frequency of structural disturbance to apple orchards, contains spider assemblages similar to those found in the orchards and is a potential colonization source.

2.6. Connecting Statement

The results from chapter 2 imply spiders immigrate into orchards from deciduous forest adjacent to the orchards. In chapter 3 I further test and characterize this immigration by determining how distance from forest, a potential source population, affects the spider colonization of apple orchards.

Chapter 3: Spider colonization of apple orchards: distance from the source affects abundance and species composition

3.1. Abstract

The colonization of a habitat by individuals dispersing between patches is important to species composition in the habitat, especially when the rate of dispersal is high. We studied the colonization of apple orchards by foliagedwelling spiders to determine how the rate and composition of colonizing spiders is affected by distance from a source habitat. We also compared the composition of colonizing spiders to spider assemblages in older, established orchards to assess the long-term influence of these species on composition. We planted 12 "micro" apple orchards at two distances, 10 and 50 m, from deciduous forest, a potential source habitat, and removed spiders weekly from mid-May to mid-September, 2006. We also collected spiders from the adjacent forest. Over 2400 spiders colonized the micro-orchards during the season, reaching rates of 35-45 spiders/ m^3 /week. In the micro-orchards, five species were more abundant in micro-orchards 10 m from the forest, while one species was more abundant in the micro-orchards 50 m from the forest. The composition of the spider assemblages, as assessed by ordination techniques, formed a gradient: the samples from the micro-orchards 10 m from the forest were intermediate in composition between the assemblages in the deciduous forest and those in the micro-orchards 50 m from the forest. The spider species found in micro-orchards were the same as those found in older, established orchards. However, the relative abundance of individuals among species was more even in the older orchards, indicating that local dynamics modify the species composition over time. These results demonstrate that spiders do colonize apple orchards from adjacent deciduous forest, but the composition of the colonizing fauna can vary at small spatial scales.

3.2. Introduction

The composition of species assemblages in a patch is affected by local factors, such as competition or response to abiotic variables, and also by the

colonization of individuals dispersing from regional species pools (Hillebrand and Blenckner 2002). High rates of colonization will have a larger influence on community composition than low rates of colonization, where species composition is more affected by local dynamics (Leibold *et al.* 2004). Measuring the rate and patterns of colonization of habitats by individuals facilitates predictions of how this immigration will affect the composition of assemblages. In agroecosystems, dispersal and colonization have a particularly important influence on arthropod natural enemy communities, as populations within the crop are periodically reduced through disturbances such as harvesting and pesticide application and the landscape is relatively fragmented (Wissinger 1997; Bianchi *et al.* 2006). Spiders are among the first arthropods to colonize recently disturbed habitats (Bishop and Riechert 1990; Marc *et al.* 1999) and are ideal taxa with which to study colonization dynamics.

Much of the work on spider dispersal has been with ground-dwelling spiders in arable farmland. The majority of studies on these epigeic spiders have focused on the Linyphiidae (sheet-web spiders), which are common in farmland, and because of their small size they are well adapted to disperse across the landscape by ballooning (Weyman *et al.* 2002). Both the species richness and abundance of epigeic spiders in agricultural fields have been found to positively correlate with landscape features, such as heterogeneity and non-crop areas, at scales from 200 m to 3 km radii around the crop (Clough *et al.* 2005; Schmidt and Tscharntke 2005b; Isaia *et al.* 2006). However, the effects of dispersal and colonization on the species composition of spider assemblages are poorly understood. Similarity between species assemblages declines with distance, but the degree to which this occurs will be dependent on the taxa and particular landscape (Kadmon and Pulliam 1993; Nekola and White 1999).

There has also been little study of the dispersal dynamics of foliagedwelling spiders, which are less common in arable farmland, but abundant and species-rich in perennial crops such as apple orchards (Dondale 1956; McCaffrey and Horsburgh 1977; Dondale *et al.* 1979; McCaffrey and Horsburgh 1980; Olszak *et al.* 1992a; Samu *et al.* 1997; Bogya *et al.* 1999; Brown *et al.* 2003).

Foliage-dwelling spiders are among the first natural enemies to colonize fruit trees (Whalon and Croft 1986; Rathman and Brunner 1988) and the proximity of adjacent habitats in the agroecosystem affects the abundance of spiders in the orchard (Miliczky and Horton 2005). Although some studies have found that habitats adjacent to crops have dissimilar spider fauna (Bishop and Riechert 1990; Samu *et al.* 1997; Topping and Lovei 1997; Samu and Szinetár 2002), suggesting that long-distance dispersal is the main source of colonists (Bishop and Riechert 1990), research in apple orchard agroecosystems has shown that immediately adjacent forests harbour similar spider assemblages, implying they act as source patches on a local scale (chapter 2).

In this study we investigate the colonization by foliage-dwelling spiders of apple orchards in southern Québec, Canada. Our first objective is to determine if distance from the potential local source habitat (deciduous forest) affects the composition of the spiders colonizing the foliage. Our second objective is to compare the composition and species that are colonizing the orchard with assemblages present in orchards that have been established for a longer time, which will indicate the relative importance of dispersal and local dynamics to the composition of the assemblages.

3.3. Materials and Methods

3.3.1. Micro-orchards

To measure colonization of apple orchards we planted small orchards ("micro-orchards") each consisting of ten 3-year-old apple trees, and collected spiders that colonized these patches. The ten trees in a micro-orchard were planted together within a 1.2-by-0.5 m plot. Orchard trees are normally planted further apart, but we wanted the foliage of the trees to grow close together and form a block of foliage approximating what is found for individual trees in an older, established orchard. We used ten cultivars of apple, and each orchard was planted with a random selection of trees from the following varieties (all on M26 rootstock): Honeycrisp, Golden Supreme, Cortland Royal Court, Pinova, McIntosh Summerland, Silken, Gala Scarlet, Jonamac, Gingergold, and Spartan.

Using multiple varieties of apple in each orchard allowed a range of foliage growth patterns. However, we standardized the overall shape of each microorchard by pruning the foliage throughout the summer to a fixed size: approximately 1.5 m long, 0.5 m wide, and 1.75 m tall, with foliage beginning at 0.5 m off the ground.

3.3.2. Experimental design

The micro-orchards were planted within hay fields east of a continuous section of deciduous forest on an Agriculture and Agri-Food Canada experimental farm in Frelighsburg (45° 03' N, -72° 50' W), Québec, Canada. This area was predominantly forest; within a 3-km radius of the farm the landscape is 80% forest and 20% orchards and fields. We planted 12 micro-orchards (total of 120 trees) along a 600-m length of forest, grouping the orchards at three sites (approximately 300 m apart), each site consisting of four micro-orchards: two at a 10-m distance from the forest, separated by 10 m, and two 50 m from the forest, also separated by 10 m. Micro-orchards at the two distances were directly in line with each other, perpendicular to the forest. The trees were planted to the east of the forest, downwind from the prevailing westerly winds (M. Audette, pers. comm.). The grass and herbaceous vegetation within 10 m of each micro-orchard was kept mown.

The adjacent forest was dominated by white birch (*Betula papyifera* Marshall), grey birch (*Betula populifolia* Marshall), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marshall), and white elm (*Ulmus americana* L.). Subdominant trees and shrubs included trembling aspen (*Populus tremuloides* Michaux), yellow birch (*Betula alleghaniensis* Britton), and staghorn sumac (*Rhus typhina* L.).

The trees were planted on 15-16 May 2006. Each patch was machine tilled and compost was added at the time of planting. In the first two weeks the patches were watered twice and fertilized with 10-50-10. Five hundred grams of 15.5-0-0+19 Ca (Calcinate tropicote, Yara Inc.) and 500 g of 0-0-22+12 Mg (sulpomag) were added to each plot on 13 June, and we added an additional 500 g

of 15.5-0-0 +19 Ca to each patch in mid-July and mid-August. Any fruit produced by the seedlings was immediately removed.

3.3.3. Spider sampling

We collected spiders from the micro-orchards 13 times over 15 weeks between 8 June and 14 September 2006. Unlike Linyphiids, which balloon even as adults (Weyman *et al.* 2002), most foliage-dwelling spiders can balloon only as early instars, and this occurs mainly during the spring and summer (Duffey 1956; Marc *et al.* 1999). Collections were done once weekly, except for the 10^{th} and 13^{th} weeks. We collected spiders by visually searching each micro-orchard for 25-30 minutes until week 6 (7 July), and for the remaining weeks (when numbers of colonizing spiders began to increase) by combining the visual search with shaking of the trees over a $1-m^2$ sheet. Spiders were collected and placed in 70% ethanol. During these collections we also removed any branches with aphids, as these attract ants, which may affect spider colonization, and any large insect herbivores (>3 cm), such as orthopterans and lepidopterans, to reduce excessive consumption and damage to the plants.

Spiders were collected from the adjacent forest on three dates: week 2 (13 June), week 8 (26 July), and week 12 (23 August). On each date, three 20-m lengths of forest within 150 m of each of the 3 sites was randomly selected, and all foliage was shaken or beaten with a stick over a $1-m^2$ sheet, and spiders were collected and placed in 70% ethanol. The 30-m length of forest closest to the micro-orchards at each site was not sampled, and the same stretch of forest was not sampled more than once.

We made two sweep collections (16 June, 26 July) of the grass in the fields adjacent to the micro-orchards. A 25-m^2 area was sampled at each site using a sweep net. The field was sampled to eliminate the possibility that it was acting as a source habitat, although previous work has indicated it harbours a very low relative abundance and number of species per unit area (chapter 2).

Spiders were identified to the lowest possible taxonomic level. Vouchers were deposited in the Lyman Entomological Museum of McGill University (Ste-Anne-de-Bellevue, Québec).

3.3.4. Data analyses

3.3.4.1. Colonization rate and species turnover in micro-orchards

To quantify colonization of the orchards and determine if the different distances from the forest affected these patterns, we compared the colonization rate and total spider abundance in micro-orchards based on their distance from the adjacent forest. We expressed the rate of colonization per week as number of individuals per m³, as the micro-orchards were kept pruned to a constant volume (0.94 m³). The two collections made in week 11 and 14 were after two weeks of colonization and were therefore not compared with rates from the other weeks.

We determined the turnover of species colonizing the micro-orchards over time by pooling the samples for every three-week period, eliminating species represented by singletons and calculating turnover from each block of time to the next (5 blocks of time in total). We calculated turnover as $(b + c) / (S_1 + S_2)$, where b=number of species present only in time 1 (and not in time 2), c=number of species present only in time 2 (and not in time 1), S₁=total number of species in time 1, and S₂=total number of species in time 2 (Brown and Kodric-Brown 1977, cited in Magurran 2004).

To determine if distance from the adjacent forest affected the total number of spiders colonizing the micro-orchards, we used a complete blocked analysis of variance (ANOVA, PROC GLM), with distance from forest as the independent variable, and site (position along the length of the forest) as a blocking factor. We also compared the abundance of each spider species colonizing the microorchards at the two distances using ANOVA. The Kolmogorov-Smirnov test was used to assess normality of error terms and Bartlett's test to determine homogeneity of variances. Non-parametric data were log-transformed to fit these assumptions. Statview version 5.0.1 (SAS Institute 1998) was used for these analyses.

3.3.4.2. Spider assemblages

Collections were from three habitats: the micro-orchards near (10 m) to the forest, farther (50 m) from the forest, and the forest itself. We compared the species richness and composition of the spider assemblages from these three habitats.

We used rarefaction curves to compare spider species richness between the three habitats using Ecosim version 7 (Gotelli and Entsminger 2001), calculating individual-based curves using an independent (with replacement) algorithm and 1000 iterations per level. To determine if differences in average species richness of each habitat were significant, we compared the species richness at the highest shared abundance level using the 95% confidence intervals provide by Ecosim.

To compare the composition of the spider assemblages collected from the three habitats we used non-metric multidimensional scaling (NMDS). Nonmetric multidimensional scaling is a non-parametric ordination technique that does not require linear relationships between variables (McCune and Grace 2002). Abundances were log_{10} (x+1) transformed to decrease the influence of common species. We pooled data from all collection dates and analysed sample units based on site (3 forest sites, 6 micro-orchards at 10 m, 6 micro-orchards at 50 m). To perform NMDS we ran a preliminary six-dimensional analysis (parameters: Sorenson distance measure, random starting configuration based on time of day, 100 iterations, 50 runs with real data, and 100 runs with randomized data (Monte Carlo test)). We re-ran the NMDS using the same parameters, but with the number of dimensions recommended by the preliminary run and the initial graph coordinates as the starting coordinates (McCune and Grace 2002).

To test if species composition was significantly different between the three habitats we used non-parametric multi-response permutation procedures (MRPP) (Zimmerman *et al.* 1985) on the log-transformed data, with a Sorenson distance measure to correspond with the NMDS metric (McCune and Grace 2002). We chose MRPP because it does not require that the data are distributed normally or have homogeneous variances. We grouped sample units by habitat and compared

all groups for significant differences in composition, followed by pair-wise comparisons between each group. We report the p-value of the MRPP test statistic as well as the agreement statistic (A), which describes within-group homogeneity as compared to random expectations and also describes the relative effect size (McCune and Grace 2002). PC-Ord version 4 was used for the NMDS and MRPP analyses (McCune and Mefford 1999).

The relative abundance per unit area of spider species from the field collections also was compared to those in the micro-orchards to assess if the field could be acting as a source population.

3.3.4.3. Comparing species in micro-orchards to older orchards

To compare the species assemblages found in micro-orchards to those found in orchards that had been established for a longer period of time, we used data from spiders collected from the foliage of nearby orchards (also on the Agriculture and Agri-Food Canada experimental farm in Frelighsburg) in 2004 (chapter 2). At the time of collection these orchards were about 15 years of age, covered 0.5 to 0.8 ha, and had been insecticide-free for nine years. Spiders had been collected from the bottom 2 m of orchard foliage on five occasions from mid-May to mid-August. Further details on the sampling methodology for these three orchards are in chapter 2.

We compared the species found in the orchards in 2004 to the species found in the micro-orchards. First, we compared the relative abundances of the most common ten species in the collections to determine if the most efficient colonizers were still dominant species in orchard foliage after the passage of time. Second, we assessed rank-abundance plots (Whittaker plots) of the collections (excluding singletons) to illustrate differences in the relative abundance of individuals among species (the evenness) of the collections (Magurran 2004). We also calculated Simpson's evenness index (E_{1-D}), a quantitative measure of evenness, for each habitat (Magurran 2004).

3.4. Results

In total, 3442 individual spiders, representing 44 species in 11 families, were collected in 2006: 981 spiders from the forest samples and 2461 from the micro-orchards. Raw data are presented in Appendix II. Ninety-one percent of the spiders were immature, and we identified 89% of the specimens to the genus or species level.

The rates of colonization of micro-orchards at both distances from the adjacent forest were lowest during May and June, peaked through late July and August, and decreased in late August and September (Figure 3-1). On most collection dates, there were more spiders landing on the micro-orchards 10 m from the forest as compared to spiders on the micro-orchards 50 m from the forest.



Figure 3-1: Spiders collected per m^3 of foliage in micro-orchards 10 m or 50 m from deciduous forest (sum for n=6 at each distance) over 15 weeks from June 6 until September 15, 2006, in southern Québec, Canada.

Species turnover was low, ranging from 6-16% from each three-week block to the next over the course of the summer.

There were significantly more spiders collected from the micro-orchards 10 m from the forest (mean \pm SE: 223 \pm 25, n=6), as compared to those 50 m away (mean \pm SE: 187 \pm 23, n=6) (F_(1,6)=9.8, p=0.02). When the relative abundances of the ten most common species or genera were compared, most taxa were more common in the near micro-orchards (Table 3-1).

Table 3-1: Mean number of spiders (\pm SE) (n=6) and results from analyses of variance between micro-orchard locations (10 and 50 m from the forest) in southern Québec, Canada, for the ten most commonly collected spider species and genera.

Species	10 m	50 m	F _(1,6)	р
Araniella displicata (Hentz)	59.2 ± 4.7	95.2 ± 7.0	18.0	0.002
Philodromus rufus vibrans Dondale	37.3 ± 4.1	39.3 ± 4.0	0.12	0.73
<i>Emblyna</i> sp.	32.2 ± 4.9	7.5 ± 0.7	49.2 ^a	< 0.001
<i>Theridion murarium</i> Emerton	22.0 ± 4.0	13.2 ± 2.1	3.8	0.08
Misumenops sp.	18.2 ± 2.5	9.2 ± 0.8	14.6 ^a	0.003
Eris sp.	11.5 ± 2.3	3.0 ± 0.5	27.1 ^a	< 0.001
Philodromus spp.	10.5 ± 1.1	4.5 ± 0.8	19.0	0.001
Misumena vatia (Clerck)	4.8 ± 1.2	1.5 ± 0.7	5.3	0.04
Pelegrina sp.	3.8 ± 1.2	1.8 ± 0.5	3.1	0.11
Hentzia mitrata (Hentz)	1.2 ± 0.3	1.0 ± 0.4	0.12	0.73

^a Abundances were log-transformed before ANOVA to homogenize the variances.

Immature individuals identified to genus for *Emblyna*, *Misumenops*, *Eris* and *Pelegrina* were pooled with the species from the same genus for analysis. For each of these genera only one species was commonly collected in studies in this area: *Emblyna sublata* (Hentz), *Misumenops asperatus* (Hentz), *Eris militaris*

(Hentz), and *Pelegrina proterva* (Walckenaer) (chapter 2, Bostanian *et al.* 1984; Dondale *et al.* 1979). *Araniella displicata* (Hentz) was the only spider significantly more numerous in the far micro-orchards.

Sixty-eight spiders were collected from the three field sites (total swept area= $150m^2$); the average density of spiders in the fields adjacent to the micro-orchards was 0.45 spiders/m². The spider species commonly found in the fields (i.e. $\ge 10\%$ of the collection) were *Misumena vatia* (Clerck) (25%), *Araniella displicata* (15%), *Misumenops asperatus* (10%) and immature *Tetragnatha* spp. (10%) (n=68).

Rarefied estimates of species richness showed no significant difference between forest and micro-orchards at the two distances, as there was overlap of 95% confidence intervals for samples containing 850 individuals (Figure 3-2).



Figure 3-2: Individual-based rarefaction curves depicting estimated spider species richness (SR) (\pm 95% confidence intervals) for the forest and the micro-orchards 10 and 50 m from deciduous forest in Southern Québec. Arrow indicates number of individuals at which species richness comparisons were made.

Ordination of the samples from each micro-orchard and forest site with NMDS produced a two-dimensional ordination that minimized stress (final stress=10.1) and explained 92% of the variance (axis 1: R^2 =0.547, axis 2: R^2 =0.375) (Figure 3-3). The samples clustered by habitat (forest, micro-orchards at 10 and 50 m), indicating that the composition of the spider assemblages in the samples in each location were similar to each other. Additionally, the samples from the near micro-orchards were more similar to the forest samples than those from the far micro-orchards.



Figure 3-3: Sample unit (by location) non-metric multidimensional scaling (NMDS) of spider collections from deciduous forest and micro-orchards 10 m and 50 m from deciduous forest in southern Québec. Numbers following symbols refer to site number.

Multi-response permutation procedures showed that these differences between samples based on habitat were significant (Table 3-2). Comparisons of micro-orchard samples grouped by site (1, 2, or 3), rather than position relative to the forest (i.e. habitat), showed that samples did not separate based on this grouping (A= -0.009, p=0.542).

Table 3-2: Significance and effect size (agreement statistic, A) of multiresponse permutation procedure (MRPP) comparisons of spider assemblages sampled from micro-orchards (10 and 50 m from forest), and adjacent deciduous forest in southern Québec, Canada.

Agreement statistic (A)	р
0.203	< 0.001
0.141	< 0.001
0.119	0.004
0.232	0.002
	Agreement statistic (A) 0.203 0.141 0.119 0.232

^a Samples are grouped by habitat (10 or 50 m micro-orchard, or forest).

Many of the spider species collected from the micro-orchards had been collected from the established orchards in the same area in 2004. Of the ten most common species found in the micro-orchards, nine of these were also the most common species collected from the established orchards, although the species had different relative abundances within the collections (Figure 3-4).

Additionally, the distribution of individuals among all species differed between the collections: the Whittaker rank abundance plot showed that the collection from the orchards in 2004 was more even compared to those from the micro-orchards (Figure 3-5), and the Simpson's evenness index (E_{1-D}) confirms this pattern: the evenness index for the 2004 orchard collection was higher (E_{1-D}) =0.54) than the indices from the micro-orchard samples (near E_{1-D} =0.26; far E_{1-D} =0.22).



Figure 3-4: Relative abundance (% of collection) in micro-orchards and older orchards (2004 collection) of the ten most common spider species from micro-orchard collections in southern Québec.

3.5. Discussion

The primary objective of our project was to assess how distance from a source at small spatial scales (10-50 m) affects the composition of spider assemblages colonizing available habitat, in this case, apple orchards. Our results indicated that the composition of spiders colonizing micro-orchards was affected by distance from the adjacent deciduous forest: the similarity to spider assemblages in the forest decreased in orchards 50 m from the forest, as compared to those 10 m from the forest. The rate of colonization and relative abundance of several common spiders also was lower in micro-orchards farther from the forest, but species richness was not affected. The clear change in spider composition over a



Figure 3-5: Rank abundance (Whittaker) plot of spider species (excluding singletons) from micro-orchards 10 and 50 m from deciduous forest, and collections from established orchards in 2004, in southern Québec.

40 m distance between the two sets of micro-orchards suggests the composition of dispersing spiders changes over a small spatial scale. Changes in species composition in identical habitats over a gradient of distance can be due to limitations in dispersal ability of species from one source habitat (Nekola and White 1999) and the immigration of individuals from different source habitats (Leibold *et al.* 2004). Of the ten most common spider species sampled in the micro-orchards, five had significantly lower abundances in far micro-orchards as compared to near micro-orchards, suggesting that these species are dispersal limited even over the 40-m distance further from the source habitat. Only one spider, *Araniella displicata*, was more common in the micro-orchards far from the forest compared to those near the forest. Although this spider composed a high proportion of the spiders in the fields near the micro-orchards, the densities were

low and so it is unlikely the fields were a major colonization source. The higher relative abundance in the far micro-orchards could be due either to dispersal from other patches in the area or to different interactions within the two types of microorchards.

The gradient of similarity in spider assemblages found from the forest through micro-orchards at two distances from this forest confirms that the immediate adjacent forest is likely the main source of colonists to apple orchards (Figure 3-3). Previous studies of spider assemblages in crops and adjacent habitats showed that in some cases the spider assemblages in adjacent habitat were very different from those in the crop (Bishop and Riechert 1990; Samu and Szinetár 2002), although the results from chapter 2 demonstrated that for apple orchards, adjacent habitats with similar vegetation structure and degree of disturbance have spider assemblages with the same composition as those in the orchard foliage.

Patterns of species richness and abundance of epigeic spiders in arable farmland (mostly Linyphiids) have been related to landscape elements at scales greater than the distances investigated in this study. The species richness of epigeic spiders in crop fields increases with higher landscape heterogeneity in radii ranging from 200-500 m from the crop (Clough et al. 2005; Isaia et al. 2006), and Linyphiid abundance in fields is positively correlated with non-crop habitat within 1-3 km radii (but not smaller), suggesting that habitats at long distances can act as source populations (Schmidt and Tscharntke 2005b). This study is the first to examine effects of distance on spider species composition, rather than just species richness or abundance. Although only two distances from one source habitat were examined, our results indicated that composition of spiders colonizing habitats changes over this relatively small scale and should be considered in addition to species richness and abundance when studying and modelling colonization patterns of spiders across a landscape. The degree to which more distant patches in the metacommunity contribute colonizers is an important research question that has yet to be addressed.

Our second objective was to compare the spiders colonizing the microorchards with assemblages present in the foliage of older orchards. We found that the orchards sampled for another study in 2004 had the same common spider species (9 of the 10 most abundant species were the same) as found in the microorchards in this study, but the relative abundance of collected individuals was more evenly distributed among species than in the micro-orchards (Figure 3-3). This indicates that, although dispersal from the adjacent forest is a source of species found in the orchards, local dynamics alter the composition of the spider community over time. These local dynamics may include colonizationcompetition trade-offs, which have been demonstrated for ground-dwelling spiders (Marshall *et al.* 2000). Other local dynamics may consist of differences between colonizers in relative survival to adulthood or fecundity, leading to a shift in relative abundances in subsequent generations.

Dispersal and subsequent colonization should have an important influence on spider communities in this landscape; there was a relatively high colonization rate in all micro-orchards, especially in late July and August (weeks 8 and later), when 30-40 spiders/m³/week were collected (Figure 3-1). The high rate of colonization will influence species assemblages most significantly in habitats with reduced populations of spiders from disturbances such as pesticide application or physical management techniques. Our results indicate that the species composition of the spiders colonizing these habitats will vary at a small spatial scale depending on the distance from the adjacent habitat. Additionally, although nearby forest provides a source of colonizers, local dynamics within the orchards will affect the composition of the spider assemblages over time.

3.6. Connecting Statement

Before beginning the spider collections for the survey presented in chapter 2, I knew that many of the spider specimens I would collect would be immature. When unidentifiable, immature spiders are generally not included in species level analyses of data. Whether or not the subsequent representation of spider assemblage composition is significantly altered from what is actually present in the environment is unknown. There is the risk that conclusions drawn regarding diversity and composition, both within one habitat and in comparisons between habitats, are incorrect. In chapter 4 I address this question.

Chapter 4: Relevance of collected juveniles to the analysis of spider community studies

4.1. Abstract.

Spider field collections often consist of a high percentage of immature specimens that are not identifiable to species; in many studies these juveniles are discarded and not used in analyses. To evaluate if this practice affects the results of a community study, we sampled foliage-dwelling spiders in two habitats, reared the collected immature spiders until maturity, and identified them to species. We tested if the results from statistical analyses (species richness, evenness, assemblage composition) changed with the exclusion of data from immature specimens by analyzing two datasets: one including mature spiders only, the other including both mature and immature spiders (complete dataset). Nine of the total 49 spider species were collected only as juveniles, but only one of these nine species, *Philodromus praelustris* Keyserling, was common ($\geq 10\%$ of collection). The distribution of individuals among species was more even in the complete dataset than the mature-only dataset, which could either indicate differences in composition or reflect sampling effort. However, species richness estimates were the same regardless of dataset, and there were only small changes in species composition of the samples between datasets, suggesting that there were not important compositional differences between the samples in each dataset. The inclusion of immature spiders in the data in this study yielded the same results that would occur with increased sampling effort.

4.2. Short Communication

In community studies, field collections of spiders often have a high proportion of immature spiders as compared to mature spiders: the percentage of juveniles may reach over 80% of the individuals collected (Samu *et al.* 1997; Brierton *et al.* 2003). As a result, the number of spiders that are identified to genus or species level varies; in some studies 70-80 % of all specimens are identified (Bostanian *et al.* 1984; Olszak *et al.* 1992a; Olszak *et al.* 1992b;

Brierton *et al.* 2003), whereas in others the number is as low as 20% (Mason *et al.* 1997; Samu *et al.* 1997). The accuracy to which an immature spider is identified to genus or species often depends on its family: Linyphiidae, Dictynidae, Clubionidae, and some Salticidae are the least commonly identified to species when collected as juveniles in foliage studies (Bostanian *et al.* 1984; Olszak *et al.* 1992b; Mason *et al.* 1997).

The composition of the mature spiders in an assemblage may differ from the composition of the assemblage that includes both immature and mature individuals owing, for instance, to differential mortality rates across species. Thus the exclusion of unidentified immature spiders may affect the results of analyses, both within one habitat and when comparing assemblages between habitats.

We used a study comparing spiders in orchards and adjacent deciduous forest (chapter 2) to test if the results of analyses change with the inclusion or exclusion of immature spider specimens in the data. After the collection of foliage-dwelling spiders, we reared the juveniles until maturity to allow species level identification. We analyzed two datasets: one with only spiders collected as mature individuals ("mature-only" dataset), and the other also containing the extra data obtained from the rearing and identification of immature spiders ("complete" dataset). The parameters of species richness, evenness, and community composition were calculated using each dataset and the results from the analyses were compared.

The collections of foliage-dwelling spiders were from four apple orchards and adjacent deciduous forest, sampled on three to five occasions from May to August 2004. Three orchards (A, B, and C) were in Frelighsburg (45° 03' N, -72° 50' W), Québec, on an Agriculture and Agri-Food Canada experimental farm. These orchards and their adjacent forests were sampled on 17-19 May, 7-8 June, 30 June-July 3, 19-22 July, and 9-11 August. Orchard D was an organic commercial orchard in Mt. St. Hilaire (45° 31' N, -73° 09' W), Québec, and this orchard and its adjacent forest were sampled during the last three sampling periods listed above. No insecticides had been used in any of the orchards for at least nine years. Apple trees and forest foliage were sampled by beating branches over a $1-m^2$ collecting sheet. In the Frelighsburg orchards we sampled trees from the two outer rows: 16 apple trees, 5 branches per tree, whilst in the Mt. St. Hilaire orchard we sampled interior trees, not edge trees, due to constraints from other research projects. In the adjacent forest, we sampled the foliage of two 5-m blocks along the edge (1 m into the forest). A complete description of orchard and forest characteristics was presented in chapter 2.

To include as many immature specimens as possible in the complete dataset, we used two strategies to identify these individuals. Some species were identified even when immature from non-reproductive characteristics: *Araniella displicata* (Hentz), *Enoplognatha ovata* (Clerck), *Philodromus rufus vibrans* Dondale, *Misumena vatia* (Clerck) and *Tmarus angulatus* (Walckenaer). Other immature spiders were reared individually in the laboratory on a diet of live *Drosophila* until reproductively mature and then identified. To increase rearing success during the latter portion of the study, the *Drosophila* were fed diet supplemented with ground dog food (Nutro: Natural Choice. Nutro Products Inc., CA, USA); the spiders were also fed various insects collected from outdoors. Spider nomenclature followed that of Platnick (2007), and vouchers were deposited in the Lyman Entomological Museum of McGill University (Ste.-Annede-Bellevue, Québec).

To estimate species richness in each habitat and with each dataset, we calculated individual-based rarefaction curves using Ecosim version 7, using an independent algorithm and 1000 iterations per abundance level (Gotelli and Entsminger 2001). First, we compared the estimated species richness of each habitat from each dataset. Then we assessed whether comparisons of species richness between habitats would differ depending on which dataset was used.

We compared the evenness of the individuals among species in the two datasets with Whitakker rank-abundance plots, separating the data by habitat and dataset and expressing the relative abundance (log transformed) of each species as a percent of the total abundance (Magurran 2004).

We assessed differences between the species composition of the samples based on location (A, B, C, or D), habitat (orchard or forest), and dataset (complete or mature-only). To compare samples we used non-metric multidimensional scaling (NMDS), a non-parametric ordination method that does not require linear relationships between variables (McCune and Grace 2002). We log transformed the abundance data to reduce the influence of common species, and then to eliminate the effect of different total abundances in each dataset, we expressed species abundance values as a percent of total abundance in each dataset. Both transformations and standardizations of data are acceptable before analysis using NMDS (McCune and Grace 2002). Using PCORD v. 4 (McCune and Mefford 1999), we did an initial six-dimensional analysis (parameters: Sorenson distance measure, random starting configuration, 100 iterations, 50 runs with real data, and 100 runs with randomized data (Monte Carlo test)). For the second run we altered the number of dimensions to that recommended by the preliminary run and used the graph coordinates from this preliminary run as the starting coordinates (McCune and Grace 2002).

Forty percent of the immature spiders were successfully reared. Mortality of juveniles occurred mainly during the early rearing period, when spiders were fed fruit flies without a supplemented diet (i.e. added dog food). The success rate of rearing was over 80% when spiders were fed fruit flies reared with supplemented diet.

Identifying immature spiders doubled the number of identified individuals included in the analyses from 402 to 809, and the number of species identified increased from 40 to 49. The species list and the life stage of the spiders when collected are presented in Appendix I. Of these nine species not represented by mature specimens, seven were singletons, one species, *Emblyna maxima* (Banks), was only found occasionally (12 specimens), but another species, *Philodromus praelustris* Keyserling, was one of the most common species found in the study (129 specimens).

Despite the increase in raw species richness when the complete dataset was used, rarefied estimations of species richness in each habitat (orchard and

forest) were the same when calculated using either dataset (Figure 4-1). The inclusion of data obtained from rearing and identifying immature specimens produced the same results as an increase in sampling effort would have done. When the rarefied species richness of orchard and forest were compared using the complete dataset, the forest had significantly more species than the orchard (Figure 4-1, point A). This significant difference between the species richness of the two habitats was not found from the rarefaction of data from the mature-only dataset (Figure 4-1, point B); this was due to the fewer individuals (lower sampling effort) in the dataset rather than changes in species richness estimations.



Figure 4-1: Individual-based rarefaction curves depicting estimated spider species richness (SR) (\pm 95% confidence intervals) for orchard and forest habitats in southern Québec using complete and mature-only ("mat.only") datasets. Arrows indicated species richness at which orchard and forest were compared for complete dataset (A) and mature-only dataset (B).

There was a more even distribution of individuals among species (rank abundance) in both orchard and forest habitats in the complete dataset as

compared to the mature-only dataset (Figure 4-2). These differences could either reflect compositional differences in the assemblages or lower sampling effort.



Figure 4-2: Rank-abundance (Whittaker) plot of relative abundance of spider species (log₁₀ abundance, expressed as percent of total) in orchard and deciduous forest in Southern Québec, and from complete and mature only ("mat.only") datasets.

The NMDS comparing samples from each location, habitat, and dataset produced a two-dimensional ordination (final stress=6.48) explaining 93.5% of the variation (axis 1: R^2 =0.796; axis 2: R^2 =0.139). In general, the two points from each particular habitat and location were close, indicating that the composition of the assemblages was similar regardless of dataset (Figure 4-3).

Sample points from the mature-only dataset tended to be below and to the left of all sample points from the complete dataset. This consistent shift in space suggests that there is also a consistent change in the sample composition between datasets. Since samples were standardized so there was no difference in


Figure 4-3: Sample unit (orchard or forest for each site, collection dates pooled) non-metric multidimensional scaling (NMDS) analysis of southern Québec spider collections from complete and mature-only ("mat.only") datasets. Labels following symbols indicate habitat (orchard: "orc", forest: "for") and site (A to D) of sample.

abundance between datasets, the main difference between the samples was the number of species and evenness, both of which were higher in samples in the complete dataset. Again, the different results from the two datasets appears to be because of a relative difference in sampling effort, rather than variations in species composition resulting from the exclusion of immature specimens. From the comparisons of the two datasets we suggest that for most community studies not concerned with identifying all species present, the results are the same whether or not data from immature specimens are included. Increasing sampling effort will provide the same increased precision to the analyses. The similarity /

dissimilarity of assemblages between habitats is mostly determined by the dominant species within the habitats, and these species will likely be collected as mature individuals. Rearing immature spiders also required considerable time, space, and effort. These results are important from a practical standpoint because we provide the first evidence that the results from community analyses that either include or exclude immature individuals are the same.

4.3. Connecting Statement

The results from chapters 2 and 3 show immigration from adjacent habitats influences the composition of spider assemblages in apple orchard foliage. The application of pesticides affects the ecology of many arthropods within the agroecosystem, including spiders. The impact of physical pest control methods such as kaolin clay on spider ecology is less well known.

Chapter 5 is the first of three chapters that examine the effects of kaolin on the ecology of spiders and a potential prey species, *Choristoneura rosaceana* (Lepidoptera: Tortricidae). Kaolin sprays reduce *C. rosaceana* populations and damage in apple orchards, and in chapter 5 I tested for kaolin-induced changes in larval behaviour that may contribute to the efficacy of kaolin. Prey behaviour is one factor that affects interactions between predators and prey, and pest management methods that alter pest behaviour can affect predation by natural enemies. The behavioural effects of kaolin tested for in this chapter may change the interactions of predators and parasitoids with *C. rosaceana*.

Chapter 5: Effect of kaolin on the fitness and behaviour of *Choristoneura rosaceana* (obliquebanded leafroller) (Lepidoptera: Tortricidae) larvae

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5.1. Abstract

The mechanisms by which kaolin, a clay particle film formulation, affects the fitness and behaviour of larvae of obliquebanded leafroller, Choristoneura rosaceana (Harris), were investigated. Feeding experiments tested kaolin as a physical barrier versus a physiological toxin for larvae that consumed kaolin applied either to apple (*Malus* spp.) leaves or mixed in artificial diet. Behavioural experiments tested the effects of kaolin applied to apple leaves on neonate dispersal and leaf rolling by third and fourth instars. When larvae fed on apple leaves sprayed with kaolin, mortality and time to pupation of larvae increased significantly whereas pupal mass significantly decreased. When larvae consumed kaolin mixed into an artificial diet, however, the effects on mortality, pupation time and pupal mass were negligible. There may be minor physiological effects from consumption because male time to pupation was delayed for larvae fed diets containing the highest concentration of kaolin. In behavioural experiments, neonate larvae dispersed more quickly off plants covered with kaolin than control plants, and kaolin delayed the construction of leaf shelters by third and fourth instars. We showed that the effects of kaolin on C. rosaceana larvae are primarily physical, causing changes in dispersal and rolling behaviours and as a physical barrier to feeding.

5.2. Introduction

Obliquebanded leafroller, *Choristoneura rosaceana* (Harris), (Lepidoptera: Tortricidae), has been considered a secondary pest in apple (*Malus* spp.) orchards for much of the history of fruit crops in North America. Since the late 1970s, however, increasing numbers of leafrollers and increasing apple

damage have been observed in fruit growing regions of Canada and the northern United States (Reissig 1978). Although there are multiple factors associated with the increased pest status of *C. rosaceana*, increased populations and fruit damage have been correlated with resistance and cross-resistance to various families of insecticides, including organophosphate, carbamoyl oxime, pyrethroid insecticides, and benzoylhydrazine insect growth regulators (Reissig *et al.* 1986; Pree *et al.* 2001; Smirle *et al.* 2002).

In this study, we investigate a cost-effective, non-chemical option for C. rosaceana control: a fine particle spray of kaolin clay. Kaolin is a white, nonabrasive aluminosilicate clay processed for agriculture and marketed as "Surround WP" Crop Protectant. Kaolin is a promising method of control for different types of orchard pests; studies have shown it effectively reduces damage on fruit by codling moth Cydia pomonella (L.) (Unruh et al. 2000), fruittree leafroller, Archips argyrospilla (Walker) (Knight et al. 2001), Mediterranean fruit fly, Ceratitis capitata (Wiedemann) (Mazor and Erez 2004), pear psylla, Cacopsylla pyricola Foerster, and pear rust mite, Epitrimerus pyri (Nalepa) (Puterka et al. 2000). Knight et al. (2000) found that kaolin reduces the overwintered population of C. rosaceana larvae when applied in apple orchards before bud break; they reasoned that kaolin affected the movement of larvae from their overwintering sites to new foliage. They also investigated the effect of kaolin on larvae when fed apple leaves treated with a kaolin formulation and found that both pupation success and mean pupal mass decrease (Knight et al. 2000). However, the mechanisms underlying the observed effects of kaolin on obliquebanded leafroller in the orchard and in feeding experiments have not been determined. For effective use of the clay as a method of control, it is important to know the mechanisms by which it affects the target organism. Therefore, in this study we investigate what physiological and behavioural changes larvae exhibit when they consume or are exposed to kaolin.

Kaolin is hypothesised to function largely as a physical barrier or irritant (Glenn *et al.* 1999), but the possibility of toxicity to insects, including *C*. *rosaceana* larvae, by ingestion of the kaolin along with plant tissue has not been

studied. To investigate for physiological effects, we compared the fitness of larvae, as measured by development time and pupal mass, in two feeding trials: kaolin fed to C. rosaceana larvae mixed in artificial diet, which eliminates physical barrier effects of the compound, versus kaolin sprayed on apple leaves. Additionally, we studied the effect of kaolin on the dispersal and establishment of C. rosaceana to determine any mechanisms by which kaolin may affect these behaviours. The movement and dispersal of C. rosaceana larvae occur typically for the spring generation when overwintered larvae move from their hibernacula beneath the bark to colonize newly flushing leaves, and for the summer generation when neonates disperse from the egg masses. Larvae of both generations will also move regularly during their development as they vacate old leaf shelters and form new ones (Waldstein et al. 2001). These periods of movement and dispersal, when larvae are outside protective leaf shelters, are opportune windows for control. In these experiments, we tested the effect of kaolin on the behaviour of C. rosaceana larvae during key life stages when there is the most movement and thus control may be most feasible: neonate dispersal and establishment of leaf shelters by overwintering third and fourth instar larvae.

This study is organized into two parts. The first two experiments examine how kaolin in the diet affects *C. rosaceana* larvae: the fitness of *C. rosaceana* larvae was compared when larvae were fed diets of either (1) apple leaves sprayed with or without kaolin or (2) kaolin mixed in artificial diet or artificial diet alone. The second two experiments investigate the effects of kaolin on the behaviour of (1) neonates and (2) third and fourth instars.

5.3. Materials and Methods

5.3.1. Laboratory rearing of C. rosaceana

All experiments used larvae obtained from a laboratory colony of *C*. *rosaceana* originally collected in 2002 from apple orchards in Southern Québec, Canada. Larvae were reared in 30-mL plastic cups on an artificial pinto-bean based diet (Shorey and Hale 1965) at 22°C and a photoperiod of 16:8 (L:D) h. Larvae in the laboratory experiments were also fed this diet and reared under these conditions.

5.3.2. Experiment 1: Kaolin in artificial diet

Five artificial diet treatments, a control and four concentrations of kaolin (Surround WP: Engelhard Corp., NJ, USA) were prepared. Kaolin was mixed into the diet before solidification at the following concentrations: 8, 25, 40, and 60 g/L diet. Because higher concentrations of kaolin are not easily dissolved into the diet, 60 g/L was the highest concentration used. Ten-millilitre aliquots of each treatment diet were put into 30-mL plastic cups, 50 replicate cups per treatment. One *C. rosaceana* neonate was placed in each cup. Larvae were randomly chosen from two egg masses and distributed so that each treatment received an equal number of larvae from each egg mass. Larvae were reared undisturbed until pupation, and mortality, time until pupation, pupal mass, and sex were recorded.

5.3.3. Experiment 2: Kaolin applied to apple leaves

Fresh apple leaves (McIntosh) were sprayed with water (control), 30 or 60 g/L solutions of kaolin in water (concentrations recommended for field use). Once dry, 2.5 cm diameter disks were cut out of the leaves using a cork borer, and disks were put into 30-mL cups containing 5 mL of agar, with 60 replicates per treatment. The agar maintained humidity in the cups; the larvae did not consume it. At the beginning of the experiment, one *C. rosaceana* neonate was placed in each cup; larvae were randomly chosen from two egg masses and distributed equally among treatments. Every two-to-three days, new leaf disks from freshly collected leaves were cut, sprayed, and added to the cups, while old leaf disks were removed. Larvae were reared until pupation, and mortality of larvae, time until pupation, pupal mass, and sex were recorded.

5.3.4. Experiment 3: Kaolin and neonate dispersal

The experiment used terminal branches bearing five leaves, cut from small potted apple trees (McIntosh) that had been sprayed with either water (control) or

a kaolin solution (60 g kaolin/L water). Twenty trees were sprayed for each treatment. In the laboratory, experimental branches were placed in 30-mL glass vials with water and arranged in a grid pattern that alternated control and kaolin branches. Branches were placed 30 cm apart. Five *C. rosaceana* neonates were placed on each experimental branch, one on each leaf. Newly hatched larvae from two egg masses were used and evenly distributed so that each treatment received an equal number of larvae from each egg mass to avoid variation in dispersal behaviour of neonate *C. rosaceana* associated with larval age and family (Carrière 1992). After three time periods - 1, 3.5, and 21 h, the larvae remaining on the branches were counted by inspecting the leaves. Additionally, the position of the larvae was recorded as either on the leaf or hanging. Larvae were often found hanging from the leaf by a silk thread, or would drop off the leaf and hang in response to the movement of the branch when being inspected.

5.3.5. Experiment 4: Kaolin and rolling behaviour of larvae

The study occurred in an orchard of 15-year-old McIntosh apple trees on the Agriculture and Agri-Food Canada experimental farm of Frelighsburg (45° 03' N - 72° 50' W), QC, Canada. The trees had been treated with fungicides during the spring but no insecticides had been used. Trees used in the experiment were in the interior of the orchard, and treatments were paired on a given tree. Experimental trees were selected based on the presence of two branches with terminal leaf whorls bearing leaves at a similar stage of expansion, at a height of 1.5 to 2 m from the ground, and all branches were on the same side of the tree (facing north-northwest). Two replications of the rolling experiments were done, one during 12-13 June 2003 and the second during 20-22 June 2003, by using third and fourth instars of *C. rosaceana* larvae, respectively. Larval instars were determined using head capsule width. There was no precipitation during the experimental periods.

A 48 g/L kaolin solution (treatment) or water (control) was applied to the tree using a Stihl BR 420 backpack sprayer at a rate of 1.4 L/min for 30 s. Branches from one treatment were covered with a plastic bag when the other

treatment spray was applied to prevent contamination. After the leaves had dried, spherical wire cages were placed over the branch terminals and muslin was placed over the cage to prevent larvae from escaping from the experimental branches. The cages were flexible to allow positioning around the branch, thus preventing the leaves from touching the muslin and the cages were about 20-25 cm in diameter and about 30-35 cm long.

Early third or fourth instars of *C. rosaceana* were placed on the caged branches one day after the spray treatments. One larva was placed on the upper surface of the smallest leaf of each of the leaf whorls at midday. Larvae were monitored four times over a period of 20 h after initial larval placement: during the first replication of the experiment at 2, 4, 6, and 18 h, and during the second experiment at 2.5, 5, 7.5, and 20 h. During these monitoring periods, if a larva had fallen onto the mesh on the inside of the cage it was placed back onto the smallest leaf of the leaf whorl. The number of larvae fallen onto the mesh was recorded at each time.

At each monitoring period, the larva was categorized as "fallen" if it had fallen off the plant onto the inside of the mesh, "non-rolling" if it was on the plant but had not begun to construct a leaf shelter, or "rolling" if it was in the process of constructing or had constructed a leaf shelter. Larvae were considered to be in the process of constructing a leaf shelter if there were multiple silken strands laid out, even though the shelter could take several more hours to complete. A leaf shelter includes any of the myriad of structures that leaf-rolling caterpillars construct from leaves, i.e. two leaf surfaces webbed together, a shelter made from the edges of leaves pulled up towards the midrib of the leaf, or a leaf roll at the edge of the leaf.

5.3.6. Statistical Analyses

SAS version 8 (SAS Institute 2000) was used for all statistical analyses.

Experiments 1 and 2 (feeding experiments): Male and female pupal data were analyzed separately. Pupal mass data were analyzed using analysis of variance (ANOVA) (PROC GLM), whereas time-to-pupation data had a non-

parametric distribution and so was analyzed using the Kruskal-Wallis test. In significant ANOVA tests, differences between treatment means were compared using the Bonferonni test (α =0.05). For significant Kruskal-Wallis tests, means were determined to be significantly different when there was no overlap of the 95% confidence intervals.

Experiment 3 (neonate dispersal experiment): Because the data were non-parametric, they were analyzed using the Kruskal-Wallis test. As in experiments 1 and 2, means were determined to be significantly different when there was no overlap of the 95% confidence intervals.

Experiment 4 (third and fourth instar rolling experiments): Data for third and fourth instars were pooled because there is no evidence that the instars behave differently. Data were analyzed using two-way contingency tables and Fisher's exact test to compare between the treatments (control and kaolin) at each time period the proportions of larvae (1) with rolls or without rolls, and (2) larvae fallen onto the mesh versus larvae still on the leaf.

5.4. Results and Discussion

5.4.1. Kaolin feeding experiments

The feeding experiments (1 and 2) demonstrate that kaolin's physical barrier effects are the main cause for reduced fitness of larvae. In experiment 1, the time to pupation and pupal mass of female *C. rosaceana* were not significantly different between the control or kaolin treatments of any concentration (time to pupation: H₄=7.5, n=111, p=0.11; and mass: F_{4,106}=0.72, p=0.58) (data not shown). For male pupal mass there were no significant differences between treatments because the ANOVA of all treatments was marginally non-significant (mass: F_{4,109} =2.44, p=0.051). Male *C. rosaceana*, however, took significantly longer to pupate for larvae on the highest kaolin dose as compared to the control (time to pupation: H₄ =13.29, n=114, p=0.01). Mixing kaolin with artificial diet was intended to remove any effects of a physical barrier that kaolin may have but still allow monitoring of effects when kaolin is ingested and indicate whether there are obvious physiological effects. Because consumption of artificial diet

was not measured, we cannot definitively say that there were no effects of kaolin in artificial diet on larvae because our experiments were not designed to detect compensatory feeding. Indeed, our experiments indicate there may be some physiological effects at high concentrations of kaolin, because male C. rosaceana larvae fed the highest kaolin dose in artificial diet took significantly longer to pupate than larvae on control diet, and male pupal masses were close to being significantly different from larvae reared on control diet. Males are on average smaller than females, which could render them more vulnerable to any physiological effect of the kaolin and could explain the different effects due to sex seen in this experiment. No physiological effects of kaolin on insects have been reported in the literature, but clays are well known to have adsorptive qualities when ingested by mammals and birds (Wilson 2003) and potential physiological effects from consumption of kaolin could include binding to toxins, proteins or salts in the gut. The mortality of larvae fed diets containing kaolin were within 2% of the control, with the exception of the highest kaolin dose (60 g/L) for which there was 18% mortality compared to 6% in the control; the 8 g/L kaolin diet had a relatively high mortality with 12% of larvae. The differences in percent mortality cannot be tested statistically to determine whether the variation is random or due to effects of kaolin.

In experiment 2, the time to pupation and pupal mass of larvae were clearly affected by kaolin when applied to the surface of apple leaves. Mortality of larvae increased as the kaolin dose applied to the leaves increased (Figure 5-1A). For both male and female *C. rosaceana*, the kaolin treatments of 30 and 60 g/L significantly decreased the average pupal mass, while the 60 g/L spray resulted in an increased time to pupation for the larvae as compared to the control (Figure 5-1B and C) (pupal mass: $F_{2,73}$ =46.0, p < 0.0001 (male); and $F_{2,63}$ =74.8, p < 0.0001 (female); time to pupation: H₂=9.2, n=76, p=0.01 (male) and H₂=26, n=66; p < 0.0001 (female)). Knight et al. (2000) found similar trends for mortality and pupal weight when larvae were fed leaves sprayed with kaolin, but the mechanism of these effects were not determined. These findings are in contrast with the results of experiment 1, where kaolin mixed with artificial diet

caused minimal effects on mortality, time to pupation and pupal mass. Our experiments are the first to demonstrate that that the physical barrier is one of the major mechanisms of action of kaolin for larvae feeding on sprayed apple leaves: kaolin directly hinders consumption of leaf material and, additionally, this physical barrier effect could also inhibit any compensatory feeding behaviour that may occur. However, our results also indicate there may be some physiological effects of kaolin because males fed kaolin in artificial diet took longer to pupate than males on control diet. Further investigation on a finer scale is needed to determine whether or not kaolin has subtle effects on larval physiology.



Figure 5-1. Mortality (A), pupal mass (B), and time to pupation (C) of *C*. *rosaceana* larvae reared on apple leaves sprayed with kaolin. For B and C, bars represent mean values \pm SE. Means were compared within sexes and bars beneath different letters are significantly different at p=0.05 (n=60).

5.4.2. Effects of kaolin on larval behaviour

The striking barrier effect of kaolin on larval feeding leads to the question of how kaolin will affect the behaviour of larvae. In experiment 3, 86 out of the initial 200 neonates placed on branches of both treatments were found at the first monitoring period (1 h). This number of neonates found on all branches remained relatively constant through the remaining two times: there were 80 larvae found on all branches at time two (3.5 h), and 86 larvae found on all branches at time three (21 h). The initial loss of about 120 larvae from the experiment was probably due to immediate loss of larvae from plants by dropping onto the table. After 1 h, the number of larvae on control and kaolin plants was not significantly different, but neonates placed on apple branches sprayed with kaolin exhibited a tendency to drop more frequently off the plants; there were significantly more larvae hanging from the kaolin leaves than from the control leaves (H₁=9.65, n=40, p=0.002) (Figure 5-2A).



Figure 5-2. Neonates hanging from the branches (A) and total number of neonates on branches (including larvae hanging from the branches) (B). Means \pm SE are presented, and within each time period bars with different letters are significantly different at p=0.05 (n=20).

For subsequent time periods, there was no difference in number of larvae hanging from the plants, but there were significantly more neonates on control branches as compared to kaolin branches: after 3.5 h, there were approximately twice as many larvae on control branches than kaolin branches (H₁=9.64, n=40, p=0.0019), and

after 21 h this difference had increased to almost five times more larvae on control branches than kaolin branches (H₁=22.08, n=40, p < 0.0001) (Figure 5-2B). Because the number of larvae observed during the three time checks remained almost constant, it seems the larvae would drop from the kaolin branches, and either crawl to adjacent plants or drift to adjacent plants, eventually settling on control branches. These results are relevant when the dispersal of second generation C. rosaceana larvae is considered: eggs are laid in masses that contain hundreds of eggs, and the larvae, upon hatching, leave the nest and either crawl to an adjacent leaf, drop down from the plant on silk to a nearby leaf, or if there are air currents they balloon away from the egg mass (Chapman and Lienk 1971). Plant characteristics associated with the propensity of neonates to balloon are not linked to plant water content or leaf age but may be associated with leaf texture (Carrière 1992; Zalucki et al. 2002). Leaf texture is one plant character that is altered by kaolin; others may include microhabitat (light and humidity) and obstruction of surface chemicals, which may also affect neonate behaviour. The net movement of larvae from kaolin to control branches, either by crawling or by ballooning to an adjacent plant, suggests that neonates on kaolin plants are more likely to drop off the plant than those on unsprayed plants. An increased rate of dropping or ballooning off plants covered with kaolin will increase the risk of mortality of the neonates in the field, as ballooning likely causes high mortality of neonates (Zalucki et al. 2002). In addition to increasing neonate mortality during dispersal, kaolin may also negatively affect other factors involved in successful establishment. Unruh et al. (2000) found that kaolin reduced the distance travelled by codling moth neonates on apple shoots and also reduced larval ability to locate and penetrate the fruit. A similar phenomenon could be expected with neonate C. rosaceana.

In experiment 4, for the 20 h that the larvae were monitored, a significantly higher proportion of larvae on control branches had initiated construction of a leaf shelter compared to larvae on kaolin branches (Table 5-1). The initiation of a leaf roll was faster for larvae on control branches, because after the first monitoring period 78% (21/27) of larvae on control branches had begun

building a leaf shelter, compared to 29% (8/28) of larvae on kaolin branches (p=0.0004). After the final monitoring period (18-20 h) the difference was still significant, with 100% of control larvae having formed leaf shelters, and 75% (21/28) of kaolin larvae (p=0.0102). It is possible that if the larvae were followed for a longer period, the difference in proportions of leaf shelters between treatments would become insignificant. There were no significant differences between the control or kaolin treatment at any time in the number of larvae dropping off the branch onto the mesh. Our results indicate that kaolin delays leaf shelter formation for at least 20 h, but it may not decrease shelter construction over a longer period. However, the significant delay in the construction of leaf shelters may affect the fitness of larvae. In orchards, there are an array of parasites of *C. rosaceana* larvae (Li *et al.* 1999; Vakenti *et al.* 2001; Wilkinson *et al.* 2004) and generalist predators (T.E.S. pers. obs., Bostanian *et al.* 1984); the increased time period during which larvae are exposed will increase their chance of being preyed upon by natural enemies.

	Control		Kac	olin	
Monitoring period	Non rolled	Rolled	Non rolled	Rolled	Fisher's exact test p-value
1	6	21	20	8	0.0004
2	2	25	12	16	0.0043
3	1	26	11	17	0.0023
4	0	27	7	21	0.0102

Table 5-1. Number of third and fourth *C. rosaceana* larvae with (rolled) or without (nonrolled) shelters (control n=27, kaolin n=28).

Our results have relevance to the use of kaolin to control *C. rosaceana* in the field. Because kaolin delays the leaf rolling behaviour of third and fourth instars, it could affect the establishment of the overwintering generation when they colonize new foliage in the spring. Knight *et al.* (2000) found that in the

field when kaolin was applied to the trees before bud break (in late March) there were fewer larvae (from the overwintering generation) present in early May, but that later sprays, just before bloom and petal fall, did not reduce the numbers of larvae. Our study indicates that kaolin can also be effective just after bud break, affecting the larvae when they are initially colonizing the foliage. Kaolin sprays to control the spring generation should therefore target the period from before bud break, when larvae are leaving their hibernacula (Knight *et al.* 2000), but can also continue into the first stages of leaf flushing when larvae are establishing their initial leaf shelters.

Our results indicate that kaolin affects the behaviour of C. rosaceana larvae and thus may subsequently affect the fitness of the larvae. When kaolin is applied to apple leaves, the main mechanism of action is as a physical barrier, increasing the developmental time of the larvae and decreasing pupal mass. Kaolin also affects the dispersal behaviour of neonates and delays leaf shelter construction by third and fourth instars. Although it is worthwhile to apply kaolin in the spring in conjunction with its use to control other early season pests, it may be difficult to quantify the relationship of the control of the spring generation of C. rosaceana with population size or damage by the summer generation (Reissig 1978). The application of kaolin during neonate dispersal of the summer generation of C. rosaceana also will be an effective time to control the leafroller. The neonate life stage is a crucial opportunity for control of *C. rosaceana*, because early life stages are vulnerable to a variety of mortality-causing factors (Zalucki et al. 2002), and the successful establishment of neonate herbivores is a crucial factor in determining subsequent population dynamics (Cornell and Hawkins 1995). Our experiments have clearly shown that neonate establishment is negatively affected by the presence of kaolin. Additionally, kaolin has been found to deter ovipositing by female C. rosaceana (Knight et al. 2000); thus, the periods of ovipositing and neonate dispersal should be targeted for kaolin application.

5.5. Connecting Statement

The results from chapter 5 show that kaolin delays the establishment of *C*. *rosaceana* larvae, both neonates and mid-instars, on apple leaves. The increased exposure of the larvae may render them more vulnerable to predation. In chapter 6 I test this hypothesis by comparing the predation rate on larvae by spiders in the common family, Salticidae (jumping spiders), on kaolin-treated and un-treated apple leaves. I also characterize the functional response of salticid spiders to various densities of *C. rosaceana* larvae.

Chapter 6: Predation of salticid spiders on neonate *Choristoneura rosaceana* (Lepidoptera: Tortricidae) and a test for indirect effects of a kaolin particle spray

6.1. Abstract

Pesticides may indirectly affect arthropod communities by changing interactions between predators and prey. Sprays of kaolin clay are used for controlling multiple pests in apple orchards, and their direct negative effects on pests have been demonstrated. Kaolin affects the behaviour of Choristoneura rosaceana larvae by slowing their establishment of protective leaf shelters. We test the hypothesis that this increases the predation risk of the larvae by characterizing the predation by the salticid spiders, *Eris* sp. and *Pelegrina* sp., on C. rosaceana larvae. First, we determine the functional response of the salticids to changing densities of neonate C. rosaceana. We then test if predation rate at one density of neonates changes if kaolin has been applied to the apple foliage. The salticids exhibit a type II functional response to changing densities of C. rosaceana neonates, although they often consume multiple larvae simultaneously. In mesocosms containing apple seedlings (8-10 leaves), kaolin on the foliage does not change the predation rate by a salticid spider. Although kaolin may delay the establishment of neonates on the apple foliage, there is no increased predation by salticids, possibly due to modulation of the interactions by the three-dimensional complexity of apple foliage.

6.2. Short Communication

Indirect effects of pesticides on arthropod communities are common, although most testing of chemicals is still for direct effects on individual species (Rohr *et al.* 2006). A potential indirect effect of pesticides is to change interactions between predators and their prey. For example, insecticides may increase predation by delaying prey development and prolonging vulnerable stages (Rohr *et al.* 2006), or through altering prey behaviour (Schulz and Dabrowski 2001; Fleeger *et al.* 2003).

Particle spray formulations of kaolin clay reduce arthropod pest populations in crops by altering behaviours such as ovipositing or feeding rate (Lapointe 2000; Unruh et al. 2000; Puterka et al. 2005). In apple orchards, kaolin sprays reduce populations of and damage by the larvae of *Choristoneura* rosaceana (Harris) (Lepidoptera: Tortricidae). Kaolin on foliage delays larval development (Knight et al. 2000), and increases the time it takes for larvae to establish protective leaf-shelters (chapter 5). Kaolin may indirectly increase the incidence of predation on the larvae through these changes in prey behaviour. However, insecticides can induce changes in predator behaviour as well by causing active avoidance of insecticide residues, resulting in reduced predation (Singh et al. 2001). We used the model system of salticid spiders (jumping spiders) preying on *C. rosaceana* larvae to test if kaolin indirectly affects interactions between predators and prey. Spiders are dominant generalist predators in apple orchards (Dondale *et al.* 1979; McCaffrey and Horsburgh 1980) and will feed on *C. rosaceana* larvae (Miliczky and Calkins 2002); predation by insects and spiders reduces C. rosaceana larval populations by 21-35% in orchard plots (Sarvary et al. 2007). The juveniles of two salticid species, Eris militaris (Hentz) and Pelegrina proterva (Hentz) are abundant in orchards in July (T. E. Sackett pers. obs.), concurrent with the hatching and development of the summer generation of C. rosaceana. The objectives of this study were to measure the predation rate of salticids on varying densities of larvae, and assess whether or not kaolin affects predation rate at one particular density.

Preliminary feeding experiments had shown no difference in predation rate of *C. rosaceana* by two salticid species, *Eris* and *Pelegrina* (data not shown). We collected immature *Eris* and *Pelegrina* spiders, 2-3 mm in length (head to spinnerets) from unsprayed apple orchards in Frelighsburg (45° 03' N, -72° 50' W), Québec, Canada, within 48 hours of beginning the experiments. The spiders were kept in test tubes with a moistened cotton plug, kept at ~22° C, and each fed one fruit fly at about 18h00 on the day before experimentation. Experiments were conducted during the day (beginning 9h00) because salticids are diurnal. Experiments used neonate *C. rosaceana* from a laboratory colony originally

collected in 2002 from apple orchards in Southern Québec. Larvae were reared in 30-mL plastic cups on an artificial pinto-bean based diet (Shorey and Hale 1965) at 22°C and a photoperiod of 16:8 (L:D) h.

In a first experiment we measured the number of larvae consumed by salticid spiders over a series of prey densities, i.e. the functional response (Holling 1966). Most invertebrate predators, including spiders, exhibit a type II functional response (Wise 1993), where attack rate remains constant regardless of prey density; prey consumption increases with increases in prey density, and the proportion of prey eaten decreases (Holling 1966; Juliano 2001). For data to fit this type of response, handling time of prey is constant, and the predator is assumed to eat one prey at a time (Juliano 2001). Salticids will attack and feed upon multiple *C. rosaceana* neonates simultaneously (T.E. Sackett, pers. obs.). As a result, the attack rate might increase as a function of prey density, producing a type III functional response where the proportion of prey eaten initially increases with prey density (Juliano 2001).

To determine the functional response of salticids to *C. rosaceana* neonates, we established five density treatments: 10, 20, 40, 70, and 100 larvae (n=5). Larvae were placed on one apple leaf in a 96-mL solo cup. One salticid spider (*Eris* or *Pelegrina*) was randomly placed in each of the cups, and after 7.5 h, the spiders were removed and remaining larvae counted. Larvae had established shelters on the leaves after this 7.5-hour period and were no longer being eaten by the spiders. We determined the type of functional response using logistic regression to fit an equation to the response curve of proportion of prey eaten versus prey density (PROC CATMOD) with SAS Version 8 (SAS Institute 2000). If the linear term is significantly less than zero (i.e. the proportion of prey eaten decreases with increased prey density), this indicates a type II response; if it is significantly greater than zero, it is a type III response (Juliano 2001).

We found that as prey densities increased, the number of prey consumed increased, but the total proportion of prey eaten decreased (Figure 6-1). No partially consumed larvae were found.



Figure 6-1: Number (A) and proportion (B) of *C. rosaceana* neonates eaten by salticid spiders at different densities of neonates (n=5 for each density).

The linear term of the function was significantly less than zero ($X^{2=}12.7$, p=0.0004) indicating a type II functional response. Despite the consumption of multiple larvae simultaneously by the spiders, the attack rate remained constant regardless of prey density. Density-dependent responses of spiders to prey are uncommon, and when observed are likely due to increasing prey activity rather than a modification of hunting strategy by the spiders (Wise 1993).

To evaluate whether kaolin affected the predation by salticids on *C*. *rosaceana* neonates, we used mesocosms that contained apple seedlings, as habitat complexity modulates interactions between predators and prey (Huffaker 1958; Price *et al.* 1980). We used only one density of neonates, as more than one density of prey was not required to detect interactions between kaolin and predation rate.

Forty-four apple seedlings (McIntosh) were grown from seed for two months in 10-cm square pots in a growth chamber and greenhouse. Before the experiment, the seedlings were pruned to 15-17 cm high, each with 8-10 leaves. Half of the seedlings were sprayed with a 60 g/L kaolin solution until dripping, at a rate of 3.2 L/min from a 1.5-m distance. The remaining seedlings were sprayed with water. After drying, the seedlings were placed in cylindrical enclosures 27.5 cm high, 13.5 cm diameter, with clear plastic sides and a mesh top. The mesh was permeable to neonates but not to spiders.

One hundred *C. rosaceana* neonates, newly emerged from egg masses, were placed on the top three leaves of each of the seedlings in four treatments (n=11): (1) control, (2) kaolin, (3) control + spider, and (4) kaolin + spider. The spider was added immediately after the neonates.

The enclosures were left for 48 hours, after which the spider was removed, and the remaining *C. rosaceana* larvae were counted by examining the enclosure and all leaves and stems of the seedling under a dissecting microscope. The number of larvae remaining was analysed using a two-factor analysis of variance (PROC GLM), with kaolin and spider presence as factors. Post-hoc Tukey tests were used to determine significant differences between treatment means. Statview version 5.0.1 (SAS Institute 1998) was used for analysis.

In the seedling experiments, the presence of the spider in the enclosure significantly reduced the number of neonates established on the seedlings by almost half ($F_{(1,40)}=32.7$, p < 0.0001), but the presence of kaolin spray did not affect the number of neonates ($F_{(1,40)}=0.013$, p=0.91) or interact with the spider treatments ($F_{(1,40)}=0.002$, p=0.96) (Figure 6-2). Previous behavioural experiments with neonates on kaolin-treated apple seedlings showed that kaolin

caused the neonates to drop off the plants and disperse away from the plant more often than on control plants (chapter 5). For lepidopteran larvae this dropping behaviour is characteristic of the initiation of aerial ballooning; after dropping, the larvae are caught in a wind current and carried away from the plant (Bell *et al.* 2005). In this experiment the plastic walls of the enclosure eliminated the breezes that allow neonates to disperse. Although about 25% of the neonates crawled upwards and actively left the enclosure, this behaviour was not affected by kaolin (Figure 6-2).



Figure 6-2: Mean number of remaining *C. rosaceana* larvae on apple seedlings sprayed with kaolin (K) or with water (C), and with the addition of a salticid spider (+S). Different lower case letters above the bars indicate significantly different means (Tukey test) (p<0.05) (n=11 for each treatment).

Because the neonates were able to leave the enclosures, the reduction in neonates in the spider treatments could have been due to spider feeding but also increased escape of neonates due to the presence of the spider. Trait-mediated effects, i.e. effects from changes in behaviour of the prey rather than direct predation, have been observed in other systems as the insect avoids or drops off the substrate in response to the presence of the spider (Mansour *et al.* 1981; Gastreich 1999).

The common salticids from apple orchards, *Eris* and *Pelegrina*, will prey upon higher numbers of neonates as densities increase, but, although they consume multiple larvae simultaneously, the attack rate remains constant. Although kaolin delays the establishment of shelters by neonates on apple leaves (chapter 5), this does not affect the predation of larvae by salticid spiders.

6.3. Connecting Statement

The laboratory experiments in chapters 5 and 6 indicated that although kaolin affected the behaviour of *C. rosaceana* larvae, it did not change the predation of salticid spiders on neonate larvae. In the field experiments presented in chapter 7 I test the direct effects of kaolin on populations of spiders and other generalist predators in apple orchards, as well as on the rate of parasitism of *C. rosaceana* larvae.

Chapter 7: Effects of kaolin on the composition of generalist predator assemblages and parasitism of *Choristoneura rosaceana* (Lepidoptera: Tortricidae) in apple orchards

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7.1. Abstract

In three apple orchards, we tested how the hydrophilic kaolin clay particle film Surround WP affected the diversity of generalist arthropod predator assemblages in orchard foliage and the parasitism of the pest species Choristoneura rosaceana (Harris) (obliquebanded leafroller) (Lepidoptera: Tortricidae). In two orchards, kaolin was applied to orchard foliage once a week for four weeks, between mid-June and mid-July in 2004 and 2005. In the third orchard kaolin was applied to foliage twice over two weeks in June 2004. We quantified the proportion of larvae C. rosaceana parasitized, larval populations, and the relative abundance and assemblage composition of generalist predators (spiders and insects) in the orchards. Kaolin altered the species composition of the generalist predator assemblages and reduced the relative abundances of certain generalist predators, most notably jumping and crab spiders (Salticidae and Philodromidae), assassin bugs (Reduviidae), ants (Formicidae), and coccinellids (Coccinellidae). In contrast, the relative abundances of web-spinning spiders (Araneidae, Dictynidae, Theridiidae) were not affected. Kaolin did not affect the proportion of parasitized C. rosaceana larvae, which ranged from 24-47% in control and kaolin treatments, or the relative proportions of parasitoid taxa. The kaolin formulation did not affect the abundance of C. rosaceana larvae, but in one orchard, kaolin did reduce the abundance of the combined numbers of C. rosaceana and another tortricid pest, Argyrotaenia velutiana. Although kaolin does not affect parasitism of C. rosaceana, it significantly changes the composition of generalist predator assemblages in orchard foliage.

7.2. Introduction

Formulations containing the aluminosilicate clay kaolin are effective at managing pests in a variety of crops (Unruh *et al.* 2000; Cottrell *et al.* 2002; Showler 2002; Saour and Makee 2004; Lapointe *et al.* 2006). In apple orchards, formulations containing kaolin can control the lepidopterans *Cydia pomonella* L. (codling moth) (Unruh *et al.* 2000), *Archips argyrospilus* (Walker) (fruittree leafroller) and *Choristoneura rosaceana* (Harris) (obliquebanded leafroller) (Knight *et al.* 2000; Knight *et al.* 2001), as well as *Dysaphis plantaginea* Passerini (rosy apple aphid) (Burgel *et al.* 2005), *Ceratitis capitata* (Wiedemann) (Mediterranean fruit fly) (Mazor and Erez 2004), and *Conotrachelus nenuphar* Herbst (plum curculio) (Thomas *et al.* 2004).

Since kaolin is a non-specific physical control method (Vincent *et al.* 2003) there may be negative effects on parasitoids and generalist predators. Knight *et al.* (2001) showed that 4-10 applications of kaolin to apple orchard foliage negatively affected densities of spiders, ants, and coccinellids, as well as reduced the rate of parasitism of the western tentiform leafminer (*Phyllonorycter elmaella* (Doganlar and Mutuura) (Gracillariidae)). In laboratory studies kaolin prevented ovipositing by the parasitoid *Diachasma alloeum* (Muesebeck) on blueberry infested by *Rhagoletis mendax* Curran (blueberry maggot) (Stelinski *et al.* 2006). The importance of parasitoids and natural enemies to pest control is well established (Stiling and Cornelissen 2005), so disruption of biocontrol agents is of concern in most agroecosystems. The effects of kaolin particle sprays on parasitoids of other pest species, as well as particular guilds and species of generalist predators, need to be examined.

We studied the effects of a hydrophilic kaolin particle spray on generalist predators and parasitism of the pest species *Choristoneura rosaceana* in apple orchards in southern Québec, Canada. *Choristoneura rosaceana* larvae are parasitized by numerous and varied species (Li *et al.* 1999; Vakenti *et al.* 2001; Cossentine *et al.* 2004; Wilkinson *et al.* 2004). Generalist predators in the orchard foliage of this area include spiders, ants, and reduviid bugs; spiders are particularly species-rich, consisting of at least 40 species, with a population peak

in mid-July (Dondale et al. 1979; Bostanian et al. 1984). Although little research has been done on the role of generalist predators in orchard biocontrol, spider assemblages have been shown theoretically and empirically to be important for biocontrol (Riechert and Lockley 1984; Riechert and Bishop 1990; Riechert and Lawrence 1997; Riechert et al. 1999; Symondson et al. 2002). We use the composition of this diverse natural enemy community as a response variable to the effects of kaolin. Kaolin disrupts the behaviour of some arthropods by physical interference (chapter 5, Stelinski et al. 2006), as opposed to having broad toxic effects, and may affect predator taxa differently depending on their foraging mode and behaviour. Hunting spiders, which are in constant contact with foliage, are more susceptible to some insecticides than web-spinners, which are provided a degree of protection by their webs (Bostanian et al. 1984; Pekár 1999b). Because major generalist predator groups (spiders, ants and coccinellids) show population decreases with kaolin application (Knight et al. 2001), we investigated if particular species, families or guilds within these arthropod groups are more severely affected than others, resulting in changes in the composition of generalist predator assemblages.

In field experiments, we applied kaolin following a program designed to control populations of *C. rosaceana*. This insect is a pest of a variety of fruit crops (Chapman and Lienk 1971), and non-chemical methods of control are needed as populations of larvae have developed resistance and cross-resistance to a variety of pesticides (Reissig 1978; Carrière *et al.* 1996; Lawson *et al.* 1997b; Waldstein *et al.* 1999; Pree *et al.* 2001; Smirle *et al.* 2002). Kaolin reduces fruit damage by summer generation *C. rosaceana* when applied for either half the season (seven applications from late March to mid-August) (Knight *et al.* 2001).

Because kaolin reduces ovipositing (Knight *et al.* 2000) and neonate dispersal (chapter 5), we applied the formulation during these life stages (coverage over four weeks, from mid-June to mid-July). We asked two questions: what is the effect of kaolin on the diversity of generalist predators in the foliage of apple orchards, and how does kaolin affect the parasitism of *C. rosaceana* larvae?

7.3. Materials and Methods

7.3.1. Orchards and kaolin treatments

The kaolin trial was done in three approximately 15-year-old orchards during 2004 and 2005. These included two orchards at the Agriculture and Agri-Food Canada Experimental Farm in Frelighsburg (45° 03' N, -72° 50' W), Québec (McIntosh, semi-dwarf root stock), and one commercial orchard near Mt. St. Hilaire (45° 31' N, -73° 09' W), Québec (Cortland and McIntosh, standard rootstock). The orchards in Frelighsburg had been free of insecticides since 1987, and no insecticides were applied during the course of the experiment, although fungicides were applied in early spring to manage apple scab. At the commercial orchard in Mt. St. Hilaire the grower had used a variety of fungicides and insecticides in recent years, but in the year of this experiment no insecticides were applied until after the experiment had finished. Effects of kaolin on generalist predators were tested in two orchards in Frelighsburg in 2004 and 2005, one orchard per year. The effects of kaolin on the parasitism of *C. rosaceana* were determined in 2004 in one orchard in Frelighsburg and one orchard in Mt. St. Hilaire.

We used a fixed-block design that alternated kaolin and control blocks to compensate for any variation in arthropod populations due to location within the orchard, and all experimental blocks were at least two rows (of trees) away from the orchard edge. In Frelighsburg, orchard F1 (2004) was 0.5 ha and was divided in 12 blocks, each with 24 trees (3 rows x 8 trees). Orchard F2 (2005) was 0.8 ha in size and was divided into 12 blocks, each with 54 trees (3 rows x 18 trees). In Mt. St. Hilaire, orchard H3 (2004) was 2 ha in size and divided into 6 blocks of 45 trees each (3 rows x 15 trees).

At each orchard, first flight of male *C. rosaceana* was detected using Pherocon II pheromone traps (Vincent *et al.* 1990). We subsequently tracked the phenology of *C. rosaceana* using a degree-day model (base 6.0°C) (Onstad *et al.* 1985), using mean daily temperatures at each orchard.

There were two treatments in each orchard, a control treatment (no spray), and a kaolin treatment, which used the hydrophilic kaolin formulation Surround WP (Engelhard Co, Iselin, NJ). In Frelighsburg, a 6 kg/100 L concentration and 1000 L/ha application rate were used, as recommended by the manufacturers. Kaolin was applied within four days of first male flight, and re-applied once per week until at least after peak egg hatch (250 DD_{6.0}). In both years this resulted in four applications: in 2004 (orchard F1), on 17 June, 23 June, 30 June and 13 July (328 DD_{6.0}), and in 2005 (orchard F2) on 23 June, 30 June, 8 July, and 15 July (390 DD_{6.0}). In orchard H3 in 2004, kaolin was applied within several days of first male flight and applied only once the following week (17 June and 23 June (140 DD_{6.0})), before peak egg hatch. This was to ensure kaolin residue would be absent on the apples at harvest, which was a major concern of the grower. Additionally, only 450 L/ha was applied ("light application") due to limitations of the grower's spraying equipment.

7.3.2. Effect of kaolin on generalist predators

Densities of generalist predators were quantified in orchards F1 and F2 in 2004 and 2005. In orchard F1 in 2004, three randomly chosen trees per block (5 branches per tree/10 beats per branch) were beaten over a 1-m² sheet, and all spiders (Araneae) were collected. There were five collection dates, one after each application of kaolin (20 June, 28 June, 12 July, 26 July), and the final collection one month after the final kaolin application (8 August). In orchard F2 in 2005, four trees per block were sampled using the same technique, but all generalist predators were counted, including spiders, harvestmen (Opiliones), beetles (Coleoptera), ants (Formicidae), stink bugs (Pentatomidae), and assassin bugs (Reduviidae). As very few spiders were found from the first three collections of 2004, in 2005 there were only two collections: immediately after the fourth and last kaolin application (25 July), and one month after this kaolin application (15 August). Insect predators were identified to family, and spiders to family and species when possible. Spiders were also divided into three age classes: spiderlings (newly hatched spiders, classified as such when less than 1.5 mm in

length), juveniles (immature spiders but not newly hatched), and adults. Since beating was the only collection method, the samples were biased towards diurnal species, as well as those found in foliage, rather than on tree bark.

Spider nomenclature follows that of the World Spider Catalog (Platnick 2007), and vouchers of spiders, insects, and parasitoids were deposited in the Lyman Entomological Museum of McGill University (Ste.-Anne-de-Bellevue, Québec).

7.3.3. Effects of kaolin on C. rosaceana parasitism

In 2004, we sampled for larval *C. rosaceana* (approximately 4th instar: 600-675 DD_{6.0}) by visually searching branches and fruit from ground height to 2m. In orchard F1, we searched 4 trees per block (6 blocks/treatment), 10 min search per tree. In orchard H3 (n=3), we searched 6 trees per block, 15 min. per tree. We counted larvae of pest species of tortricids, which included mainly *Choristoneura rosaceana* but also *Argyrotaenia velutinana* (Walker). *C. rosaceana* larvae were brought back to laboratory to be reared, species confirmed, and emergent endoparasitoids were collected. Tortricid larvae and emerging adults were identified using Chapman and Lienk (1971). Parasitoids were classified to family, and the rate of parasitism and proportion of each family were compared in kaolin and control treatments.

7.3.4. Statistical analyses

The relative abundances of generalist predators, *C. rosaceana* larvae, and the proportion of larvae parasitized, were compared between control and kaolin treatments using analysis of variance (ANOVA, PROC GLM). Relative abundance of generalist predator taxa was analyzed using raw data, unless the data for a particular group were non-normal or had heterogeneous variances, in which case they were square root transformed. To compare proportion of larvae parasitized, raw data were arcsine-square root transformed before analysis. SAS version 8 (SAS Institute 2000) and Statview version 5.0.1 (SAS Institute 1998) were used for these statistical tests. The proportions of each parasitoid order and family in kaolin and control treatments were compared using Fisher's exact tests. On-line applets with expanded contingency tables (Lowry 2006) were used for Fisher's exact tests, allowing analysis of tables with expected cell frequencies below 5, for which Chi-square analysis is inappropriate.

We used non-metric multidimensional scaling (NMDS) to examine patterns of generalist predator community composition (based on family data) and to see whether kaolin affected this composition. Data from 2004 and 2005 were analyzed separately, and samples from each treatment block and collection date were analyzed to determine if either treatment or time affected the assemblages. Non-metric multidimensional scaling was chosen over other ordination methods because it does not require linear relationships among variables, it does not limit configurations based on a predetermined model, and its distance measure can be specified (McCune and Grace 2002). We used PC-Ord version 4 (McCune and Mefford 1999) to perform NMDS using the following procedure: we ran a preliminary six-dimensional analysis to determine the number of dimensions to minimize stress (parameters: Sorenson distance measure; random starting configuration based on time of day; 200 iterations; 50 runs with real data and with randomized data (Monte Carlo test)). Using the number of dimensions recommended by the preliminary run and the saved starting configuration, we ran the NMDS again and report these results (McCune and Grace 2002).

To determine the statistical significance of the differences in predator composition between the treatments, we used non-parametric multi-response permutation procedures (MRPP) (Zimmerman *et al.* 1985), using a Sorenson distance measure to correspond with the NMDS metric (McCune and Grace 2002). Samples were grouped by treatment block and collection date, as with the NMDS. We report the p-value of the MRPP test statistic as well as the agreement statistic, A, which describes the within-group homogeneity as compared to random expectations, and reflects effect size (McCune and Grace 2002).

7.4. Results

7.4.1. Effect of kaolin on generalist predators

In 2004, 654 spiders were collected over the five sampling dates. The relative abundances of spiders in both plots in the first three sampling dates (20 June – 12 July) were several times lower than the 26 July (fourth) and 8 August (fifth) samples (Figure 7-1). There was a significant decrease in the relative abundance of total spiders in the kaolin plots after the fourth application of kaolin in July ($F_{(1,10)}=11.42$, p=0.007), but catch rates were no longer significantly lower one month after this final application in August ($F_{(1,10)}=3.8$, p=0.08) (Figure 7-1). The increase in collected spiders on 26 July was mainly due to an increase in the number of spiderlings and immature spiders, as many orchard spider species reproduce during July. On this sampling date, both spiderlings and older spiders (includes juveniles and matures) were significantly lower in kaolin plots than control plots (spiderlings: $F_{(1,10)}=4.9$, p=0.05; matures/juveniles: $F_{(1,10)}=12.6$, p=0.005).



Figure 7-1: Relative abundance of all spiders collected from orchard F1 in 2004 in control and kaolin plots (n=6) after each of four kaolin applications, and one month after the fourth application. Different letters above bars within one sampling event indicate significantly different means (p < 0.05).

Spiders were the most common generalist predators in the orchards, in both control and kaolin blocks. In 2005, from the two sampling dates pooled, spiders accounted for 59% of the total predators (total n=571) in the control treatment, and 80% in the kaolin treatment (total n=251). Ants were the second most common taxa in both treatments, accounting for 22% and 16% of individuals in control and kaolin treatments, respectively. Most other groups (harvestmen, beetles, and lacewings (Neuroptera)) accounted for less than 1% each of collected arthropods, except the assassin bugs (mainly *Zelus luridus* Stal), which were 15% of the predators in the control treatment, but less than 1% in the kaolin treatment. The last two sampling dates of 2004 (July and August), along with the samples from 2005 (July and August), were examined in more detail by determining the response of all generalist predators at the family level.

Two spider families were significantly affected by kaolin: the Salticidae (jumping spiders) and Philodromidae (crab spiders) (Table 7-1). These hunting spiders, the two most common families in the orchards, made up 55% of all spiders collected over the two years (total spiders n=1195). Fewer salticids were collected in both July and August sampling periods of both years, while philodromids were only significantly lower during July of 2004. One-third (397/1195) of collected spiders from both years were identified to species, and fifteen different species were collected from the orchards, although not all were common; eight of these species were only found in 1-2% of the collections from either treatment (Table 7-2). Since two-thirds of the spiders were not identified to species (many of the immature specimens), we did not test for statistical differences between the relative abundances of individual species in each treatment. Of the insect generalist predators, the assassin bugs had a significantly lower abundance in kaolin plots at both sampling periods, the coccinellids in the July sampling period, and the ants in the August sampling period (Table 7-1).

	July 2004		August 2004		July 2005		August 2005	
	Control	Kaolin	Control	Kaolin	Control	Kaolin	Control	Kaolin
Salticidae	$11.7 \pm 2.4a^{a}$	$5.5\pm1.2b$	$10 \pm 1.1a$	$6.3\pm1.0b$	$13 \pm 2.1a$	$6.8\pm1.4b$	$10.3\pm1.5a$	$4.7\pm1.0b$
Philodromidae	$5.7 \pm 0.6a$	$2.3\pm0.6b$	3.8 ± 1.0	3.2 ± 1.2	$3.3\pm0.9a$	$1.2\pm0.5b$	2.3 ± 0.7	1.8 ± 0.3
Clubionidae	0	0	0.2 ± 0.2	0.2 ± 0.2	0.3 ± 0.3	0.3 ± 0.2	0.3 ± 0.2	0
Thomisidae	0.2 ± 0.2	0.5 ± 0.2	0.3 ± 0.2	0.3 ± 0.2	2.2 ± 1.8	1.3 ± 1.2	1.5 ± 0.7	0.7 ± 0.3
Araneidae	1.0 ± 0.5	1.2 ± 0.6	1.8 ± 1.0	1.0 ± 0.6	4.7 ± 1.4	2.3 ± 0.8	5.3 ± 1.0	4.2 ± 0.9
Dictynidae	2.2 ± 0.6	1.2 ± 0.8	2.3 ± 0.9	2.2 ± 0.7	0.8 ± 0.5	1.3 ± 0.5	2.7 ± 0.8	1.5 ± 0.6
Theridiidae	2.3 ± 0.8	0.8 ± 0.5	1.8 ± 0.5	0.8 ± 0.3	1.8 ± 0.5	0.7 ± 0.5	1.3 ± 0.5	0.8 ± 0.3
Opilionidae	n/c ^b	n/c	n/c	n/c	0.8 ± 0.2	0.3 ± 0.2	0.3 ± 0.3	0.2 ± 0.2
Reduviidae	n/c	n/c	n/c	n/c	$6.3 \pm 1.5a$	0b	$7.5\pm0.9a$	$0.2\pm0.2b$
Pentatomidae	n/c	n/c	n/c	n/c	1.5 ± 0.6	0.5 ± 0.2	0.3 ± 0.2	0.3 ± 0.3
Formicidae	n/c	n/c	n/c	n/c	13.2 ± 4.1	4.2 ± 1.1	$7.8 \pm 2.2a$	$2.7\pm0.7b$
Coccinellidae	n/c	n/c	n/c	n/c	$0.7\pm0.2a$	0b	0.5 ± 0.3	0.2 ± 0.2
Total spiders	128	87	146	75	192	115	149	85
Total other	n/c	n/c	n/c	n/c	135	30	95	21
Grand Total	128	87	146	75	327	145	244	106

Table 7-1: Relative abundances (mean \pm SE) (n=6) and total number of generalist predators collected immediately after (July) and 1 month after (August) the final kaolin application in orchards F1 (2004) and F2 (2005) in southern Québec, Canada.

^a Means within a row (for each date) followed by a different letter are significantly different (P < 0.05, ANOVA). ^b Only spiders were collected in 2004 (other arthropods not collected (n/c)).

Family	Species	% in Control (n=226)	% in Kaolin (n=171)
Salticidae	Eris militaris (Hentz)	24	19
	Pelegrina proterva (Walckenaer)	21	12
Theridiidae	Enoplognatha ovata (Clerck)	11	16
	Theridion murarium Emerton	4	2
Philodromidae	Takayus lyricus (Walckenaer)	0	2
	Philodromus praelustris Keyserling	13	23
	<i>Philodromus rufus vibrans</i> Dondale	6	7
Thomisidae	<i>Philodromus cespitum</i> (Walckenaer)	1	1
	Bassaniana utahensis (Gertsch)	1	1
	Misumena vatia (Clerck)	1	1
	Misumenops asperatus (Hentz)	1	0
	Tmarus angulatus (Walckenaer)	0	1
Dictynidae	Emblyna sublata (Hentz)	3	7
Araneidae	Araniella displicata (Hentz)	13	8
Linyphiidae	Walckenaeria spiralis (Emerton)	1	0

Table 7-2: Spider species collected from Frelighsburg (Québec, Canada) orchards (F1 and F2) and percent composition of identified spiders from collections (2004 and 2005 combined).

Non-metric multidimensional scaling of the 2004 spider assemblage data by treatment block (n=6 for each treatment) and date (n=2) produced a threedimensional solution that minimized stress (final stress=9.8) and explained 91% of the variance. Four of the six kaolin samples from July are separated from the other samples along axis 1 (axis 1: R^2 =0.465, axis 2: R^2 =0.232) (Figure 7-2, showing two axes explaining the majority of the variance). Multi-response permutation procedures confirm that the July collections from control and kaolin


Figure 7-2: Sample unit (treatment block and date) non-metric multidimensional scaling (NMDS) of the final two spider collections from orchard F1 in Frelighsburg (Québec, Canada) in 2004. Symbols represent spider samples from control (C) and kaolin (K) blocks (n=6) in July and August.

treatments were the only assemblages that were significantly different in composition (Table 7-3).

The NMDS ordination of the generalist predator assemblages (both spiders and insects) by treatment block (n=6 for each treatment) and date (n=2) in 2005 also produced a three-dimensional solution that minimized stress (final stress=12.5) and explained 86.9% of the variance. The samples from the control and kaolin treatments from both dates are separated from each other along the two axes that explain the majority of the variance (Figure 7-3) (axis 1: R^2 =0.448; axis

2: $R^{2=}0.224$). Multi-response permutation procedures analyzing all groups indicated significant differences (p < 0.001, A=0.175), and pair-wise comparisons

Table 7-3: Effect size (agreement statistic, A) from multi-response permutation procedure (MRPP) comparisons of generalist predator assemblages sampled from Frelighsburg (Québec, Can.) orchards from control and kaolin plots in July and August of 2004 and 2005.

Groups ^a compared	Agreement statistic (A)							
Groups compared	Orchard F1 (2004)	Orchard F2 (2005)						
All groups	0.042	0.18 ^b						
C-1 vs K-1	0.11 ^b	0.12 ^b						
C-2 vs K-2	-0.0043	0.17 ^b						
C-1 vs C-2	-0.0073	0.031						
K-1 vs K-2	-0.019	0.064 ^b						

^a Groups consist of the samples from the 6 replicate blocks from each treatment and sampling date. C=control, K=Kaolin, 1=July, 2=August ^b groups are significantly different at p<0.05 (n=6)

showed significant differences in species composition between all samples, except for the control pair. The relative differences in assemblages in the control and kaolin treatments at each date were larger than the differences between the assemblages in the two kaolin treatments, as shown by the agreement statistics (effect size) (Table 7-3).

7.4.2. Choristoneura rosaceana parasitism and density

The proportion of parasitized *C. rosaceana* larvae was not affected by kaolin in either orchard F1 (four kaolin applications) or H3 (two kaolin applications). In F1, the percent parasitism was 47% (11/23 larvae) in control plots and 37% (6/16 larvae) in kaolin blocks, and there was no significant difference between the treatments (F1: $F_{(1,10)}=0.0004$, p=0.98). In orchard H3, the percent parasitism was 44% (25/61 larvae) in control blocks and 24% (17/71 larvae) in kaolin blocks



Figure 7-3: Sample unit (treatment block and date) non-metric multidimensional scaling (NMDS) of arthropod (spider and insect) collections from orchard F2 in Frelighsburg (Québec, Canada) in 2005. Symbols represent arthropod samples from control (C) and kaolin (K) blocks (n=6) in July and August.

and was not significantly different ($F_{(1,10)}=5.5$, p=0.08). Four families of parasitoids were collected: one Dipteran family, Tachinidae, and the Hymenoptera families Braconidae, Ichneumonidae, and the superfamily Chalcidoidea. There was no difference in the proportion of Diptera versus Hymenoptera in each treatment (Fishers exact test. F1: p=0.6; H3: p=1.0) or differences in the proportions of each taxa within Hymenoptera (Fisher's exact test. F1: p=0.8; H3: p=1.0).

There was no significant effect of kaolin on *C. rosaceana* populations in either orchard (F1: $F_{(1,10)}=0.88$, p=0.37. H3: $F_{(1,10)}=0.55$, p=0.50). However,

when *A. velutiana* was included in the analysis for F1, there were significantly fewer larvae of these two species in kaolin blocks as compared to control blocks $(F_{(1,10)}=6.1, p=0.033)$.

7.5. Discussion

The kaolin treatment significantly altered the species composition of generalist predator assemblages in the Frelighsburg orchards in both years and reduced the relative abundance of the most common families of spiders as well as important insect predators such as assassin bugs, ants, and coccinellids. Kaolin did not affect the overall percent parasitism, or the composition of parasitoids, of *C. rosaceana* larvae.

The community structure of generalist predators in July of both years and in August 2005 was different in kaolin plots as compared to control plots (Figures 7-2, 7-3, Table 7-3). These changes were caused by a reduction in the relative abundance of wandering generalist predators, mainly salticid and philodromid spiders, ants, and the almost complete elimination of assassin bugs in the kaolin plots (Table 7-1). The changes in the insect populations had a significant effect on the overall diversity of the assemblages: when insects are included in diversity analyses (2005 data), control and kaolin plots in both July and August are significantly different from each other. In contrast, in 2004, when only spider species were included in analyses, the assemblages were only significantly different between control and kaolin blocks in July, and not August. This may indicate a different response based on year, a higher impact of kaolin on the insect groups, or a more rapid recolonization of disturbed plots in August by spiders as compared to the other arthropods; spiders are well known to be early colonizers of disturbed habitat (Bishop and Riechert 1990). A similar decrease in spider relative abundance and diversity occurs in apple orchards treated with broadspectrum insecticides as compared to orchards under integrated or organic management (Bostanian et al. 1984; Wisniewska and Prokopy 1997; Pekár 1999a; Bogya et al. 2000).

It is not clear if the decrease in wandering predator relative abundance in kaolin plots is due to kaolin directly affecting the arthropod, its predation ability, or because of a decrease in prey. Wandering predators, characterized by continuous movement within the foliage while hunting, were adversely affected by kaolin, but no families of web-spinning spiders were significantly affected by kaolin, nor were the sit-and-wait crab spiders (Thomisidae) (Table 7-1). Laboratory studies have shown that hunting spiders are more susceptible to insecticide residues than web-spinners because of their direct contact with the substrate (Pekár 1999b). The few assassin bug nymphs found in the kaolin plots had clay particles covering the sticky hairs on their legs (T. E. Sackett pers. obs.). Spiders detect and avoid surfaces with freshly applied pesticides, although after one day this avoidance behaviour disappears, presumably because the chemical is no longer detected (Pekár and Haddad 2005). Kaolin, as a particle film, is weathered off more gradually, after one to several weeks, depending on precipitation (T. E. Sackett pers. obs.).

The reduction in spider numbers due to kaolin could carry over to the following year, as significantly fewer spiderlings (pooled from all spider families) were collected from kaolin plots than control plots. Since many generalist predators, especially spiders, reach their peak abundance concurrent with summer generation *C. rosaceana* emergence and development in mid-July (Figure 7-1), kaolin applied at this time will have a large impact on seasonal generalist predator populations. Little is known about the role of generalist predators in apple orchards, so the impact of disruption of these assemblages by kaolin is unknown; spiders likely contribute to pest control as members of natural enemy assemblages (Symondson *et al.* 2002) rather than via the actions of individual species (Riechert and Bishop 1990; Miliczky and Calkins 2002).

The rate of parasitism of *C. rosaceana* larvae in all plots ranged between 24% and 47%, and there was no evidence that kaolin affects this rate or any of the families of endoparasitoids that emerged from collected larvae. *C. rosaceana* larval parasitism has been found to be similarly high in other studies, for example, 16-60 % in British Columbia (Cossentine *et al.* 2004) and 21-37% in Michigan

(Wilkinson *et al.* 2004). Knight *et al.* (2000) found that kaolin reduced rates of parasitism of western tentiform leafminer, and ovipositing by *D. alloeum* on *R. mendax* was prevented by kaolin (Stelinski *et al.* 2006). Differences in host location strategies (Vinson 1998) as well as larval habits (degree of enclosure of larvae inside fruit, leaf mines, or leaf folds) may affect the interactions between kaolin and parasitism and explain why *C. rosaceana* parasitism was unaffected.

The kaolin treatments did not affect the densities of *C. rosaceana* larvae. In a previous study, kaolin was effective against summer generation *C. rosaceana* when 7-10 applications of the product were used (Knight *et al.* 2001). When *A. velutiana* larvae were included in the analysis of F1 data, the four applications of kaolin did lower the combined density of both these leafrollers, indicating that kaolin did affect tortricid populations.

Although kaolin is a promising method of pest control in many crops, its application to apple orchard foliage caused significant changes to the relative abundance and composition of generalist predator communities. However, the rates of endoparasitism of the leafroller *C. rosaceana* and the composition of the parasitoid taxa were not affected by the kaolin treatment.

Chapter 8: Research summary, synthesis, and future work

8.1. Introduction

One criticism of IPM research is that much effort is spent finding direct replacements for pesticides, i.e. curatives, rather than redesigning the agroecosystem so that immediate measures are not so often required (Hill *et al.* 1999). This is a valid point when considering long-term management, but the fact remains that curative control strategies for many insects are still needed (Vincent and Roy 1992; Prokopy 2003). An ecological perspective, which quantifies how communities are affected by disturbance (e.g. curatives), local dynamics such as interactions between species (predation, parasitism), and regional influences such as immigration and emigration, is essential for the effective management of an agroecosystem. In this thesis I examined the ecology of spiders and other natural enemies in apple orchards from this perspective.

8.2. Research Summary

8.2.1. Spider assemblages in orchards and adjacent habitats

In chapter 2, I explored the idea that natural habitats that were typically adjacent to apple orchards had similar spider assemblages to the orchard foliage, could they therefore act as source populations for colonization. I hypothesized (hypothesis 1, Introduction) that natural habitats that are similar with respect to two factors, vegetation structure and frequency of structural disturbance of the habitat, would also have similar spider assemblages.

Three types of natural habitat were commonly found near orchards: deciduous forest, fields, and the ecotone between the forest and fields, consisting of perennial and annual non-woody plants. At four sites within two locations in the eastern townships of Québec, I compared the spider assemblages found in orchards to these three types of adjacent habitat. As predicted, spider assemblages in deciduous forest were similar to those in nearby orchards; in three out of the four sites the composition of the collected samples from the orchard were not statistically different from the samples from the forest, as compared with multi-

response permutation procedures and non-metric multidimensional scaling (Figure 2-2). Assemblages in orchards were dissimilar to those in low-growing vegetation and field. These results indicated that orchards, as crops, do not have a specialized agrobiont fauna, but there is a correlation between spider assemblage composition and the vegetation structure and frequency of structural disturbance in the habitat.

The similarity in spider assemblage composition found between deciduous forest and orchard foliage in chapter 2 suggests that the forest is an important source population for spiders to recolonize orchards. However, these results do not demonstrate that there are spiders moving from the forest to the orchard. This issue is addressed in chapter 3.

8.2.2. Spider colonization of apple orchards

In chapter 3, I tested how distance at a small scale (10-50 m) from deciduous forest affected the rate and species composition of the spiders colonizing apple orchards. I hypothesized (hypothesis 2, Introduction) that the deciduous forest would be a source of the same spider species found in orchard foliage, but I did not expect significant differences in species composition due to these small-scale differences in distance from the source. I also compared the spider assemblages that recently colonized orchards to the assemblages found in orchards that had been established for longer periods of time (15 years). I hypothesized (hypothesis 3, Introduction) that the same species would be found in the older orchards, although the relative abundances would change over time as not all spiders have equal dispersal abilities.

I planted small orchards of young trees ("micro-orchards") at two distances, 10 m and 50 m, from deciduous forest, at three sites separated by approximately 300 m. I made weekly collections of the spiders that colonized these micro-orchards, measured their abundance, and identified them to the lowest possible taxonomic level. I also compared these assemblages to the collections made in 2004 from older orchards (chapter 2).

I found that the assemblages in the micro-orchards 10 m from the forest were more similar to the forest assemblages than the ones in the micro-orchards 50 m from the forest. The composition of the assemblages in these three habitats were significantly different from each other, indicating that the composition of the spiders colonizing the micro-orchards from the forest changed even at this small spatial scale (Figure 3-3; Table 3-2). There were also interesting patterns when the spider assemblages from the micro-orchards were compared to the spiders collected in orchards in the same area two years previously. The most common species in older orchards and micro-orchards were the same, indicating that the spiders colonizing the orchards played an important role in longer-term community assembly (Figure 3-4). However, the assemblages in the older orchards were much more even than those in the micro-orchards, suggesting that local dynamics after colonization were also important to the community (Figure 3-5).

8.2.3. Relevance of juvenile spiders to community studies

My spider collections were typical of most spider community studies in that a large proportion of the collected individuals were juveniles. If these immature specimens are excluded from analysis because they are not identifiable to species, will this affect the results and conclusions of community studies? I hypothesized (hypothesis 4, Introduction) that the composition of the samples would be different if only adults were included, as opposed to the inclusion of both juveniles and adults, because of factors such as differential mortality rates between species.

To test this question, I analyzed two datasets from the community study presented in chapter 2: a dataset containing only the mature spiders ("matureonly"), and a "complete" dataset containing both mature and immature spiders. The second dataset, containing species information for spiders collected as juveniles, was available because when I collected immature spiders, I had reared them until maturity and then identified them to species. Other specimens I was able to identify when they were still immature because many foliage-dwelling spider species have unique non-reproductive characteristics. The original community study (chapter 2) had compared the species assemblages in orchard and deciduous forest. I made these same comparisons, using species richness estimations, relative evenness, and species composition of samples (using non-metric multidimensional scaling), but compared results produced by the two datasets.

There were twice as many individuals in the complete dataset than the mature-only dataset (402 and 809, respectively), and 9 extra species were identified that hadn't been collected as mature specimens (40 species were identified from the collected mature individuals). The extra data resulting from the inclusion of immature spiders did not provide any different information other than what would be gained from increased sampling effort (i.e. collecting more mature spiders). Species richness estimates for orchard and forest habitats did not change between datasets (Figure 3-1). The distribution of individuals among species was less even in the mature-only dataset, but that is to be expected because of the lower number of individuals (Figure 3-2). The ordination of samples by site, habitat (forest or orchard), and dataset produced an ordination where the sample points from a given site and habitat were very close together, regardless of dataset (Figure 3-3). Although rearing immature spiders yielded more species identifications, including this data did not change the analysis and comparison of assemblage data. Increasing the size of the dataset through increased sampling effort will be easier and produce the same results.

8.2.4. Kaolin and orchard arthropods

The results from chapters 2 and 3 indicated that immigration into orchards plays an important role in structuring the spider assemblages in orchard foliage. Another major influence on spider assemblages in orchard foliage is the application of pesticides. Spider populations are reduced by insecticide application, and the composition of the assemblages also changes (Bostanian *et al.* 1984; Olszak *et al.* 1992a; Wisniewska and Prokopy 1997; Pekár 1999a; Pekár 1999b). Physical pest control methods alter the physical environment of the pest to reduce its impact on the crop (Vincent *et al.* 2003). Kaolin clay formulations, although sprayed on the foliage much like conventional insecticides, are physical control methods, as their mechanism of action is by physically changing the environment of the crop.

In chapters 5 to 7 I explored the effects of kaolin on spider and other natural enemy assemblages and ecology. First, in laboratory and mesocosm experiments I determined how kaolin affected the behaviour of a potential prey item of spiders, larvae of the Tortricid moth, *Choristoneura rosaceana*, and how kaolin affected spider interactions with these larvae. Second, in field experiments, I investigated the effect of kaolin on spider and generalist predator communities as well as parasitism of *C. rosaceana* larvae.

8.2.5. Effects of kaolin on C. rosaceana larval behaviour

Interactions between pests and predators are modulated by many factors, including prey behaviour. If pest management methods such as kaolin alter the behaviour of a pest, they may also alter these predator-prey interactions. Kaolin sprays are effective in reducing *C. rosaceana* populations and damage in orchards, and in chapter 5 I investigated the mechanisms responsible for the negative effects of kaolin on *C. rosaceana* larvae.

I tested if kaolin had physiological effects when ingested as previous studies had shown negative effects of larvae when consumed, but these were mainly attributed to kaolin being an actual physical barrier. Because clays can adsorb to nutrients preventing assimilation, I tested if there were potentially physiological effects as well. Second, I tested if kaolin affects the establishment (leaf-shelter formation) on apple leaves of two instars of *C. rosaceana*: third instar and neonates. I hypothesized (hypothesis 5, Introduction) that kaolin would hinder the establishment of leaf shelters because of delayed recognition of the host plant or direct physical interference.

The feeding experiments indicated that the mechanisms behind kaolin's negative effects on *C. rosaceana* upon consumption were mainly physical (i.e.

delayed feeding), although there may be minor physiological effects from consumption (Figure 5-1). Kaolin delayed the construction of leaf shelters by third and fourth instar larvae (Table 5-1), neonates dispersed off kaolin-covered leaves more rapidly than off control leaves, and fewer neonates settled on kaolincovered leaves as well (Figure 5-2). Thus kaolin may increase the risk of predation or parasitism because the larvae are exposed for a longer period of time when colonizing spring leaves or when dispersing as neonates.

8.2.6. Predation on *C. rosaceana* by salticid spiders and interactions with kaolin

One of the most common spider families in Québec apple orchards is the Salticidae, or jumping spiders, and many species in this family reproduce and reach peak abundances in July concurrent with the dispersal of *C. rosaceana* neonates. Most invertebrate predators have a type II functional response to prey density (i.e. increasing consumption of prey with increasing prey densities, but decreasing proportion of prey eaten). I hypothesized (hypothesis 6a, Introduction) that the salticid spiders would have this type of response to changing densities of *C. rosaceana* neonates, but that there was the possibility of an increasing proportion of neonates eaten with increasing densities (type III response) because salticid spiderlings will eat multiple neonates simultaneously. I also tested if the presence of kaolin on leaves affected the rate of predation of salticids (*Eris* sp. and *Pelegrina* sp.) on one density of neonates placed in mesocosms containing apple seedlings. I hypothesized (hypothesis 6b, Introduction) that kaolin would increase the rate of predation on neonates as it delays their rate of establishment on apple leaves.

Salticid spiders exhibited a type II functional response to changing densities of neonate larvae (Figure 7-1). Surprisingly, kaolin did not affect the predation rate by salticid spiders on neonates (Figure 7-2). The kaolin did not affect the number of neonates establishing on the apple seedlings, unlike the results from chapter 5, probably because the design of the mesocosm prevented the increased ballooning from the plants. I suspect that the kaolin did not affect

the predation rate by salticids because the complexity of the foliage in the mesocosms modulated the interactions between the spiders and neonates enough to compensate for the delay in leaf-shelter formation by the neonates.

8.2.7. Effects of kaolin on generalist predator assemblages in orchards and on parasitism of *C. rosaceana* larvae

Although kaolin does not affect the interactions between one common spider family, the Salticidae, and its prey, it is essential to determine what the response of entire spider assemblages are to kaolin in field experiments. In chapter 7, I measured the effect of kaolin applications, designed for controlling populations of *C. rosaceana* summer generation larvae, on the abundance and composition of generalist predator assemblages in the orchards and the rate of parasitism on *C. rosaceana* larvae. I hypothesized (hypothesis 7, Introduction) that kaolin would negatively affect the generalist predators in the orchards, but that it would affect some spider guilds and predators more than others, due to their different foraging behaviours. I also expected that kaolin would negatively affect the parasitism of *C. rosaceana* larvae.

Kaolin reduced the relative abundances of many of the common wandering predators, including certain families of hunting spiders (salticids and philodromids), assassin bugs, ants, and coccinellids (Table 7-1). As a result of these changes, the composition of the spider assemblages as a whole was significantly different between kaolin plots and unsprayed plots (Figure 7-2). Kaolin did not significantly affect the rate of parasitism of *C. rosaceana* larvae or the proportion of parasitoids in Hymenopteran families or Diptera in each treatment.

8.3. Synthesis and Suggested Future Directions

Although kaolin reduced the densities of generalist predators in the orchards, the mechanisms by which it affected the predators are not clear. In the laboratory, kaolin did not affect the predation ability of salticids, the most common hunting spider found in the orchards, even though it affected prey (*C*.

rosaceana) behaviour. Other possibilities are that kaolin reduced the amount of prey available, or it was physically disturbing to predators that are in continuous contact with the foliage. Spider emigration is usually associated with one of three factors: environmental conditions (e.g. temperature and humidity), low prey availability, or disturbance (Riechert and Lockley 1984). Kaolin could be associated with all three of these factors; the mechanisms through which kaolin affects predators in agricultural crops still need to be experimentally determined.

Although kaolin reduces predator densities in orchards, it is preferable to the use of broad-spectrum insecticides: there is no evidence that it causes predator mortality, and it does not affect the rate of parasitism of some pests, such as *Choristoneura rosaceana*. Kaolin negatively affects the parasitoids of other arthropods in orchards, such as the lepidopteran leafminer *Phyllonorycter elmaella* (Knight *et al.* 2001). The effects of kaolin on parasitism will not be uniform as host-parasitoid relationships differ with respect to factors such as host behaviour or host location strategies of the parasitoid (Vinson 1998). If we are to understand and quantify the comparative disadvantages of kaolin and other curative methods, field trials must be done.

Despite the alteration and lower densities of spider assemblages as a result of kaolin application, this research demonstrated that deciduous forest adjacent to orchards has spider assemblages similar to those in the orchard foliage, and the rate of colonization of orchards was from 35-40 spiders/m³/ week at peak times. Low densities of spiders in orchard foliage are not due to lack of colonization potential, but to the distance of the orchard from source habitats, the populations of spiders within source habitats, and the pest management regime in the crop. Management regimes may affect spider mortality directly, as in the case of certain insecticides, and they will also indirectly affect the propensity of spiders to emigrate depending on how they interact with prey density and microhabitat characteristics.

There was a more even distribution of individuals among spider species in assemblages in older orchards than in assemblages of recently colonized spiders. The interaction between colonization and local dynamics such as relative fecundity and survival, relative emigration, and competition or predation will shape the composition of the spider assemblages over time. The guild composition of spider communities in crops is remarkably constant across agroecosystems; each guild (i.e. runners, stalkers, orb-web weavers, etc.) occupies a fairly fixed proportion of the assemblage (Uetz *et al.* 1999). This suggests that the factors, both external and internal, that shape spider assemblages may be similar across communities. Further research can examine how colonization and local interactions interact during community assembly. The micro-orchard system used here, in a landscape with about 80% of forested area, was ideal for studying spider colonization as the number of colonizing spiders was high enough to observe statistically significant patterns for indices species composition. The micro-orchard system will be useful in further research in arthropod community assembly in orchard foliage, providing insight into ecological processes that are interesting both for integrated pest management strategies and for ecology in general.

Brown *et al.* (2003) report that in North America, sprayed orchards are dominated by web-spinning guilds, while IPM and unsprayed orchards have a higher relative number of hunting spiders. The results of my research suggest two mechanisms by which this pattern is created. First, kaolin negatively affected hunting spiders more than web-spinners, similar to the effects from more conventional insecticides (Pekár 1999b). Second, my research showed that the spider assemblages colonizing orchards also have a higher proportion of webspinners than hunting spiders relative to the composition of spiders found in longer established orchards. Therefore the composition of the initial spider colonizers, in addition to curative pest management techniques, will cause orchard assemblages to be characterized by fewer hunting spiders and more web-spinners as compared to orchards where fewer insecticides are applied.

We do not know the significance of changes in spider assemblages in orchards with respect to pest management because we know little of the biocontrol role of foliage-dwelling spiders. Predation of *C. rosaceana* larvae in orchards can range from 21% to 35%, and spiders are a main component of the

predatory fauna (Sarvary *et al.* 2007). However, orchard communities are complex, potentially containing more than 20 pest species (Chouinard *et al.* 2001), and numerous spider species, insect predators, parasitoids, and countless neutral arthropods. Additionally, because orchards are perennial and can be composed of trees of different varieties and ages, different habitat structure may modulate interactions. Despite these difficulties, the role of spiders and generalist insect predators as biocontrol agents can be determined using classic methods, such as excluding spiders from plots and measuring the response of the community as a result (Bishop and Riechert 1990). We can subsequently address the complexities of the system and tease apart the influences of particular taxa.

The same factors and processes, whether in natural or agricultural habitats, influence ecological communities. These are local factors, such as abiotic conditions, environmental disturbance, and interactions (i.e. competition, predation), and regional factors: the immigration and emigration of species to and from the regional species pool (Hillebrand and Blenckner 2002). The research described in this thesis provides a greater understanding of the influence of colonization on spider assemblages in apple orchards and the effects on spider and natural enemy ecology of an increasingly common and effective pest control method, kaolin clay. Future work examining the interactions between spiders and other arthropods in the orchards will provide a greater understanding of the ecology and biocontrol role of these arthropods.

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Appendix I. Data from Chapter 2

Table AI-1: Counts of spiders, and life-stage when collected, of spiders from sites (A, B, C, and D) and habitats (orchard (orc.), forest (for.), field (fie.), and ecotone (eco.)) in 2004 in apple agroecosystems in Québec. Sample dates were pooled.

	Site and Habitat															
	А				В				С			D			Collected	Collected
Species	Orc.	For.	Fie.	Eco.	Orc.	For.	Fie.	Eco.	Orc.	For.	Eco.	Orc.	For.	Fie.	mature	immature
Admestina tibialis (C. L. Koch)	1														1	
Araneus diadematus Clerck												1				1
Araniella displicata (Hentz)	29	27	2	1	37	1		1	38	13	2				21	27
Bassaniana versicolor (Keyserling)		1													1	
Ceraticelus similis (Banks)	1														1	
Cheiracanthium mildei L. Koch													1		1	
Clubiona abbotii L. Koch												1			1	
Clubiona canadensis Emerton										1						1
Clubiona obesa Hentz		1													1	
Clubiona spiralis Emerton	1														1	
<i>Emblyna</i> spp.	6	20			7	7			4							44
Dipoena nigra (Emerton)	1					1									2	
Elaver excepta (L. Koch)						1										1
Emblyna maxima (Banks)	1	9						2								12
Emblyna sublata (Hentz)	21	25			14	1		4	8				1		33	41
Enoplognatha ovata (Clerck)	33	39		7	36	6		1	8		2	10	11		134	19

	А				В				С			D			Collected	Collected
	Orc.	For.	Fie.	Eco.	Orc.	For.	Fie.	Eco.	Orc.	For.	Eco	Orc.	For.	Fie.	mature	immature
Erigone atra Blackwall	1														1	
Eris militaris (Hentz)	45	12		1	21	11		3	8	1		1	2		51	54
Eustala anastera (Walckenaer)		2													2	
Evarcha hoyi (Peckham & Peckham)								2							1	1
Gonatium crassipalpum Bryant						1										1
Grammonota gentilis Banks							1								1	
Hentzia mitrata (Hentz)						1		1							1	1
Hypselistes florens (O. P		1													1	
Mangora placida (Hentz)		3													3	
Misumena vatia (Clerck)	6	8	1	7	8	3	5	1	6	1	26		1	2	10	65
Misumenops asperatus (Hentz)	2			1	8		2		12	1	5				1	30
Neoscona arabesca (Walckenaer)				1				1	1						3	
Neottiura bimaculata (Linnaeus)	1														1	
Pardosa moesta Banks			1												1	
Pelegrina flaviceps (Kaston)	1														1	
Pelegrina proterva (Walckenaer)	14	15		1	7	5		5	18	9					35	39
Philodromus spp.	20	15	1		20	7	1	1	5			15	15			100
Philodromus cespitum (Walckenaer)	3	2							1			39	16		11	50
Philodromus praelustris Keyserling	25	18			59	5			22				1			130
Philodromus rufus vibrans Dondale	17	37			26	3		1	12	5					31	70
Philodromus vulgaris (Hentz)	2														1	1

	А				В				С			D			Collected	Collected
	Orc.	For.	Fie.	Eco.	Orc.	For.	Fie.	Eco	. Orc.	For.	Eco.	Orc.	For.	Fie	mature	immature
Pityohyphantes costatus (Hentz)	3	2													1	4
Tetragnatha spp.		2														2
Tetragnatha laboriosa Hentz							1									1
Tetragnatha versicolor Walckenaer		1														1
Theridion albidum (Banks)						1				1					2	
Theridion differens Emerton					1				2						3	
Theridion frondeum Hentz		2				4		1							7	
Takayus lyricus (Walckenaer)	2	1			1										3	1
Theridion murarium Emerton	17	7			9	3		1	15	2		1	1		52	4
Thymoites minnesota Levi							1								1	
Tibellus oblongus (Walckenaer)														5	5	
Tmarus angulatus (Walckenaer)	4	3			1	8		1		1					3	15
Tutelina similis (Banks)	1														1	
Xysticus elegans Keyserling						1			1							2
<i>Xysticus ferox</i> (Hentz)						1										1
Immature Araneidae	1	2	1				2		1			4	1			12
Immature Clubionidae	9	24		1	2	3		1	1	1				1		43
Immature Lycosidae						1					1					2
Immature Salticidae	93	31		5	31	45		16	32	15	10	8	11			89
Immature Theridiidae	27	18			20	3			22	2			3			95
Immature Thomisidae	3	6		1	12	2	4		7	21	8		1			65

Appendix II. Data from Chapter 3

Table AII-1: Counts of spiders collected from habitats (micro-orchards 10 and 50 m from forest, forest, and field) in apple agroecosystems in Québec in 2006. Sample dates were pooled.

Species	10m	50m	Forest	Field
Acanthepeira stellata (Walckenaer)				1
Achaearanea tabulata Levi	1			
Araneus diadematus Clerck	1			
Araneus guttulatus (Walckenaer)		1		
Araneus marmoreus Clerck	1			
Araneus trifolium (Hentz)		1		
Araniella displicata (Hentz)	355	571	144	10
Ceraticelus fissiceps (O.PCambridge)	1			
Ceratinops latus (Emerton)	1			
Clubiona canadensis Emerton			1	
Clubiona obesa Hentz			1	
Clubiona spiralis Emerton			1	
Collinsia plumosa (Emerton)	1			1
Diplocephalus cristatus (Blackwall)	1			
Dipoena nigra (Emerton)		1		
Emblyna spp.	163	39	288	
Emblyna sublata (Hentz)	30	6	17	5
Enoplognatha ovata (Clerck)	8	2	15	
Eridantes erigonoides (Emerton)	1			
Erigone atra Blackwall	3	1		
Erigone autumnalis Emerton		1		
Eris militaris (Hentz)	11		8	
Eris sp.	59	18	27	
Euryopis argentea Emerton	1			
Eustala anastera (Walckenaer)	1			
Evarcha hoyi (Peckham & Peckham)			1	
Habronattus decorus (Blackwall)	1	1		1
Hentzia mitrata (Hentz)	7	6	3	
Hypsosinga rubens (Hentz)			1	
Hyptiotes sp.			2	
Misumena vatia (Clerck)	29	9	8	17

Species	10m	50m	Forest	Field
Misumenops asperatus (Hentz)	1	2		7
Misumenops sp.	108	53	18	
Neoscona arabesca (Walckenaer)	1	2		
Neriene clathrata (Sundevall)		1		
Pardosa moesta Banks		1		
Pelegrina insignis (Banks)		1		1
Pelegrina proterva (Walckenaer)		1	3	
Pelegrina spp.	23	8	94	1
Philodromus cespitum (Walckenaer)	2	4	12	
Philodromus rufus vibrans Dondale	224	236	151	3
Philodromus spp.	63	29	47	
Pityohyphantes costatus (Hentz)			2	
Tetragnathus spp.	7	2	3	7
Theridion albidum (Banks)	1		1	
Theridion differens Emerton		1		
Theridion murarium Emerton	132	79	47	1
Theridula emertoni Levi	1		2	
Tmarus angulatus (Walckenaer)	1		6	
Tutelina similis (Banks)	1	1		
Xysticus canadensis Gertsch	1			
Xysticus discurans Keyserling		1		3
Immature Araneidae	11	8	14	3
Immature Clubionidae	10	3	26	
Immature Dictynidae	8			
Immature Linyphiidae	2		2	2
Immature Lycosidae	1	5		3
Immature Salticidae	29	9	3	
Immature Theridiidae	8	2	26	
Immature Thomisidae	7	10	6	2
Unknown	21	6	1	