

INVASIVE EXOTIC PLANTS AND THEIR NON-INVASIVE RELATIVES: THE
ROLE OF ENEMY-RELEASE FROM GENERALIST AND FAMILY-SPECIALIST
HERBIVORES, NOVEL DEFENSE, TAXONOMIC ISOLATION AND
POLYPLOIDY IN CONFERRING INVASION POTENTIAL.

by

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Master of Science.

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ABSTRACT

In this study, I looked at whether invasive exotic plants were more likely to escape herbivory compared to confamilial non-invasive exotics and whether enemy escape could be attributed to generalist and/or family-specific herbivores in the introduced range. Additionally, I examined the role of novel defenses, taxonomic isolation and polyploidy in conferring invasion potential.

Plants that were more invasive had lower herbivore damage in the field and were less palatable to the generalist herbivore *Pseudaletia unipuncta*. However, herbivory by the generalist, *Heliothis zea*, did not depend on the invasiveness of the plant and family-specialist herbivores were not less likely to survive on invasive exotics. In addition, I found no evidence that invasive exotics were better defended or more taxonomically isolated than non-invasive exotics. However, a preliminary analysis indicated that invasive plants were more likely to be polyploid. These results broadly suggest that escape from generalist herbivores might account for the low foliar herbivory observed on invasive exotic plants and that polyploidy may play an important role in facilitating exotic plant invasions.

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TABLE OF CONTENTS

ABSTRACT	i
ACKNOWLEDGEMENTS	ii
TABLE OF CONTENTS	iii
LIST OF TABLES	v
LIST OF FIGURES	vi
LIST OF APPENDICIES	viii
CHAPTER ONE: GENERAL INTRODUCTION	1
Exotic plant invasions	1
Mechanisms facilitating exotic plant invasions	3
Escape from natural enemies	5
Escape from plant competitors	9
Adaptive evolution in invasive plants	10
The Novel Weapons/ Defense hypothesis	12
Taxonomic isolation	13
CHAPTER TWO: HERBIVORY, NOVEL DEFENSE, TAXONOMIC ISOLATION AND THE ENEMY-RELEASE HYPOTHESIS	15
Study Rationale	15
Biology of plant families	17
Apiaceae	17
Brassicaceae	19
Fabaceae	21
Materials and Methods	24
Plant Species	24
Field herbivore damage	26
Generalist herbivores	27
Family-specialist herbivores	29
Defensive chemistry	34
Furanocoumarin extractions	35
Taxonomic isolation	36
Results	
Field herbivore damage	37

Generalist herbivores	37
Family-specialist herbivores	46
Defensive chemistry.....	56
Taxonomic isolation.....	56
Discussion	59
Conclusions.....	72
CHAPTER THREE: POLYPLOIDY AND THE INVASIVENESS OF EXOTIC PLANTS.	73
Introduction	73
Materials and Methods.....	75
Results.....	75
Discussion	77
Conclusions.....	79
LITERATURE CITED	80
APPENDICIES.....	95
Appendix 1.....	95

LIST OF TABLES

Table 1: Introduced species from 3 plant families, Apiaceae, Brassicaceae and Fabaceae, in the Ottawa region and the invasiveness ranks derived from the NatureServe I-Rank (NatureServe : www.natureserve.org). Higher ranks are more invasive.....	25
Table 2: Exotic invasive and non-invasive plant species that supported > 50% survival to pupation, initiation of feeding and continuation of feeding of family-specialist herbivores. Relationships are analyzed using a G-test of independence.....	54
Table 3: No-choice oviposition by <i>P. polyxenes</i> females on introduced Apiaceae plant species. Eggs counts indicate the average number of eggs laid by over the lifetime of one female.....	55
Table 4: Choice oviposition by <i>P. rapae</i> females on introduced Brassicaceae plant species. Eggs counts indicate total number of eggs found on each plant species.....	55
Table 5: Distribution and concentration of furanocoumarin compounds in five exotic Apiaceae plants. Concentrations are measured as $\mu\text{g} / \text{mg}$ of dry leaf weight. Furanocoumarin compounds detected and compared to known standards via HPLC methods.....	57
Table 6: Exotic invasive and non-invasive plant species that are diploid and polyploidy. Relationships are analyzed using Fisher's Exact test.....	76

LIST OF FIGURES

- Figure 1: Relationship between leaf damage (%) sustained in the field and the numerical invasiveness ranking obtained from the NatureServe I-Rank (www.natureserve.com). Points are species means for leaf damage across different populations with 20 replicates in each population. Correlation between average leaf damage (%) and invasiveness is significant. $R^2 = 0.199$, Spearman's Rho = -0.41, $P = 0.03$38
- Figure 2: Comparison of average leaf damage (%) sustained in the field between the plant families; Apiaceae, Brassicaceae and Fabaceae. Box plots indicate the median and 3rd quartiles of the mean damage incurred in the family. Difference in leaf damage between the families is not significant, Kruskal-Wallis test, Chi-sq = 2.927, $P = 0.231$39
- Figure 3 a: Relationship between leaf area consumed (cm²) by *Pseudaletia unipuncta* and the numerical invasiveness ranking obtained from the NatureServe I-Rank (www.natureserve.com). Points indicate mean feeding damage on each plant species. Correlation between feeding damage and invasiveness is significant. $R^2 = 0.215$, Spearman's Rho = -0.45, $P = 0.03$ 40
- Figure 3 b: Relationship between leaf weight consumed (mg) by *Pseudaletia unipuncta* and the numerical invasiveness ranking obtained from the NatureServe I-Rank (www.natureserve.com). Points indicate mean feeding damage on each plant species. Correlation between feeding damage and invasiveness is significant. $R^2 = 0.2$, Spearman's Rho = -0.46, $P = 0.02$ 41
- Figure 4: Comparison of feeding damage (leaf area eaten cm²) by *Pseudaletia unipuncta* between the plant families; Apiaceae, Brassicaceae and Fabaceae. Box plots indicate the median and 3rd quartiles of the mean damage incurred in the family. Difference in leaf damage between the families is not significant, Kruskal-Wallis test, Chi-sq = 5.10, $P = 0.08$42
- Figure 5 a: Relationship between leaf area consumed (cm²) by *Heliothis zea* and the numerical invasiveness ranking obtained from the NatureServe I-Rank (www.natureserve.com). Points indicate mean feeding damage on each plant species. Correlation between feeding damage and invasiveness is not significant. $R^2 = 0.012$, Spearman's Rho = 0.02, $P = 0.46$ 43
- Figure 5 b: Relationship between leaf weight consumed (mg) by *Heliothis zea* and the numerical invasiveness ranking obtained from the NatureServe I-Rank (www.natureserve.com). Points indicate mean feeding damage on each plant species. Correlation between feeding damage and invasiveness is not significant. $R^2 = 1.47 \text{ E-}4$, Spearman's Rho = -0.002, $P = 0.49$ 44
- Figure 6: Comparison of feeding damage (leaf area eaten cm²) by *Heliothis zea* between the plant families; Apiaceae, Brassicaceae and Fabaceae. Box plots indicate the median

and 3rd quartiles of the mean damage incurred in the family. Difference in leaf damage between the families is significant, Kruskal-Wallis test, Chi-sq = 6.67, P = 0.03.....45

Figure 7: Percentage of *P. polyxenes* larvae that initiated feeding, continued feeding and survived to pupation on each exotic Apiaceae species. 20 larval replicates were reared on each exotic species. (Ap = *Aegopodium podagraria*, As = *Angelica sylvestris*, Dc = *Daucus carota*, Ps = *Pastinaca sativa*, Hm = *Heracleum mantegazzianum*).....48

Figure 8: Average time taken for *P. polyxenes* larvae to develop from egg to pupation (in days) on each plant. Error bars are ± Standard Error. 20 larval replicates were reared on each exotic species. (Ap = *Aegopodium podagraria*, As = *Angelica sylvestris*, Dc = *Daucus carota*, Ps = *Pastinaca sativa*, Hm = *Heracleum mantegazzianum*).....49

Figure 9: Percentage of *P. rapae* larvae that initiated feeding, continued feeding and survived to pupation on each exotic Brassicaceae species. 20 larval replicates were reared on each exotic species. (Bv = *Barbarea vulgaris*, Bi = *Berteroa incana*, Sa = *Sinapis alba*, Cb = *Capsella bursa-pastoris*, Ec = *Erysimum cheiranthoides*, Ta = *Thlaspi arvense*, Ap = *Alliaria petiolata*, Hm = *Hesperis matronalis*).....50

Figure 10: Average time taken for *P. rapae* larvae to develop from egg to pupation (in days) on each plant. Error bars are ± Standard Error. 20 larval replicates were reared on each exotic species. (Bv = *Barbarea vulgaris*, Bi = *Berteroa incana*, Sa = *Sinapis alba*, Cb = *Capsella bursa-pastoris*, Ec = *Erysimum cheiranthoides*, Ta = *Thlaspi arvense*, Ap = *Alliaria petiolata*, Hm = *Hesperis matronalis*).....51

Figure 11: Percentage of *C. philodice* larvae that initiated feeding, continued feeding and survived to pupation on each exotic Fabaceae species. 20 larval replicates were reared on each exotic species. (Ls = *Lathyrus sylvestris*, Ms = *Medicago sativa*, Ta = *Trifolium aureum*, Tp = *Trifolium pratense*, Vc = *Vicia cracca*, Cv = *Coronilla varia*, Lc = *Lotus corniculatus*, Ma = *Melilotus alba*, Tr = *Trifolium repens*).....52

Figure 12: Average time taken for *C. philodice* larvae to develop from egg to pupation (in days) on each plant. Error bars are ± Standard Error. 20 larval replicates were reared on each exotic species. (Ls = *Lathyrus sylvestris*, Ms = *Medicago sativa*, Ta = *Trifolium aureum*, Tp = *Trifolium pratense*, Vc = *Vicia cracca*, Cv = *Coronilla varia*, Lc = *Lotus corniculatus*, Ma = *Melilotus alba*, Tr = *Trifolium repens*).....53

Figure 13: Relationship between the relatedness of an introduced plant species to North American taxa and the numerical invasiveness ranking, obtained from the NatureServe I-Rank (www.natureserve.com). Relatedness for each species is calculated as the number of native congeneric plants occurring in North America. Correlation between relatedness and invasiveness is not significant $R^2 = 0.024$, Spearman's Rho = -0.249, P = 0.126.....58

LIST OF APPENDICIES

Appendix 1. List of defensive phytochemicals recorded for each of the exotic species in this study 94

CHAPTER ONE: GENERAL INTRODUCTION

Exotic plant invasions

Anthropogenic transportation of organisms, whether purposeful or accidental, has led to the occurrence of thousands of species far beyond their natural range (Mack *et al.*, 2000). A large proportion of plants in North America have been introduced intentionally, as agricultural crops or garden ornamentals and some may have been introduced accidentally, as hitchhikers on other imported material (Mack and Lonsdale, 2001). Pimentel *et al.* (2005) have reported over 5000 exotic escapees from deliberate introduction into the United States. The economic cost associated with controlling exotic invasions is staggering and the ecological consequences of these introductions can be far-reaching (Pimentel *et al.*, 2005; Vitousek *et al.*, 1997; Mooney and Cleland, 2001).

Exotic invasions are one of the leading causes of biodiversity loss and can negatively impact native communities in a myriad of ways (Didham *et al.*, 2005). While most introduced plants are restricted to disturbed habitats, a number have invaded intact natural communities (Vitousek *et al.*, 1997). Competitive exclusion of native plants by invading exotics has been frequently cited (Minchinton *et al.*, 2006) and the presence of exotic invaders has often been correlated to lower native plant diversity (Pimentel *et al.*, 2005). Large portions of the North American Great Plains are dominated by exotic grass invaders, which are strong resource competitors and effectively exclude several native perennials (D'Antonio and Vitousek, 1992). In addition to direct competition for resources, some exotic invaders like *Centaurea maculosa* and *Alliaria petiolata* competitively exclude native species via allelopathy (Hierro and Callaway, 2003). Other impacts on native plants include competition for common mutualistic species such as

pollinators (Totland *et al.*, 2004) and disruption of soil mutualisms in native plants (Stinson *et al.*, 2006).

The impacts of exotic invaders can extend to higher trophic levels in native communities (Levine *et al.*, 2003). The formation of *Lythrum salicaria* monocultures in eastern North America have been accompanied by the displacement of several native wetland species such as the bog turtle, *Glyptemys muhlenbergii* (Blossey, 1999). Old field habitats occupied by the invasive vine, *Vincetoxicum rossicum*, are associated with lower arthropod diversity (Ernst and Cappuccino, 2005). Additionally, exotic shrubs such as *Rhamnus cathartica* and *Lonicera maackii* can act as ecological traps for song birds. Robins (*Turdus migratorius*) prefer nesting on these plants, in spite of the fact that they experience higher nest predation rates on these species compared to native shrubs (Schmidt and Whelen, 1999).

Exotic invaders also impact large-scale ecological processes including nitrogen and carbon cycling, ecosystem hydrology and natural fire regimes (Levine *et al.*, 2003). Comparisons of ecosystems dominated by exotic and native plants have revealed that exotics can increase the net primary productivity, nitrogen availability and produce litter with high decomposition rates that can alter carbon and nitrogen cycling in the ecosystem (Ehrenfeld, 2003; Liao *et al.*, 2008). For example, the invasive trees, *Myrica faya* and *Falcatoria moluccana* in Hawaii drastically increase the amount of available soil nitrogen resulting in an overall change in the canopy chemistry of invaded forests (Asner and Vitousek, 2005). Increased soil nitrogen availability caused by the exotic tree, *Acacia saligna*, encourages the growth of another invasive grass species (Yelenik *et al.*, 2004). Some exotics grasses such as, *Carpobrotus edulis*, *Bromus tectorum* and *Tamarix spp.*,

decrease the amount of soil water available for native species (Levine *et al.*, 2003). Introduced grasses like *Bromus tectorum* severely alter natural fire regimes by increasing the frequency and intensity of fires, resulting in the loss of several native species (D'Antonio and Vitousek, 1992). Further, exotic grasses are better able to recover after a fire compared to native species (D'Antonio and Vitousek, 1992). The most compelling evidence for large-scale ecological impacts driven by exotic species comes from a recent study by Anser *et al.* (2008). Through remote sensing techniques, they show that five invasive plants in Hawaii have radically altered the under-story and canopy structure of multiple undisturbed native forest communities.

While the ecological impacts of some invasive plants can be extensive, not all introduced plant species become strong invaders (Mack *et al.*, 2000; Richardson *et al.*, 2000). Only a small proportion of plants that are introduced establish populations and an even smaller percentage of established plants become ecological threats (Lockwood *et al.*, 2001; Williamson and Fitter, 1996). By definition, invasive exotic plants differ from non-invasive exotic species in their ability to proliferate, spread and negatively impact native biota (Mack *et al.*, 2000). Attributes of invasive exotics have been studied extensively in the last few decades and a number of contending hypotheses have been proposed to explain why certain exotic plants become invasive.

Mechanisms facilitating exotic plant invasions

A plethora of studies have attempted to find common life-history traits amongst invaders (Hayes and Barry, 2005). Different comparisons (native vs exotic; invasive vs non-invasive etc.) for a variety of different traits and species have yielded mixed results (Pyšek and Richardson, 2005). Phylogenetically controlled comparisons between invasive

and non-invasive plants are expected to be more meaningful (Muth and Pigliucci, 2006). A few of these comparisons have shown that invasive plants tend to have a higher relative seedling growth rate, higher specific leaf area, shorter juvenile period, shorter intervals between seed set and smaller seed sizes (Grotkopp and Rejmánek, 2007, Grotkopp *et al.*, 2002; Rejmánek and Richardson, 1996). In general, these traits suggest that invasives are likely to be more opportunistic (Grotkopp *et al.*, 2002). On the other hand, some studies fail to find common life-history attributes amongst related invaders (Muth and Pigliucci, 2006; Pyšek and Richardson, 2005).

Invasive exotic plants might not specifically gain an advantage from certain traits but benefit overall from the phenotypic plasticity of these traits. Phenotypic plasticity of a trait implies that the expression of the trait varies with environmental conditions (Richards *et al.*, 2006). This could potentially render an adaptive advantage under novel circumstances. Several comparisons between related exotic and native as well as invasive and non-invasive plants broadly indicate that invasive plants tend to have higher plasticity for fitness traits (reviewed by Richards *et al.*, 2006). For example, Funk (2008) found that five exotic species displayed higher plasticity in several physiological and morphological traits compared to phylogenetically related native plants. This trend was consistent even in low-resource environments suggesting that the invasive plants were better able to deal with stressful conditions (Funk, 2008). Further, Leishman and Thompson (2005) found that exotic invasive species performed better under high resource conditions compared to non-invasive and native species. Together, these results suggest that phenotypic plasticity might allow some invasive exotics to perform well under unfavorable conditions as well as be opportunistic under favorable conditions.

Exotic invaders are often more successful in their introduced range compared to their native range (Hierro *et al.*, 2005). Increased density in the introduced range has been measured for a few species including: *Hypericum perforatum* in North America (Vilà *et al.*, 2004), *Solidago gigantea* in Europe (Jakob *et al.*, 2004), *Cytisus scoparius* in Australia (Paynter *et al.*, 2003), and reported anecdotally for others (Hierro *et al.*, 2005). Based on this premise, it has been postulated that biotic differences in the native and introduced range are important drivers of exotic plant invasions (Keene and Crawley, 2002, Mitchell *et al.*, 2006). When a plant is introduced into a novel range, it leaves behind a number of coevolved natural enemies, mutualists and competitors, and establishes new relationships with organisms in the introduced range. The loss of some potentially regulatory relationships and the gain of some advantageous relationships have given rise to a suite of different hypotheses concerning the role of biotic interactions in facilitating the invasiveness of exotic plants (Mitchell *et al.*, 2006). Some of the main hypotheses are discussed in the following sections.

Escape from Natural Enemies

The Enemy Release Hypothesis (ERH) is one of the most commonly cited explanations for the invasiveness of some exotic plant species (Keene and Crawley, 2002). The ERH states that exotic plants leave behind herbivores and pathogens and face decreased control in the introduced range, giving them a competitive advantage against native plants (Keene and Crawley, 2002). The ERH posits two fundamental assumptions; 1. Exotic plants have lower natural enemy loads in their introduced range 2. Release from enemies results in a greater population growth rate and gives the exotic plant a competitive advantage (Keene and Crawley, 2002). These assumptions have prompted

two different approaches to testing the ERH. The biogeographical approach has been used to compare natural enemies on native and introduced populations of an invasive exotic plant while the community approach has been used to compare natural enemy regulation between invasive exotics and non-invasive exotics or native plants in the introduced range (Colautti *et al.*, 2004).

A number of exotics appear to lose herbivores when introduced. For example, *Solidago altissima* L. has a plethora of specialist feeders in North America, its native range (Fontes, 1994), but sustains few generalist herbivores and an inconsequential number of specialists in Europe, where it is highly invasive (Jobin *et al.*, 1996). Most of the studies reviewed by Colautti *et al.* (2004) support the idea that invasive exotics support fewer herbivores in their introduced range. In addition, Mitchell and Power (2002) found that exotic plants from introduced populations are infected by fewer viral and fungal pathogens compared to native populations. Even though some natural enemies might be left behind in the native range, the level of control by natural enemies might not differ between the introduced and native range. Comparisons of damage might provide more rigorous evidence for decreased control in the introduced range, from both herbivores and pathogens. This has been tested with a few invasive exotics. Introduced populations of *Silene latifolia* experience substantially lower herbivore damage because species specialists present in the native range are absent in the introduced range (Wolfe, 2002). Similarly, *Hypericum perforatum* and *Ambrosia artemisiifolia* incur lower levels of damage in the introduced range (Vilà *et al.*, 2004; Genton *et al.*, 2005).

While biogeographical studies can provide evidence for the loss of natural enemies in the introduced range, community-wide comparisons are important in

elucidating the relative impact of natural enemies on exotic invasive plants compared to native or non-invasive plants. However, comparisons between exotic and native plants in a community have been more equivocal (reviewed by Colautti *et al.*, 2004; Liu and Stiling, 2006). A number of studies even suggest that exotics suffer greater levels of herbivore damage in comparison to native plants (Agrawal and Kotenen, 2001; Novotny *et al.*, 2003; Parker and Hay 2005; Siemann and Rogers, 2003; Daehler and Strong, 1997). These results do not necessarily refute the ERH as native natural enemies (generalists in the native range and specialists on closely related native species) are expected to incorporate a large proportion of exotic plants into their host range, the Biotic Resistance Hypothesis (Levine *et al.*, 2004). Invasive and non-invasive exotic plants might differ in their ability to escape native natural enemies. The increased success of some exotic species as compared to others highlights the importance of incorporating a measure of invasiveness when testing the ERH (Cappuccino and Carpenter, 2005; Liu and Stiling, 2006).

Recent studies that compare herbivore damage and pathogen loads on a number of invasive and non-invasive exotic plants have found that invasive exotics tend to suffer lower levels of damage and harbor fewer viral and fungal pathogens in comparison to non-invasive plants (Cappuccino and Carpenter 2005; Mitchell and Power, 2002). These broad correlative studies seem to suggest that enemy release is important for a number of highly invasive exotic plants. On the other hand, there are a few invasive/non-invasive comparisons that have yielded contrasting results (Liu *et al.*, 2007; Parker and Gilbert, 2007). Disagreement between such studies could be attributed to the ambiguity in what qualifies as an invasive species versus a non-invasive one. Also, it is unlikely that enemy

release is the underlying mechanism in all exotic plant invasions and broad multi-species studies are more likely to find a pattern whereas comparisons between a few congeners might not.

A key assumption of the ERH is that natural enemies impose a significant negative impact on the fitness and competitive ability of a plant (Maron and Vilà, 2001; Keene and Crawley, 2002). Maron and Vilà (2001) suggest that top-down regulation by natural enemies should be important in short-lived plants and those that have a limited seed bank. In a meta-analysis, Levine *et al.* (2004) found that native herbivores have a strong impact on the establishment and performance of exotic species. However, a majority of the studies used in the meta-analysis focused on mammalian herbivores (Levine *et al.*, 2004). Similarly, Parker *et al.* (2006) found that native herbivores decreased the relative and overall abundance of exotic plant species and the effect was higher for vertebrate herbivores compared to invertebrates. Parker and Gilbert (2007) found that the presence of herbivores and fungi was marginally correlated with higher mortality in 18 *Trifolium* and *Medicago* spp. These studies broadly suggest that exotic plants can be controlled by natural enemies. However, the relative impacts of generalists and specialists is largely unknown but certain types of specialist herbivores, for instance seed predators, are expected to have large impacts on fitness (Maron and Vilà, 2001; Liu and Stiling, 2006). Escape from these specialist herbivores might provide a greater opportunity for invasion. Comparisons of herbivore impact on the demographic success of an exotic plant, in native and introduced populations, are needed to determine whether enemy release in the introduced range actually translates to increased fitness and competitive ability (Hierro *et al.*, 2005).

Escape from plant competitors

Escape from interspecific competition is considered an important factor in facilitating exotic plant invasions (Vilà and Weiner, 2004). Several studies suggest that invasive exotics are better competitors as compared to native species (reviewed by Vilà and Weiner, 2004). Invasive exotic plants might be better able to obtain resources. For example, *Centaurea solstitialis* out-competes several native perennial grass species because of its ability to utilize soil water that is inaccessible to natives (Enloe *et al.*, 2004). Competition can also occur via allelopathy, which is the negative impact of a plant on neighboring species through the addition of phytotoxic chemicals to the soil (Hierro and Callaway, 2003). Several highly invasive plant species including *Centaurea maculosa* (Ridenour and Callaway, 2001), *Centaurea diffusa* (Callaway and Aschehoug, 2000), *Alliaria petiolata* (Prati and Bossdorf, 2004) and *Lantana camara* (Gentle and Duggin, 1997), are known to produce allelopathic compounds that deter native plant species. Further, Callaway and Aschehoug (2000) found that North American native grasses were more negatively affected by *C. diffusa* exudates than grasses in *C. diffusa*'s native range. Increased competitive advantage against native plants, which have not evolved resistance to allelopathic phytotoxins, might explain the disproportionate success of exotic plants in the introduced range.

Competition might occur through indirect means as well. *Alliaria petiolata* has been found to produce leaf litter that negatively affects the growth of several native tree species (Stinson *et al.*, 2006). *A. petiolata* leaf litter contains compounds that reduce the germination of mutualistic mycorrhizal spores that native trees depend on (Stinson *et al.*, 2006). Some invasive exotic plants also compete with native plants for pollinators

(Levine *et al.*, 2003). For example, the exotic *Phacelia tanacetifolia* reduced the bumblebee flower visitation rate on the native species, *Melampyrum pratense* (Totland *et al.*, 2006). Chittka and Schurkens (2001) found that pollinators were more attracted to the invasive exotic, *Impatiens glandulifera*, owing to its rich nectar source and the loss of pollinators on native species considerably reduced their fitness. Seed predation could potentially exacerbate pollinator loss in native species while invasive might escape specialist seed predators in the introduced range (Ghazoul, 2002). Invasive exotics can alter the abundance of herbivores and indirectly impact native plants (Levine *et al.*, 2003). For example, small herbivorous mammals are attracted to shelter provided by monocultures of the invasive exotic, *Brassica nigra*, but these herbivores disproportionately feed on an adjacent native plant, *Nassella pulchra*, as they are deterred by chemical defenses in *B. nigra* (Orrock *et al.*, 2008). Increased competitive advantage, via direct and indirect means can interact and drive the success of invasive exotics.

Adaptive Evolution in Exotic Plants

Blossey and Nötzold (1995) hypothesized that escape from natural enemies in the introduced range results in adaptive evolution in exotic plants, where resources are reallocated from the plant's defenses to growth, thereby increasing the competitive ability the plant and facilitating invasiveness, the Evolution of Increased Competitive Ability (EICA) hypothesis. EICA has been proposed as an explanation for the increased vigor and growth of some invasive exotic plants in their introduced range (Blossey and Nötzold, 1995). The reallocation of resources to increase growth also implies that exotic plants should be less well defended in introduced populations (Blossey and Nötzold, 1995).

The EICA hypothesis has been tested extensively with mixed results so far (reviewed by Bossdorf *et al.*, 2005). A number of studies suggest that exotic plants, including *Sapium sebiferum* (Siemann and Rogers, 2003), *Eschscholzia californica* (Leger and Rice, 2003), *Solidago gigantea* (Jakobs *et al.*, 2004), *Lythrum salicaria* (Blossey and Nötzold, 1995) and *Senecio jacobea* (Stastny *et al.*, 2005), are bigger and more fecund in introduced populations. On the other hand, some exotic species do not appear to be larger in introduced populations (Willis *et al.*, 2000; Vilà *et al.*, 2004). A few studies indicate that introduced genotypes are more susceptible to specialist herbivores found in the native range, indicating a loss of defenses (reviewed by Bossdorf *et al.*, 2005), but others suggest increased defenses in introduced populations (Wikstrom *et al.*, 2006; Joshi and Vrieling, 2005; Ridenour *et al.*, 2008). When a plant is introduced in to a new range, specialist herbivores are left behind but the exotic plant still must contend with generalist herbivores in the introduced range. Under the selective pressure of generalists, it seems unlikely that an exotic plant would completely reallocate resources from defense to growth. Joshi and Vrieling (2005) found that introduced populations of *Senecio jacobea* contain higher concentrations of pyrrolizidine alkaloids. Pyrrolizidine alkaloids are effective defenses against generalist herbivores but specialists are able to detoxify these compounds and are even attracted to them, suggesting that release from specialist herbivores might drive the evolution of increased defenses in this case (Joshi and Vrieling, 2005).

Rapid adaptive evolution of exotic plants in the introduced range has increasingly been considered as a means to confer invasion potential (Muller-Scharer *et al.*, 2004). Contrary to the assumption that exotic plants suffer genetic bottlenecks on introduction,

Bossdorf et al. (2005) found no difference in neutral genetic variation between introduced and native populations. These findings suggest that the potential for adaptive evolution exists in introduced populations and that multiple introductions for exotic species are the norm rather than the exception (Bossdorf *et al.*, 2005). In addition, hybridization has been implicated in generating novel phenotypes of exotic plants, increasing the amount of genetic variation in introduced populations and escalating the potential for adaptive evolution in a novel environment (Lavergne and Molofsky, 2007). For example, reed canary grass (*Phalaris arundinacea*) has higher genetic diversity and heritable phenotypic variation in the introduced range owing to hybridization between genotypes spanning the entire European continent (Lavergne and Molofsky, 2007). Further, it has been suggested that invasive plants tend to be more polyploid in general, implying that introduced polyploid genotypes are more likely to succeed (Prentis *et al.*, 2008). Polyploidy has been associated with increased fitness, increased phenotypic plasticity and is known to impact higher trophic interactions (Soltis *et al.*, 2003).

The Novel Weapons/ Novel Defense Hypothesis

The loss of co-evolutionary relationships appears to be important in fostering exotic plant invasions; however, most exotic plants are expected to accumulate new herbivores, pathogens and competitors in the introduced ranges (Levine *et al.*, 2003). The Novel Weapons/Defense Hypothesis states that escape from enemies and competitors in invasive exotics might be facilitated by defenses that are novel to the introduced range (Callaway and Ridenour, 2004; Cappuccino and Arnason, 2006). For example, *Centaurea maculosa* and *Centaurea diffusa* are known to produce allelopathic compounds that have not been reported from any native plants and these compounds are disproportionately

more toxic to un-adapted plants in the introduced range compared to those in the native range (Callaway and Ridenour, 2004). Similarly, Cappuccino and Arnason (2006) reported that highly invasive exotic plants were more likely to be defended by potent secondary compounds that are not commonly found in North American taxa, and plants with uncommon defenses suffered lower leaf damage. Numerous examples of novel defense facilitating enemy escape exist. The highly invasive plant, *Alliaria petiolata* is known to synthesize a novel flavone glycoside, alliarinocide, which deters feeding by specialists on closely related Brassicaceae (Renwick, 2002). Similarly, the invasive vine, *Vincetoxicum rossicum*, has been found to contain a novel compound, antofine which inhibits root pathogens and another compound that deters foliar feeders (Mogg *et al.*, 2008). Defenses uncommon to the introduced range might be responsible for deterring native herbivores, pathogens and competitors that have no co-evolutionary history with these defenses and are not equipped to deal with them (Cappuccino and Arnason, 2006).

Taxonomic Isolation

Enemy escape should be stronger for taxonomically isolated species as they are unlikely to accumulate herbivores and pathogens from native species (Lockwood *et al.*, 2001). Novel exotic taxa are more inclined to be defended by uncommon or unusual phytochemicals, which might deter native herbivores, pathogens and competitors (Callaway and Ridenour, 2004). Novel exotic taxa are also more likely to utilize resources unavailable to native species (Lockwood *et al.*, 2001). A phylogenetic study on exotic grasses in California showed that those that were highly invasive were, on average, less related to natives as compared to non-invasive exotics (Strauss *et al.*, 2006). Cappuccino and Carpenter (2005) found that exotic plants with fewer native genera were

more invasive but herbivore damage on these plants was not lower on more taxonomically isolated species. A more recent study found that herbivore damage was lower on more taxonomically isolated exotic plants, but invasive exotics were not more taxonomically isolated (Dawson *et al.*, 2008). Different methods employed to measure taxonomic isolation, invasiveness and herbivore damage might explain the discrepancy between these studies.

CHAPTER TWO: HERBIVORY, NOVEL DEFENSE, TAXONOMIC ISOLATION AND THE ENEMY-RELEASE HYPOTHESIS

STUDY RATIONALE

In this study, I focus on the mechanisms underlying enemy release in invasive exotic plants. Decreased control by natural enemies could confer a competitive advantage on some exotic species which might allow them to become aggressive invaders, the Enemy Release Hypothesis (Keene and Crawley, 2002). Empirical support for the ERH has been mixed (reviewed by Colautti *et al.*, 2004; Liu and Stiling, 2006). However, recent studies have incorporated the idea that only a few exotic plants become highly invasive. These studies include a measure of invasiveness and support the prediction that highly invasive plants have lower herbivore damage (Carpenter and Cappuccino, 2004; Cappuccino and Carpenter, 2005) and lower pathogen loads (Mitchell and Power, 2002). As most exotic plants leave behind species-specific herbivores, herbivory on exotic plants can usually be attributed to generalist herbivores found in the introduced range and oligophagous (family- or genus- specific) herbivores that feed on closely related native plants (Keene and Crawley, 2002). Generalist herbivores might feed on an exotic plant if the plant is equipped only with defenses which are easy for the herbivores to overcome because they are present in native plant community that these herbivores commonly encounter. Likewise, oligophagous herbivores on closely related native species would incorporate an exotic plant in their diet if the plant has defenses similar to those of its native relatives. Taxonomically isolated plants are more likely to have unusual or uncommon defenses and are therefore more likely to become invasive via enemy release. By definition, if enemy release is a common driver of invasive plant success, I predict

that: 1) Invasive plants will sustain lower levels of leaf damage compared to non-invasive plants 2) Generalist and family specialist herbivores will avoid feeding on invasive plants compared to non-invasive exotics and 3) Invasive plants will be more taxonomically isolated from native flora than non-invasive plants. Along with empirically testing these predictions, I also looked for uncommon phytochemical defenses that might facilitate escape by deterring generalist and specialist feeders.

I test these predictions on plants belonging to three plant families: the Apiaceae, the Brassicaceae and the Fabaceae. These families make excellent candidates for this study as a number of plants in each family, both invasive and non-invasive, have been introduced to North America. Also, each one of these families supports at least one family-specialist herbivore, in the introduced range, that could potentially incorporate exotic species into their diet.

BIOLOGY AND CHEMISTRY OF PLANT FAMILIES

Apiaceae

There are over 300 genera and 3000 species in the Apiaceae, distributed primarily in the temperate regions of the world (Berenbaum, 2001). Members of this family are characterized by their umbellate inflorescence, inferior bicarpellate ovary, pentamerous flowers and schizocarp fruit (Rodriguez, 1971). A large proportion of the family is biennial and breeding systems are predominantly protoandrous and andromonoecious (Berenbaum 1990). The Apiaceae is an ecologically diverse family with species occurring in a variety of habitats including deserts, marshes, forests, tundra, and wastelands (Berenbaum, 2001). The family is split into three distinct sub-families-- Hydrocotyloidea, Saniculoidea and Apoidea-- of which the Apoidea are the most diverse (Rodriguez, 1971).

The Apiaceae are phytochemically diverse and include an assortment of coumarin derivatives that are unrivaled by any other plant family (Berenbaum, 1990). While simple coumarin compounds occur extensively throughout the family, furano- and pyrano- coumarins are limited to the Apoidea (Berenbaum, 1990). Furanocoumarins occur as two structurally different types, linear and angular (Nielson, 1971). Linear furanocoumarins are potent defensive compounds and react with tissue DNA, fatty acids and proteins in the presence of UV light (Lee and Berenbaum, 1990). This photo-activation renders the molecule extremely toxic to herbivores that are not specialized to feed on it (Berenbaum, 1978). Angular furanocoumarins are not photo-activated but are toxic to some specialists that have adapted to feed on linear furanocoumarins (Berenbaum, 1983). These compounds are, however, less common, occur in lower

concentrations and have been reported from only 4 Apiodea tribes (Berenbaum, 1983). Pyranocoumarins are more biosynthetically derived as compared to furanocoumarins and occur much less frequently in the family (Berenbaum, 2001).

Other important defensive secondary metabolites in the Apiaceae include polyacetalenes, triterpenes and methylenedioxyphenyls (MDP) (Hegnauer, 1971). Polyacetalenes, like farcaninone, are ubiquitous in the Apiaceae. Some Apiaceae polyacetalenes are highly toxic and plants such as poison hemlock, *Cicuta maculate*, store these compounds in large quantities (Hegnauer, 1971). MDP compounds such as myristicin occur in the leaves of several species. These compounds interfere with the metabolism of furanocoumarins, increasing their toxicity to herbivores (Berenbaum and Neal, 1985). Some secondary metabolites have a limited distribution within the family. For example, piperidine alkaloids occur only in the genus *Conium* and these compounds are extremely toxic to vertebrates (Castells and Berenbaum, 2005).

Owing to the potent defensive compounds in the Apiaceae, plants in this family generally support low herbivore loads and are chiefly associated with oligophagous herbivores (Berenbaum 1990). The invertebrate herbivore fauna on Apiaceae is comprised predominantly of Lepidopterans in the genera *Papilio*, *Depressaria* and *Agonopterix* (Berenbaum 1990). Several of these herbivores have evolved the capacity to metabolize the furanocoumarins of their hosts (Berenbaum, 1983).

While a number of Apiaceae plants have been introduced into North America, some, including *Pastinaca sativa* and *Daucus carota*, have become agricultural weeds and only a few, including *Heracleum mantegazzianum* and *Conium maculatum*, have been reported as substantial threats to natural areas (NatureServe: www.natureserve.org).

Brassicaceae

There are over 340 genera and 3350 species in the Brassicaceae, occurring in several regions of the world, with much of the diversity concentrated in the Northern temperate zones (Koch *et al.*, 2003). Like the Apiaceae, reproductive morphology is highly conserved in most Brassicaceae. Reproductive parts are characterized by radially symmetrical tetramerous flowers, bicarpellate ovaries and fruit capsules with a false septum (Hedge, 1976). Most Brassicaceae are annual or perennial herbaceous plants with a few woody species in some genera (Hedge, 1976). They occur in most habitats and some species have evolved to grow under extremely harsh conditions (Hedge, 1976). Taxonomically, traits such as size and shape of the fruit, embryological features, nectar-gland morphology, trichome structure and chromosome number have been used to determine phylogenetic relationships within the family (Koch *et al.*, 2003). However, there is little concordance between morphological and molecular studies on the number and monophyly of tribes in the family (Bailey *et al.*, 2006).

The most ubiquitous defensive phytochemicals in the Brassicaceae are glucosinolates (Feeny, 1977). There are over 70 different glucosinolate compounds varying only in the side-chain of a core thioglucoside structure (Kjaer, 1976). They are distributed in the order Capparales and occur frequently in the families Capparaceae, Brassicaceae and Resedaceae (Kjaer, 1976). Hydrolysis of the glucosinolate molecule yields volatile isothiocyanates, nitriles, epithionitriles and thiocyanates, all of which can be phytotoxic, deter herbivory and/or inhibit pathogen growth (Rask *et al.*, 2000). Myrosinase is the chief enzyme responsible for glucosinolate hydrolysis and is released

on tissue damage. The glucosinolate-myrosinase system is highly conserved in all Brassicaceae (Kjaer, 1976).

In addition to glucosinolates, several taxa in the Brassicaceae have evolved a secondary line of defense (Feeny, 1977). For example, plants within the genera *Erysimum* and *Cheiranthus* contain cardiac glycosides, the genus *Iberis* contains cucurbitacin glycosides and *Alliaria petiolata* contains a novel cyanopropenyl glycoside, alliarinoside (Renwick, 2002). Some genotypes of *Barbarea vulgaris* are additionally defended by a triterpenoid saponin (Agerbirk *et al.*, 2003). Several plants in the Brassicaceae also contain nortropane alkaloids (Brock *et al.*, 2007).

Both generalist and specialist herbivores feed on the Brassicaceae (Feeny, 1977). Several butterflies in the sub-family Pierinae specialize on the Brassicaceae and are able to detoxify glucosinolate compounds efficiently (Wheat *et al.*, 2007). Cabbage flea beetles, *Phyllotreta* spp., are also common specialists on this family (Feeny, 1977). Generalist species such as, *Tricoplusia ni*, *Spodoptera eridania* and *Myzus persicae* that utilize these plants, must have developed mechanisms to tolerate or detoxify glucosinolate defenses (Feeny, 1977).

Quite a few species in the Brassicaceae are of dietary importance to humans, owing to which, several have been introduced outside their native range. A large proportion of these have escaped cultivation and become weeds in disturbed areas but only a few exotic species are deemed as significant threats to native ecosystems (Daelher, 1998). Some invasive Brassicaceae in North America include *Alliaria petiolata*, *Lepidium latifolium*, *Hesperis matronalis* and *Rorripa sylvestris* (NatureServe: www.natureserve.org).

Fabaceae

The Fabaceae is the third largest angiosperm family, comprising approximately 720 genera and 19,400 species (Wojciechowski *et al.*, 2004). This family is well represented in both tropical and temperate areas of the world and its members range from large trees to small herbaceous plants (Wojciechowski *et al.*, 2004). Morphologically, Fabaceous species are typically characterized by bisexual, pentamerous flowers and leguminous fruits, which are one-chambered pods with parital placentation along the axial suture (Wojciechowski *et al.*, 2004). The Fabaceae are also renowned for their ability to form closely knit associations with nitrogen-fixing bacteria and increase the amount of nitrogen available in the soil (Sprenst, 2002). The continual availability of nitrogen has allowed members of this family to be opportunistic and do well under a variety of different conditions (Wojciechowski *et al.*, 2004). Owing to this trait, plants in this family have significant impacts on nitrogen cycling in the ecosystem and invariably influence all other species in the community (Wojciechowski *et al.*, 2004).

Morphological and molecular data support three sub-families within the Fabaceae: Caesalpinioideae, Mimosoideae, and Papilionoideae (Wojciechowski, 2003). Papilionoideae is the largest of the three sub-families with over 476 genera and is widely distributed in all regions and habitats (Wojciechowski, 2003). Plants in this sub-family share typical 'pea-like' flower morphology and have the ability to synthesize quinolizidine alkaloids, isoflavones, and non-protein amino acids (Wojciechowski *et al.*, 2004).

Given the ability of numerous Fabaceae to fix and obtain nitrogen, nitrogen-containing secondary metabolites such as alkaloids, non-protein amino acids, cyanogens,

protease inhibitors and lectins, are prominent defensive secondary compounds in this family. Quinolizidine alkaloids are potent defensive compounds against herbivores and pathogens and are distributed in the tribes Sophoreae, Podalyrieae and Genisteae but also occur sporadically in several other taxa (Wink, 1987). Pyrrolizidine alkaloids, which are potent defensive compounds, also occur in some genera of the Fabaceae (Wink, 2003). Non-protein amino acids function both as defensive compounds and as nitrogen storage sites for seedlings (Wink, 2003). Non-protein amino acids such as canavine, commonly occur in several tribes while others including lathyrine are restricted to only a few genera (Wink and Mohammad, 2002). Several nitrogen-free secondary metabolites have also been isolated from the Fabaceae (Wink and Mohammad, 2003). Flavinoids are ubiquitous in the family, coumarins and furanocoumarins occur in some genera like including *Psoralea* and *Melilotus*, cardiac glycosides occur in the genera *Coronilla* and *Securigera* and catechins and proanthocyanins occur in several woody Fabaceae (Wink, 2003).

Plants in the Fabaceae host a wide range of generalist and specialist herbivores including several homopteran sap feeders, as well as coleopteran and lepidopteran seed pod borers and foliage feeders (Edwards and Singh, 2006). Lepidoptera in the sub-families Colinae and Dismorpiinae are almost exclusively Fabaceae specialists (Wheat *et al.*, 2007).

Numerous introduced Fabaceae, ranging from small herbaceous annuals to large trees, have become prominent invaders in natural areas (Daehler, 1998). The invasion potential of plants in this family is partly attributed to their nitrogen-fixing capacity and their ability to colonize low-resource environments (Daehler, 1998). For the same reason, invasive Fabaceae have a disproportionately larger impact on native ecosystems

(Daehler, 1998). Invasive plants in this family include: *Pueraria montana*, *Coronilla varia*, *Cytisus scoparius*, *Lespedeza cuneata*, *Lotus corniculatus*, *Robinia pseudo-acacia*, *Wisteria sinensis*, *Falcataria moluccana* and *Ulex europaeus* (NatureServe: www.natureserve.org, Global Invasive Species Database, www.issg.org/database).

MATERIAL AND METHODS

Plant Species

Twenty-three introduced species in the families Apiaceae, Brassicaceae and Fabaceae that occur in the Ottawa region were used for this study (Table 1). A plant was considered introduced if it was not native to any part of the North American continent. I used a ranking system compiled by NatureServe (www.natureserve.org), a non-governmental organization, to assess the invasiveness of all plant species in the study. The organization assigns a categorical Invasive Species Impact Rank (I-Rank) based on the negative impacts of the plant. The overall rank given to a plant is an indicator of four characteristics: its ecological impact, current distribution and abundance, trend in distribution and abundance, and management difficulty (Morse *et al.*, 2004). I assigned a corresponding numerical rank, ranging from zero to six, based on the categorical I-Rank for each species (Table 1).

Table 1: Introduced species from 3 plant families, Apiaceae, Brassicaceae and Fabaceae, in the Ottawa region and the invasiveness ranks derived from the NatureServe I-Rank (NatureServe : www.natureserve.org). Higher ranks are more invasive.

Species	Family	Categorical I-Rank www.natureserve.org	Numerical Invasiveness Rank
<i>Aegopodium podagraria</i> L.	Apiaceae	Low	3
<i>Angelica sylvestris</i> L.	Apiaceae	Not yet assessed	0
<i>Daucus carota</i> L.	Apiaceae	Low	3
<i>Heracleum mantegazzianum</i> Sommier & Levier	Apiaceae	Medium/low	4
<i>Pastinaca sativa</i> L.	Apiaceae	Low/insignificant	2
<i>Alliaria petiolata</i> (M. Bieb.) Cavara & Grande	Brassicaceae	High/medium	5
<i>Barbarea vulgaris</i> W.T. Aiton	Brassicaceae	Low/insignificant	2
<i>Berteroa incana</i> (L.) DC.	Brassicaceae	Low/insignificant	2
<i>Sinapis arvensis</i> L.	Brassicaceae	Low/insignificant	2
<i>Capsella bursa-pastoris</i> (L.) Medik.	Brassicaceae	Insignificant	1
<i>Erysimum cheiranthoides</i> L.	Brassicaceae	Not yet assessed	0
<i>Hesperis matronalis</i> L.	Brassicaceae	Medium/low	4
<i>Sisymbrium altissimum</i> L.	Brassicaceae	Not yet assessed	0
<i>Thlaspi arvense</i> L.	Brassicaceae	Low/insignificant	2
<i>Coronilla varia</i> L.	Fabaceae	High	6
<i>Lathyrus sylvestris</i> L.	Fabaceae	Not yet assessed	0
<i>Lotus corniculatus</i> L.	Fabaceae	Medium/low	4
<i>Medicago sativa</i> L.	Fabaceae	Insignificant	1
<i>Melilotus officinalis</i> (L.) Lam.	Fabaceae	Medium/low	4
<i>Trifolium repens</i> L.	Fabaceae	Medium/low	4
<i>Trifolium aureum</i> Pollich	Fabaceae	Not yet assessed	0
<i>Trifolium pratense</i> L.	Fabaceae	Low/insignificant	2
<i>Vicia cracca</i> L.	Fabaceae	Not yet assessed	0

Field Herbivore Damage

In the summer of 2007, I measured the amount of leaf damage sustained in the field for all 23 species in this study. For each species, 20 leaves were randomly collected from a population and this was repeated for three to four different populations whenever possible. It was not always possible to sample multiple populations as some plants are limited to a single population in the Ottawa region. Populations were chosen such that they were a minimum of 5 kilometers apart. All collection sites were areas with low human interference that had minimal chances of being fertilized or sprayed with pesticides. Leaves were sampled during the flowering phase for all plants in order to maintain consistency in the life-stage when damage was incurred. Leaves were scanned and leaf area measured using imaging software (Scion Image Beta 4.02, Scion Corporation, Frederick, Maryland, USA, <http://www.scioncorp.com>). Damage caused by chewers, miners and gall makers was measured along with the initial area of the leaf. In cases where a substantial portion was eaten, the initial area was estimated. The level of leaf damage sustained was estimated as the percentage of the entire leaf that showed evidence of herbivory.

Analysis

Leaf damage (%) was averaged across all populations for a given species. Owing to unequal variance in the leaf damage data, I could not use parametric methods to analyze the data. Average leaf damage was correlated to the numerical invasiveness ranking using a non-parametric Spearman's rank correlation. A Kruskal-Wallis non-parametric test was also used to test whether percent damage differed between plant families.

Generalist herbivores

In the summer of 2007, I tested the palatability of 21 introduced plants on two generalist herbivores, *Heliothis zea* Boddie (Lepidoptera: Noctuidae) and *Pseudaletia unipuncta* Haw. (Lepidoptera: Noctuidae).

The corn ear worm *Heliothis zea* occurs through most of North America except for Northern Canada and Alaska (Capinera, 2001). The larvae are highly polyphagous and have been reported to feed on over 100 different host plants including several weeds (Gore et al., 2003).

The true-armyworm *Pseudaletia unipuncta* occurs east of the Rocky Mountains. *P. unipuncta* maintains permanent populations in southern North America and migrates north up to Ontario every summer (McNeil, 1987). They are chiefly grassland herbivores but are known to feed on plants belonging to several different families (Usher *et al.*, 1988).

Generalist Feeding trials

Both generalist insects, *Pseudaletia unipuncta* and *Heliothis zea*, were obtained as eggs from a laboratory colony and the larvae were reared in individual vials at an average temperature of 27°C and average 16-hour day length. *Pseudaletia unipuncta* larvae were reared on a diet consisting of wheat grass, romaine lettuce and oats. *Heliothis zea* larvae were reared primarily on corn cobs and wheat grass. Larvae in their 4th instar were used for the feeding trials.

The experiments were carried out from early June to the end of September. I used a no-choice feeding assay for both generalist herbivores. The plant material was field collected on the day of the feeding trial or the day before and refrigerated. Medium-sized

leaves with the least amount of prior damage were used for the trials. The larvae were presented with 4.0 cm² leaf cuttings from each plant. When the leaves were too small to make a cutting, I used the entire leaf or several leaves yielding a total area of 4.0 cm². I set up 12 feeding trial replicates per plant species and a single replicate consisted of a 4th instar larva along with a leaf cutting of the plant. Each trial was carried out in a 90 mm Petri dish, which was lined with moist filter paper to prevent the leaf material from wilting. I ran the trials for 24 hours in an incubator at 27 ± 2 °C. After each trial, the leaf cutting was scanned and the leaf area consumed was measured. I used the area of leaf material consumed as an indicator of feeding damage. Prior to the feeding trials, all leaf cuttings were weighed using a precision digital balance (Mettler Toledo PG2002-S) and an average wet weight per cm² was obtained for the plant species. Weight per cm² was used to derive the wet leaf weight consumed from the area of the leaf material eaten. Leaf weight consumed was measured as an additional indicator of damage in order to account for differences in leaf thickness between species.

Analysis

The leaf area and weight consumed was averaged over the 12 replicates for each species. Non-parametric tests were used for both generalist feeding trials as the data did not meet the assumption of normality. A Spearman's rank correlation was calculated for average feeding damage and the numerical invasiveness ranking. A Kruskal-Wallis non-parametric test was also used to test whether percent damage differed between plant families.

Family-Specialist Herbivores

Apiaceae specialist

The black swallowtail butterfly, *Papilio polyxenes* Fabricius (Lepidoptera: Papilionidae), is a commonly occurring native Apiaceae specialist in North America (Layberry *et al.*, 1998). *P. polyxenes* larvae feed almost exclusively on the foliage of Apiaceae plants and are well adapted to tolerate the defensive furanocoumarin compounds found in these plants (Berenbaum, 1981). *P. polyxenes* has two generations in Ontario with flight occurring mid-May and early July (Layberry *et al.*, 1998). Adults live up to two weeks in the field and have been reported to live for over 5 weeks under laboratory conditions (Feeny *et al.*, 1985). Females oviposit on leaves of suitable host plants and the larvae go through five instars before pupation (Feeny *et al.*, 1985). The larval stage has been reported to take approximately 3-4 weeks to complete (Feeny *et al.*, 1985). Common larval hosts in the northern range include the introduced plants, *Daucus carota*, wild carrot and *Pastinaca sativa*, wild parsnip (Berenbaum, 1981).

Brassicaceae specialists

Pieris rapae L. (Lepidoptera: Pieridae), is a European Brassicaceae specialist, introduced to North America in the 1960's (Layberry *et al.*, 1998). It occurs throughout North America in the introduced range (Layberry *et al.*, 1998). The larvae are well adapted to feeding on the foliage of several species of Brassicaceae and are capable of metabolizing defensive glucosinolate compounds, which are ubiquitous in the Brassicaceae (Wheat *et al.*, 2007). The flight period ranges from mid-May to mid-October in Ontario with several overlapping generations (Layberry *et al.*, 1998). The

females oviposit on singly on the leaves and the larvae go through five instars before pupation (Benrey and Denno, 1997).

Pieris napi oleraceae Harris (Lepidoptera: Pieridae) is a native Brassicaceae specialist that occurs throughout North America but restricts its habitat to wooded areas and forest edges (Chew, 1981). They can have up to four generations in southern Ontario and the adults are in flight between mid-April to mid-September (Layberry *et al.*, 1998). Their chief native host plants include toothworts (*Dentaria* spp.), rock cress (*Arabis* spp.) and a few other mustards (Chew, 1981).

Fabaceae specialist

Colias philodice Godart (Lepidoptera: Pieridae), is a native Fabaceae specialist (Karowe, 1989). It occurs throughout Canada and the United States except in Labrador, northern Quebec and the Arctic (Layberry *et al.*, 1998). Native hosts of *C. philodice* include *Vicia americana* and *Lathyrus leucanthus*. *C. philodice* has expanded its host range to a few introduced plants including alfalfa, *Medicago sativa*, which is now one of its most preferred host plants (Tabashnik, 1983). They have two or more overlapping generations in Ontario and the butterflies are in flight from May to late-October (Layberry *et al.*, 1998). Females lay eggs singly on suitable host plants and the larvae take 5 – 8 weeks to eclosion (Stanton and Cook, 1983).

Insect collection and rearing

Female *P. polyxenes* butterflies were caught in early May, 2008, and housed in small cages, along with potted *Daucus carota* plants, in the laboratory. The plants were grown in the greenhouse from commercially bought carrot seeds (Imperator variety, OSC seeds, Waterloo, Ontario). *P. polyxenes* is known to oviposit readily on *D. carota* (Heinz

and Feeny, 2005). The butterflies were fed a solution of 1:2 honey water at least once daily and began ovipositing 2 – 3 days after capture. The eggs were removed from the plant using a soft paint brush and placed on a sheet of Parafilm, which was checked daily for newly hatched larvae.

Female *P. rapae* butterflies were caught in late June, 2008 and *C. philodice* females were caught mid-July, 2008. The butterflies were transferred to a cage in the greenhouse along with a suitable plant for oviposition and a pot of yellow *Lantana camara* plants to provide nectar. Greenhouse-grown cabbage, *Brassica oleracea*, (Savoy Chieftan variety, OSC seeds, Waterloo, Ontario) was used as an oviposition site for *P. rapae* and cuttings of alfalfa (*Medicago sativa*) were used for *C. philodice*. Cabbage and alfalfa are known to stimulate oviposition in *P. rapae* and *C. philodice* females, respectively. The butterflies readily oviposited on the substrate, which was replaced every day. Plants were checked daily for newly hatched larvae.

P. napi oleraceae eggs were shipped to Carleton University in early May from a permanent colony reared at the University of Rhode Island. The eggs were maintained on a sheet of Parafilm until hatching.

Larval Survivorship

I measured the survivorship of *P. polyxenes*, *P. rapae* and *C. philodice* larvae on introduced plants from Apiaceae, Brassicaceae and Fabaceae, respectively. I also tested a native Brassicaceae specialist, *P. napi oleraceae*, on a few exotic Brassicaceae. The rearing methods were consistent for all three family specialists. Neonate larvae were transferred to 90 mm diameter plastic Petri dishes along with leaf material from one of the introduced plant species used in the study (Table 1). Leaf material was always

provided in excess of consumption. Leaves were collected from the field at least once a week and refrigerated until used in the feeding trial. Twenty replicates, each consisting of a Petri dish with one larva and leaf cuttings, were set up for each plant species. The larvae were reared in the laboratory under 16:8 day length maintained by a 60W light bulb. The day: night temperature was on average $27: 20 \pm 2^{\circ}\text{C}$. The larvae were observed daily for feeding damage, mortality and molting until pupation. The presence of a shed head-capsule was used as evidence for molting. The filter paper along with the leaf material was replaced every other day. For each plant species, I measured a) The percentage of neonates that initiated feeding b) The percentage that continued feeding c) Percentage of larvae that survived to each instar and to pupation d) Time taken (days) to develop to each instar and to pupation.

Analysis

As the percentage of larvae that survived to pupation on a plant species appeared to fall within high and low extremes, survival was analyzed as a categorical variable. Introduced plants with a low numerical ranking (0-3) were categorized as Non-invasive and plants with a high ranking (4-6) were categorized as Invasive. Owing to the low number of introduced plants in each family, the data from all three plants families was pooled together. I analyzed the relationship between survival to pupation on a plant species and the plant's invasiveness, using a G-test of independence (Sokal and Rohlf, 1987). The relationship between neonate initiation of feeding, continuation of feeding and plant invasiveness was analyzed using a G-test of independence as well. *Pieris napi oleraceae* survival data were not included in the analysis as *P. napi oleraceae* did poorly on all plants tested including *Brassica oleraceae*, which was used as a control.

Oviposition trials

As I was unable to induce mating in *P. napi. oleraceae* and *C. philodice*, oviposition trials were only conducted for *P. polyxenes* and *P. rapae*.

P. polyxenes oviposition

Eggs collected from wild caught *P. polyxenes* were reared on greenhouse grown *D. carota* plants. Multiple larvae were raised on a single plant in a 35x35x30 cm cage in the laboratory under 16:8 day/night cycle. The plants were replaced when all the leaf material was consumed. Fourth instar larvae were capable of consuming an entire plant within 24 hours and were raised individually in Petri dishes until pupation. The pupae were collected from the dishes, glued to a piece of cotton and suspended on a section of mosquito netting using insect pins. The netting was then screwed to the top of a 13 x 7 cm, 500 ml Mason jar (Bernardin, Toronto, ON) and the pupae were left to emerge. One day after eclosion, the butterflies were hand-fed a solution of 1:2 honey-water and hand-mated following the procedure outlined in Clarke and Sheppard (1956). Mated females were transferred to an oviposition cage (35x35x30 cm) along with a single potted plant of one of the introduced Apiaceae for this experiment. All five species of Apiaceae were directly transplanted from the field and placed singly in ProMix soil (Premier Horticulture, Ltd., Dorval, QC) in a 6" plastic pot. The females were hand-fed daily until they died. The eggs were counted every second day, removed from the plant using a soft bristled paint brush and placed on a piece of Parafilm. The eggs obtained were used to set up a second generation of swallowtail butterflies. The rearing procedure was identical for the second generation larvae. As the number of butterflies from the first generation was not sufficient to conduct all oviposition experiments, a second generation of butterflies

was required. *Daucus carota* was the only plant tested with 1st generation of females that emerged in the lab. All other Apiaceae were tested with 2nd generation butterflies.

P. rapae oviposition

Eggs collected from wild caught *P. rapae* were raised on greenhouse grown cabbage plants. All cabbage plants and larvae were placed in a large cage (60x60x60 cm) in the Carleton University greenhouse. The plants were watered regularly and replaced when all the leaves were consumed. The larvae were allowed to pupate on the plant or anywhere in the cage. The pupae were left undisturbed until the butterflies emerged.

I was unable to hand-mate *P. rapae* as they were easily damaged on handling. Butterflies were observed mating in the rearing cage but as it was difficult to differentiate between mated and unmated females, I could not set up individual no-choice mating arenas. Instead, I set up a choice experiment by placing pots of seven introduced Brassicaceae plants in the rearing cage. The plants were directly transplanted from the field and placed singly in ProMix soil in 6" plastic pots. The plants were checked every other day for eggs. The plants were also randomly rearranged to ensure that choice was not based on the position of the plant. The eggs were counted until all butterflies died.

Analysis

Insufficient replicates were obtained to perform robust statistical analyses. General oviposition trends are presented instead.

Defensive Chemistry

In addition to testing whether invasive plants were less palatable to herbivores, I was also interested in looking for unusual defenses that might render invasive exotics more deterrent compared to non-invasive exotics. I consulted Harborne *et al* (1999), Dr.

Duke's phytochemical and ethnobotanical database (<http://www.ars-grin.gov/duke/>) and ISI Web of Science in order to obtain information on the chemical defenses present in each of the test species (Appendix 1). For exotic plants in the Apiaceae, I also examined the distribution and concentration of six furanocoumarin compounds, occurring in the leaves of the Apiaceae that were sampled for this study. I detected and measured the concentration of these compounds with available furanocoumarin standards, using HPLC techniques.

Furanocoumarin Extraction Methods

Plant material was collected from each of the Apiaceae species (Table 1) during the month of September, 2008. Leaves were separated from other plant parts and frozen at -20°C for 72 hours. The frozen leaf material was then freeze dried for 48 hours in a EC-Modulyo Freeze Dryer. The dried material was finely ground using an industrial grade Warring blender. Crude leaf extracts were obtained using 80 % ethanol as a solvent.

10 g of crude leaf material from each plant was dissolved in 100 ml of 80% ethanol. The solution was homogenized in a New Brunswick Scientific Rotary Shaker for 24 hours. The material was filtered through 90mm Wattman filter paper (Cat#1001 090) using a Buchner Funnel and a KNF Neuberger Laboport bidirectional pump. The filtrate was stored in a refrigerator at 4°C. The solids were re-dissolved, in order to obtain furanocoumarin compounds that might not have been pulled out in the first extraction. Solids were dissolved in 100 ml of 80% ethanol, homogenized and filtered using the same techniques. The filtrates from the first and second extractions were then pooled. The crude extract obtained was centrifuged in a Thermo IEC Micromax RF refrigerated

microcentrifuge. The supernatant was removed and filtered through at 0.2 μ M Chromspec syringe filter to remove an excess of chlorophyll and particulates. The resulting filtrate used for the HPLC analysis at 1:10 dry mass: volume EtOH.

The identity of furanocoumarin compounds were confirmed using commercial furanocoumarin standards as well as furanocoumarin standards previously isolated in Dr. John Arnason's lab at the University of Ottawa. Serial dilutions of the standards were used to create a calibration curve and obtain furanocoumarin concentrations in the test species. Peaks were detected using a Sourbus Fr at wavelengths between 210 nm and 280 nm. HPLC grade Acetonitrile and Water were used as the mobile phase. Injection was through a YMC-13 (YMC-ODS, AM-100x2.1), 3 micrometer particle size syringe. The column was run for 25 min at 0.4 ml/min with a column temperature of 45C.

Taxonomic Isolation

For each plant species in the study, I used the number of native congeneric plants as an indicator of the plants taxonomic isolation. I consulted the United States Department of Agriculture database (plants.usda.gov) to obtain the number of native plants for all genera, in this study.

Analysis

The correlation between Invasiveness of a plant and its relatedness to native plants was determined using a non-parametric Spearman's rank correlation

RESULTS

Field Herbivore Damage

Introduced plants with higher invasiveness ranks sustained lower levels of leaf damage in the field (Figure 1, Spearman's Rho = -0.41, P-value = 0.03). The two highly invasive plants in this study, *Alliaria petiolata* (rank = 5) and *Coronilla varia* (rank = 6), had less than 1% leaf damage on average. Mean leaf damage did not differ between plants from the Apiaceae, Brassicaceae and Fabaceae (Figure 2, Kruskal-Wallis, Chi-sq = 2.927, P-value = 0.23). Interestingly, of the five species of Apiaceae in the study, four plants had marginal levels of leaf damage and only *Angelica sylvestris* suffered substantial levels of leaf herbivory.

Generalist herbivores

Feeding trials

Pseudaletia unipuncta feeding damage, indicated by leaf area and leaf weight consumed, was significantly correlated to plant invasiveness (Figure 3a, Leaf area: Spearman's Rho = -0.46, P-value = 0.02, Figure 3b, Leaf Weight: Spearman's Rho = -0.46, P-value = 0.02). *P. unipuncta* ate low amounts of leaf material from highly invasive plants or avoided sampling the leaf material altogether. *Alliaria petiolata* had no feeding damage and *Coronilla varia* was sampled but not consumed. *P. unipuncta* fed less on most Apiaceae. However, average feeding damage was not significantly different between plant families (Figure 4, Kruskal-Wallis, Chi-sq = 5.10, P-value = 0.08)

Heliothis zea feeding damage was not correlated to plant invasiveness (Figure 5a Leaf Area: Spearman's Rho = 0.02, P-value = 0.45, Figure 5b, Leaf Weight: Spearman's Rho = -0.002 P-value = 0.49). While there was no relationship between feeding damage

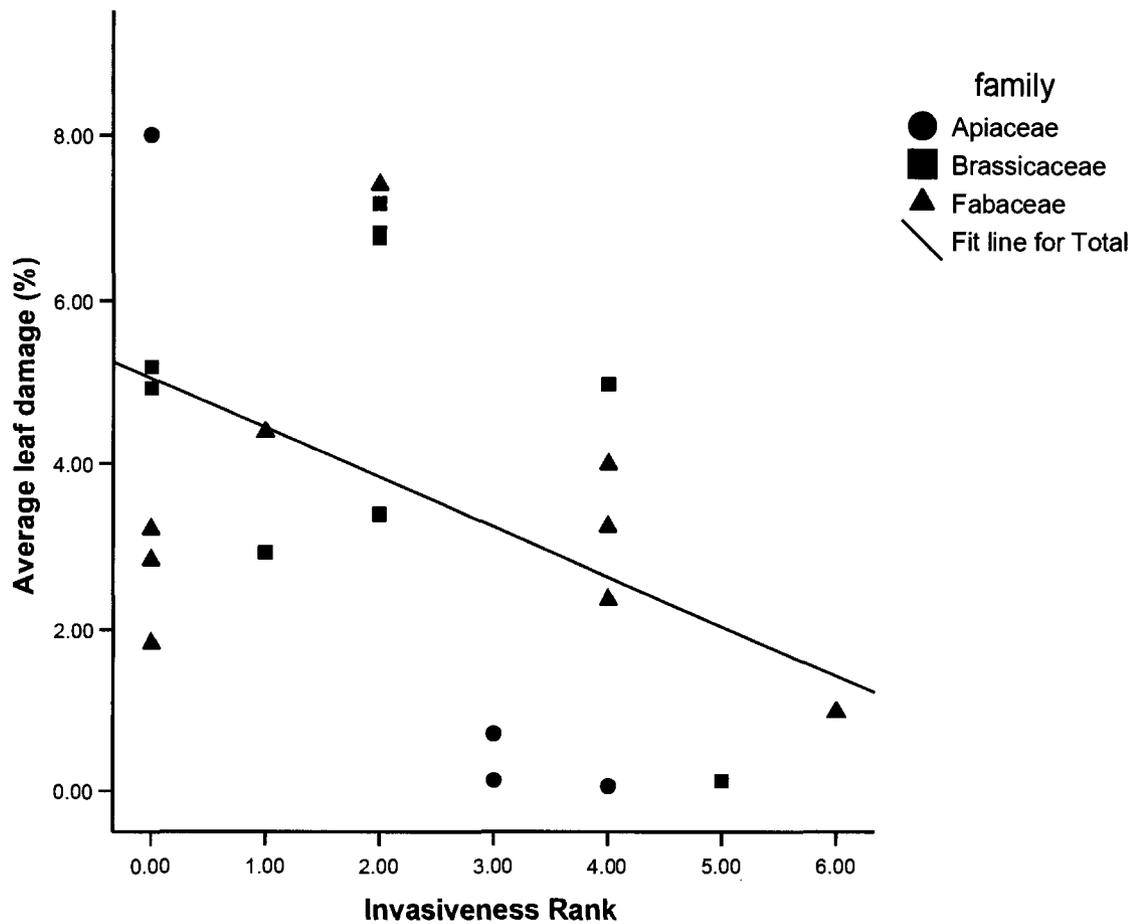


Figure 1: Relationship between leaf damage (%) sustained in the field and the numerical invasiveness ranking obtained from the NatureServe I-Rank (www.natureserve.com). Points are species means for leaf damage across different populations with 20 replicates in each population. Correlation between average leaf damage (%) and invasiveness is significant. $R^2 = 0.199$, Spearman's Rho = -0.41, $P = 0.03$.

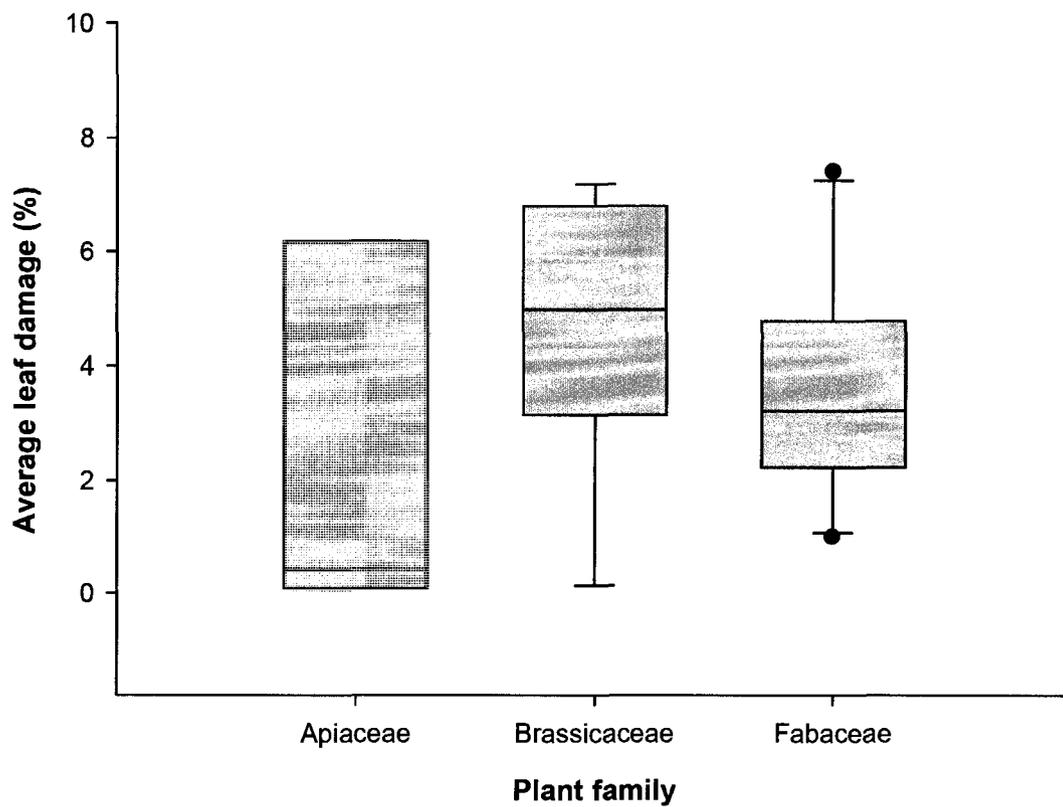


Figure 2: Comparison of average leaf damage (%) sustained in the field between the plant families; Apiaceae, Brassicaceae and Fabaceae. Box plots indicate the median and 3rd quartiles of the mean damage incurred in the family. Difference in leaf damage between the families is not significant, Kruskal-Wallis test, Chi-sq = 2.927, P = 0.231

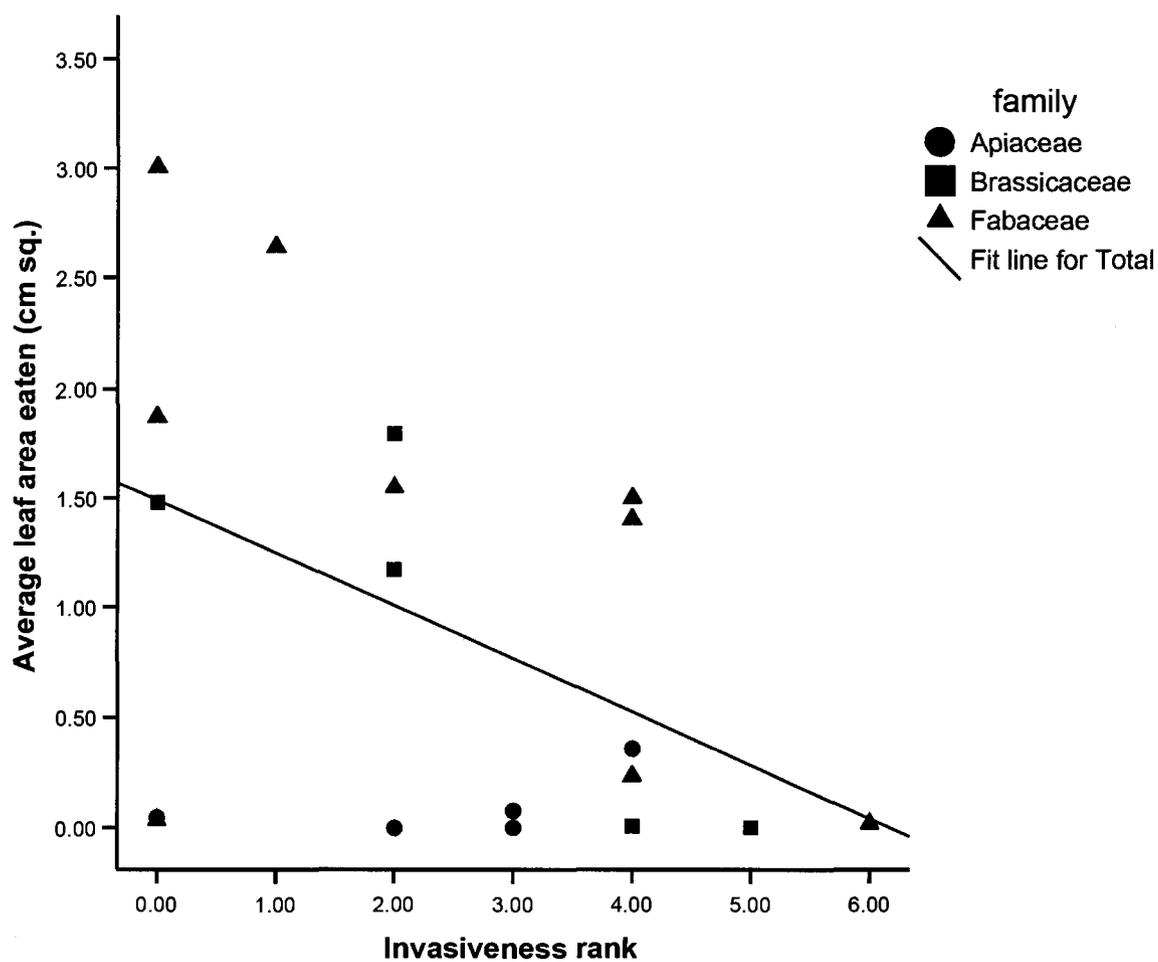


Figure 3 a: Relationship between leaf area consumed (cm^2) by *Pseudaletia unipuncta* and the numerical invasiveness ranking obtained from the NatureServe I-Rank (www.natureserve.com). Points indicate mean feeding damage on each plant species. Correlation between feeding damage and invasiveness is significant. $R^2 = 0.215$, Spearman's Rho = -0.45, $P = 0.03$

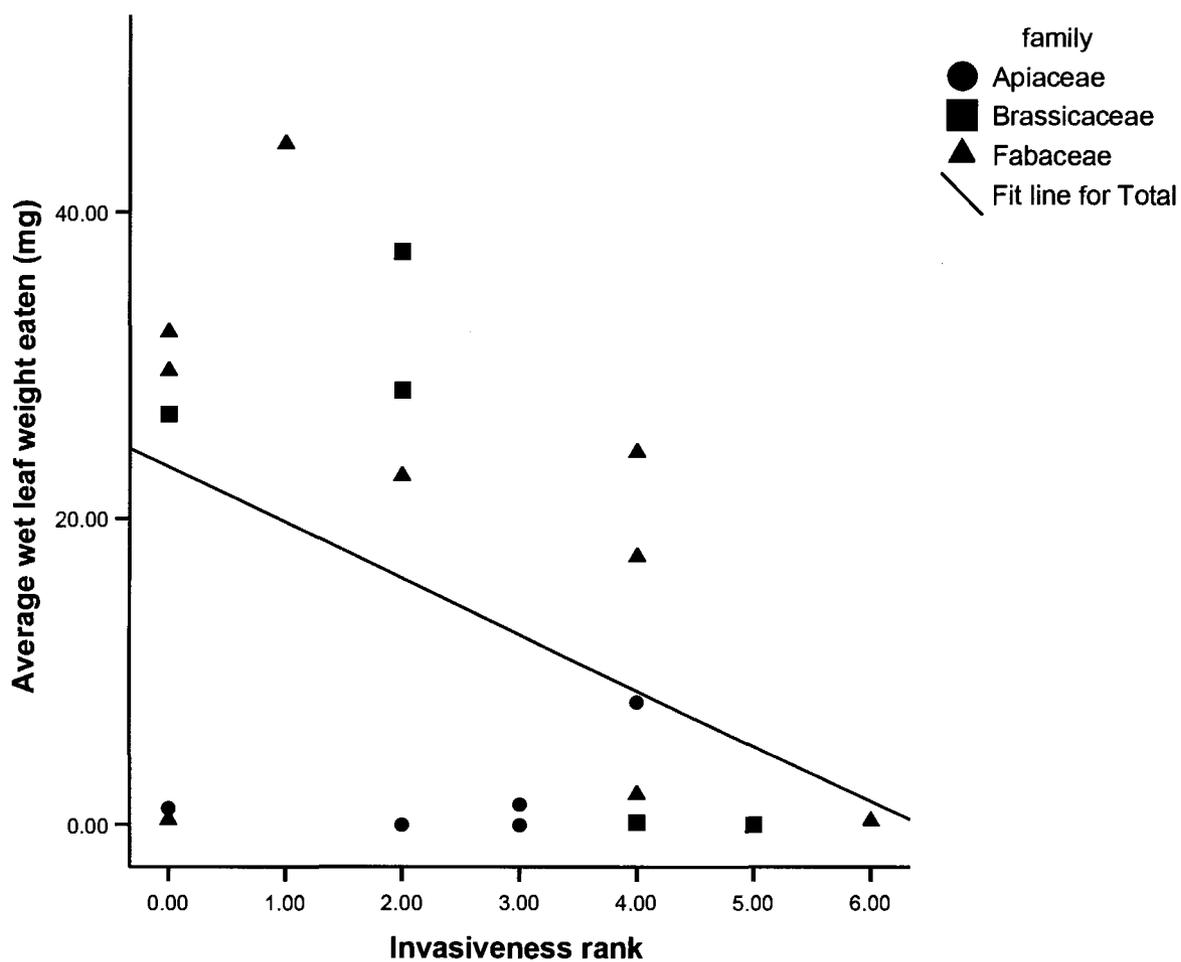


Figure 3 b: Relationship between leaf weight consumed (mg) by *Pseudaletia unipuncta* and the numerical invasiveness ranking obtained from the NatureServe I-Rank (www.natureserve.com). Points indicate mean feeding damage on each plant species. Correlation between feeding damage and invasiveness is significant. $R^2 = 0.2$, Spearman's Rho = -0.46, $P = 0.02$.

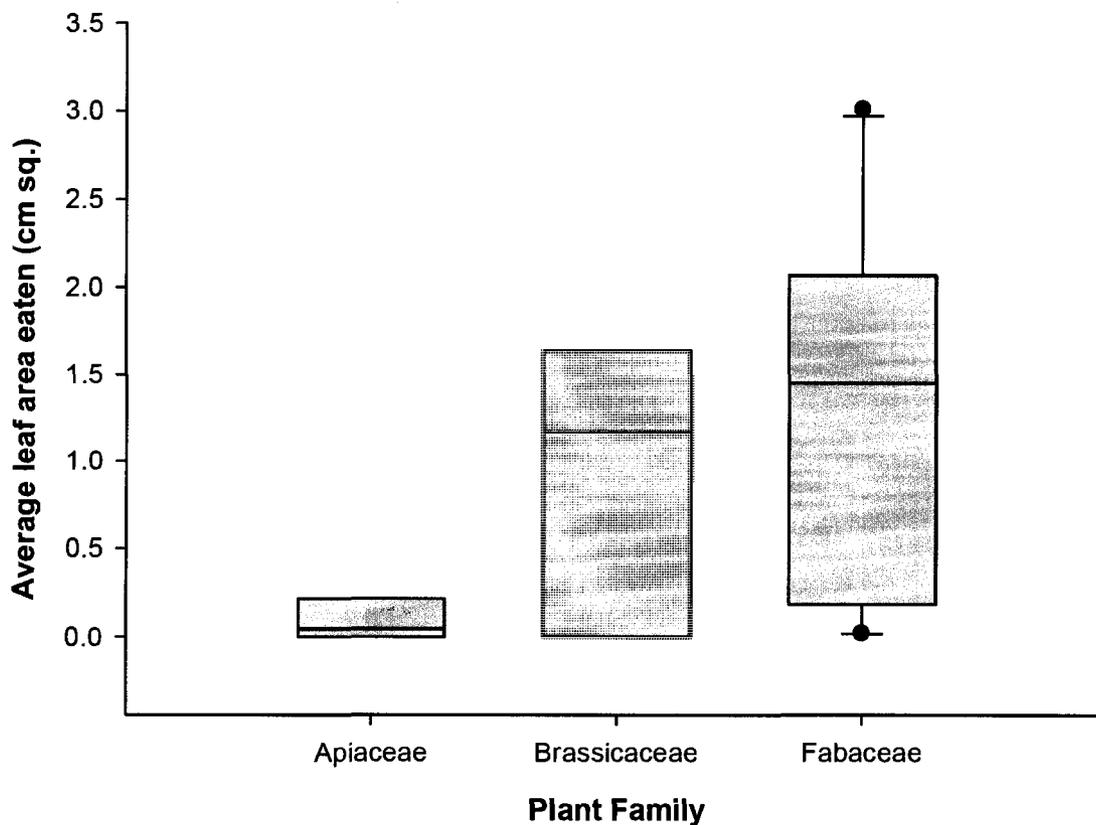


Figure 4: Comparison of feeding damage (leaf area eaten cm^2) by *Pseudaletia unipuncta* between the plant families; Apiaceae, Brassicaceae and Fabaceae. Box plots indicate the median and 3rd quartiles of the mean damage incurred in the family. Difference in leaf damage between the families is not significant, Kruskal-Wallis test, Chi-sq = 5.10, P = 0.08

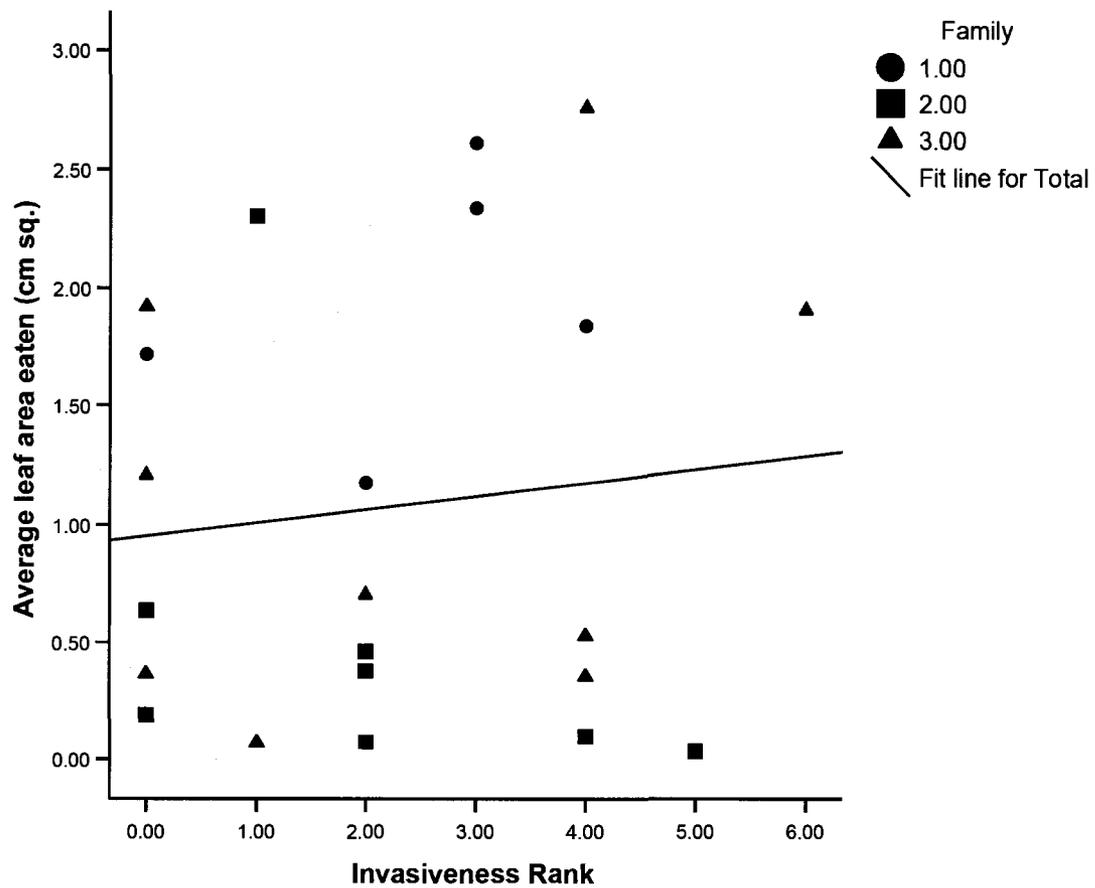


Figure 5 a: Relationship between leaf area consumed (cm^2) by *Heliothis zea* and the numerical invasiveness ranking obtained from the NatureServe I-Rank (www.natureserve.com). Points indicate mean feeding damage on each plant species. Correlation between feeding damage and invasiveness is not significant. $R^2 = 0.012$, Spearman's Rho = 0.02, $P = 0.46$

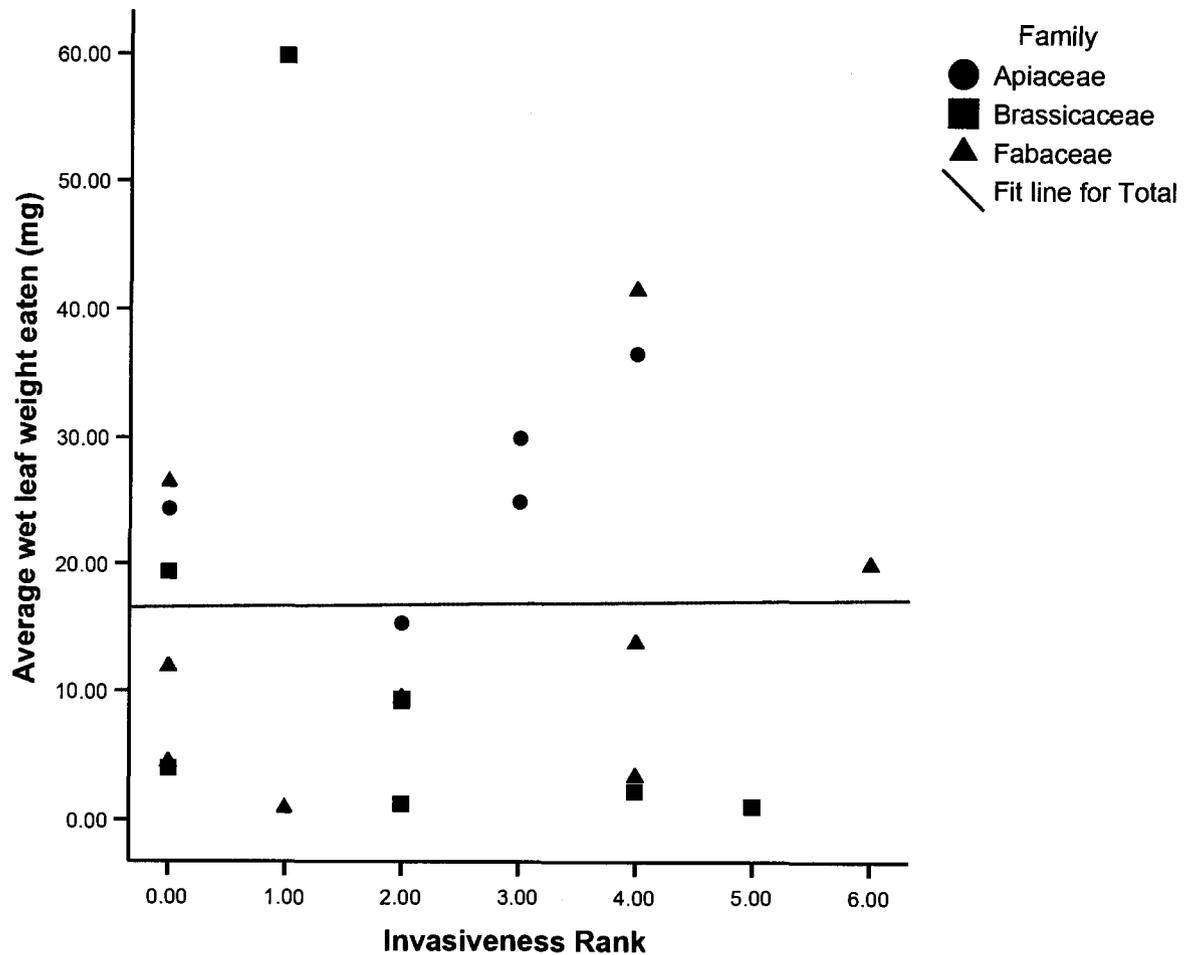


Figure 5: Relationship between leaf weight consumed (mg) by *Heliothis zea* and the numerical invasiveness ranking obtained from the NatureServe I-Rank (www.natureserve.com). Points indicate mean feeding damage on each plant species. Correlation between feeding damage and invasiveness is not significant. $R^2 = 1.47 \text{ E-}4$, Spearman's Rho = -0.002, $P = 0.49$.

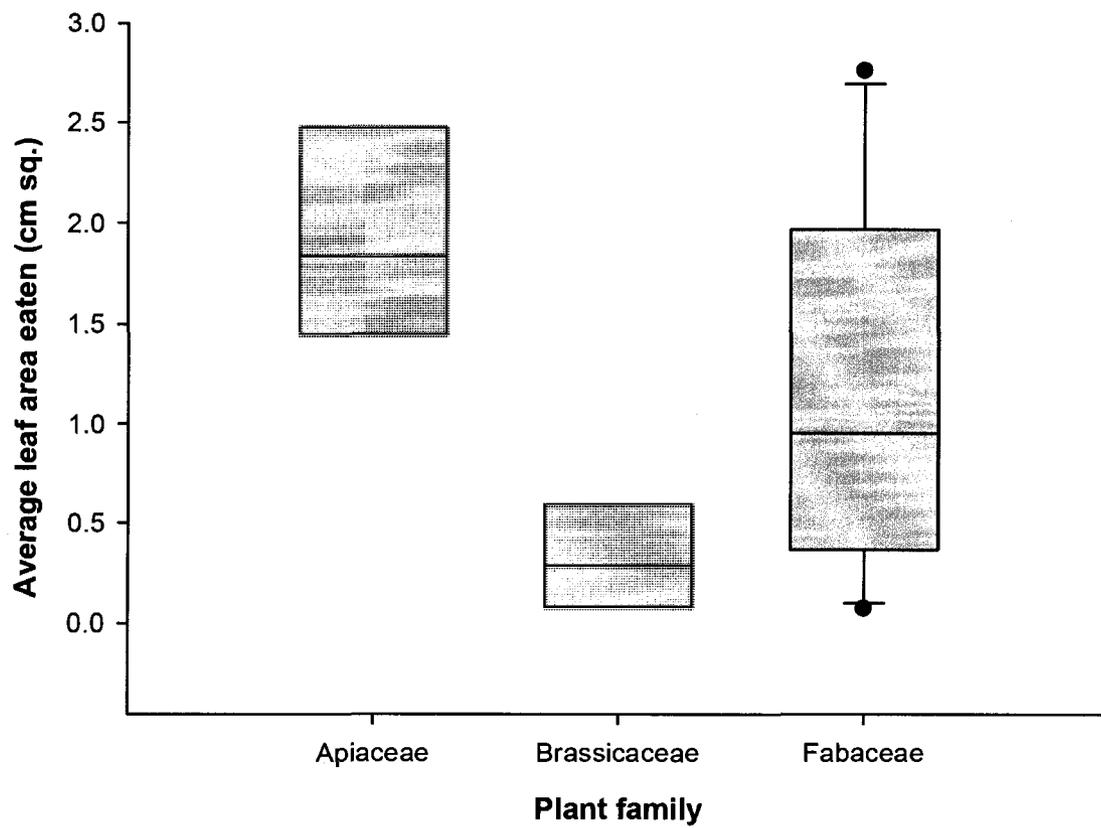


Figure 6: Comparison of feeding damage (leaf area eaten cm^2) by *Heliothis zea* between the plant families; Apiaceae, Brassicaceae and Fabaceae. Box plots indicate the median and 3rd quartiles of the mean damage incurred in the family. Difference in leaf damage between the families is significant, Kruskal-Wallis test, Chi-sq = 6.67, P = 0.03

and invasiveness, *H. zea* did not feed on the invasive plant, *Alliaria petiolata*.

Interestingly, *H. zea* avoided feeding on a number of Brassicaceae plants and the difference in average feeding damage between families is statistically significant (Figure 6, Kruskal-Wallis, Chi-sq = 6.67, P-value = 0.03).

Family-specialist herbivores

Larval Survivorship

Oligophagous specialist herbivores did not have lower survival on invasive plants as compared to non-invasive plants. There appeared to be no relationship between survival to pupation and the plant's invasiveness for all three plant families pooled together (Table 2). There was also no relationship between larval initiation and continuation of feeding on a plant and the plant's invasiveness, as well (Table 2).

P. polyxenes larval survival on *Heracleum mantegazzianum*, the most invasive Apiaceae in this study, was relatively high (75% survived to pupation). However, *P. polyxenes* larvae did poorly on *Aegopodium podagraria* (45% survived to pupation) and *Angelica sylvestris* (35% survived to pupation), both of which are non-invasive (Figures 7 & 8).

P. rapae larvae did poorly on the invasive plant, *Hesperis matronalis*, (50% survived to pupation) but had high survivorship on another invasive, *Alliaria petiolata* (95% survived to pupation). Interestingly, *P. rapae* larvae had zero survivorship on two non-invasive plants, *Capsella bursa-pastoris* and *Erysimum cheiranthoides*. Most of the larvae refused to initiate feeding on these plants (10% initiated feeding on *C. bursa-pastoris*, 5% initiated feeding on *E. cheiranthoides*), none of the larvae continued feeding and none survived past the 1st instar (Figures 9 & 10).

Two invasive Fabaceae plants, *Lotus corniculatus* and *Melilotus officinalis*, did not support *C. philodice* larval development. Over 80 % of larvae initiated and continued feeding on both plants but almost none survived past the 2nd instar. *C. philodice* had zero survival on the non-invasive plant, *Lathyrus sylvestris*, as well. However, *C. philodice* larval survivorship on the invasive plant, *Coronilla varia*, was high (70% survived to pupation) (Figures 11 & 12).

Oviposition trials

The number of eggs laid on each plant was extremely variable and dropped significantly in second-generation females. *P. polyxenes* laid the highest number of eggs on *Daucus carota*, an average of 113.2 eggs over the lifetime of a female. The number of eggs laid was extremely variable and ranged from 329 to 8 eggs per female. The average female lifespan was 20.6 days, in the *D. carota* oviposition trials. Second generation *P. polyxenes* females had a shorter life span on average (14.5 days). The average number of eggs laid by second generation females ranged from 8 eggs on *Pastinaca sativa* to zero on *Heracleum mantegazzianum* and *Aegopodium podagraria*, over the lifetime of a female (Table 3).

In the *P. rapae* choice oviposition experiment, the highest number of eggs were found on *Barbarea vulgaris* (Table 4, 292 over 5 days). *P. rapae* females laid a fairly large proportion of eggs on the highly invasive plant, *Alliaria petiolata* (40 eggs over 5 days) but none were found on the other invasive plant, *Hesperis matronalis*. Few eggs were found on *Berteroa incana* (8 eggs), *Capsella bursa-pastoris* (11 eggs) and *Erysimum cheiranthoides* (2 eggs).

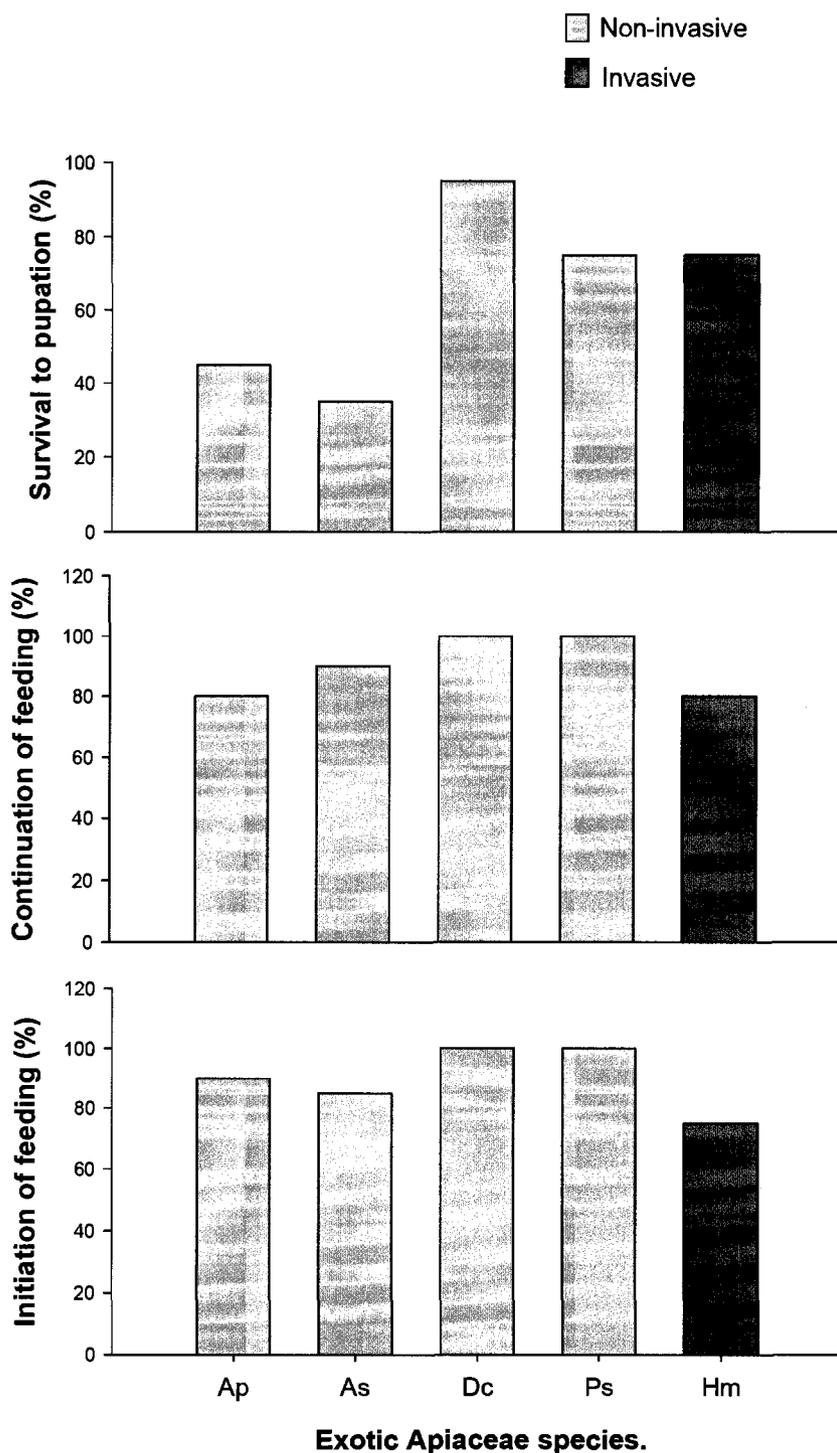


Figure 7: Percentage of *P. polyxenes* larvae that initiated feeding, continued feeding and survived to pupation on each exotic Apiaceae species. 20 larval replicates were reared on each exotic species. (Ap = *Aegopodium podagraria*, As = *Angelica sylvestris*, Dc = *Daucus carota*, Ps = *Pastinaca sativa*, Hm = *Heracleum mantegazzianum*)

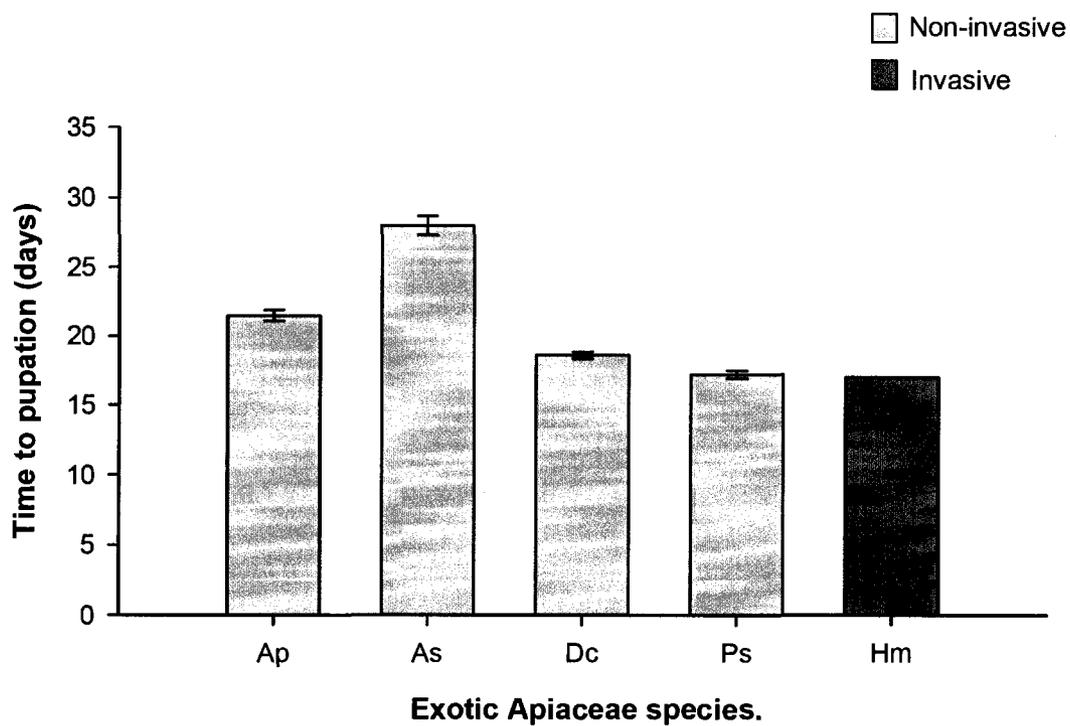


Figure 8: Average time taken for *P. polyxenes* larvae to develop from egg to pupation (in days) on each plant. Error bars are \pm Standard Error. 20 larval replicates were reared on each exotic species. (Ap = *Aegopodium podagraria*, As = *Angelica sylvestris*, Dc = *Daucus carota*, Ps = *Pastinaca sativa*, Hm = *Heracleum mantegazzianum*)

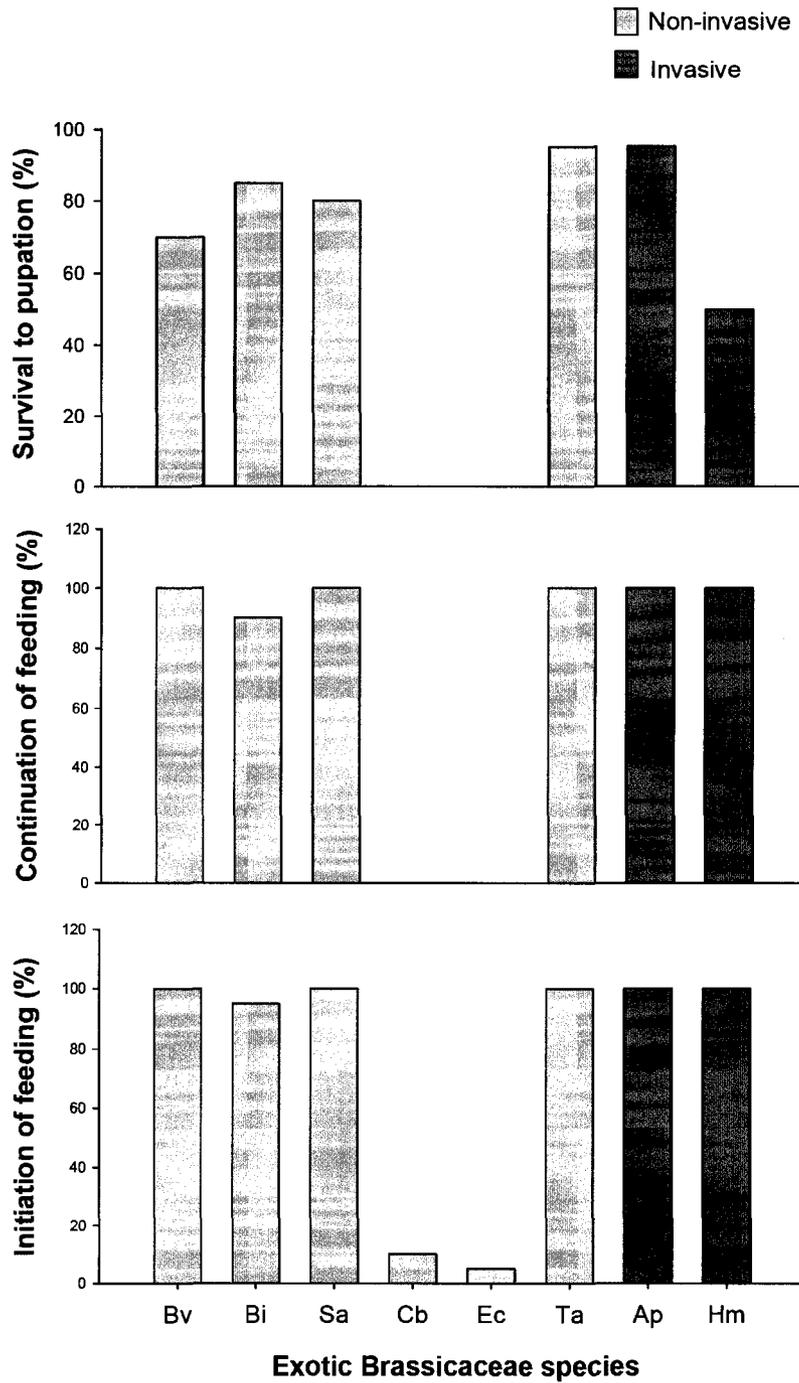


Figure 9: Percentage of *P. rapae* larvae that initiated feeding, continued feeding and survived to pupation on each exotic Brassicaceae species. 20 larval replicates were reared on each exotic species. (Bv = *Barbarea vulgaris*, Bi = *Berteroa incana*, Sa = *Sinapis alba*, Cb = *Capsella bursa-pastoris*, Ec = *Erysimum cheiranthoides*, Ta = *Thlaspi arvense*, Ap = *Alliaria petiolata*, Hm = *Hesperis matronalis*)

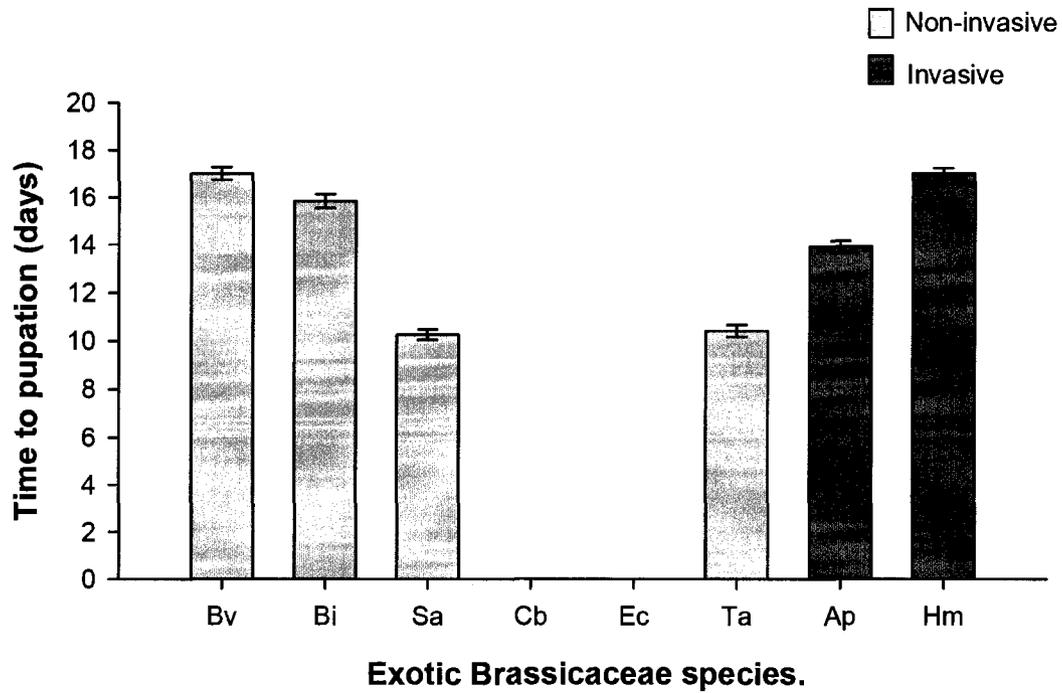


Figure 10: Average time taken for *P. rapae* larvae to develop from egg to pupation (in days) on each plant. Error bars are \pm Standard Error. 20 larval replicates were reared on each exotic species. (Bv = *Barbarea vulgaris*, Bi = *Berteroa incana*, Sa = *Sinapis alba*, Cb = *Capsella bursa-pastoris*, Ec = *Erysimum cheiranthoides*, Ta = *Thlaspi arvense*, Ap = *Alliaria petiolata*, Hm = *Hesperis matronalis*)

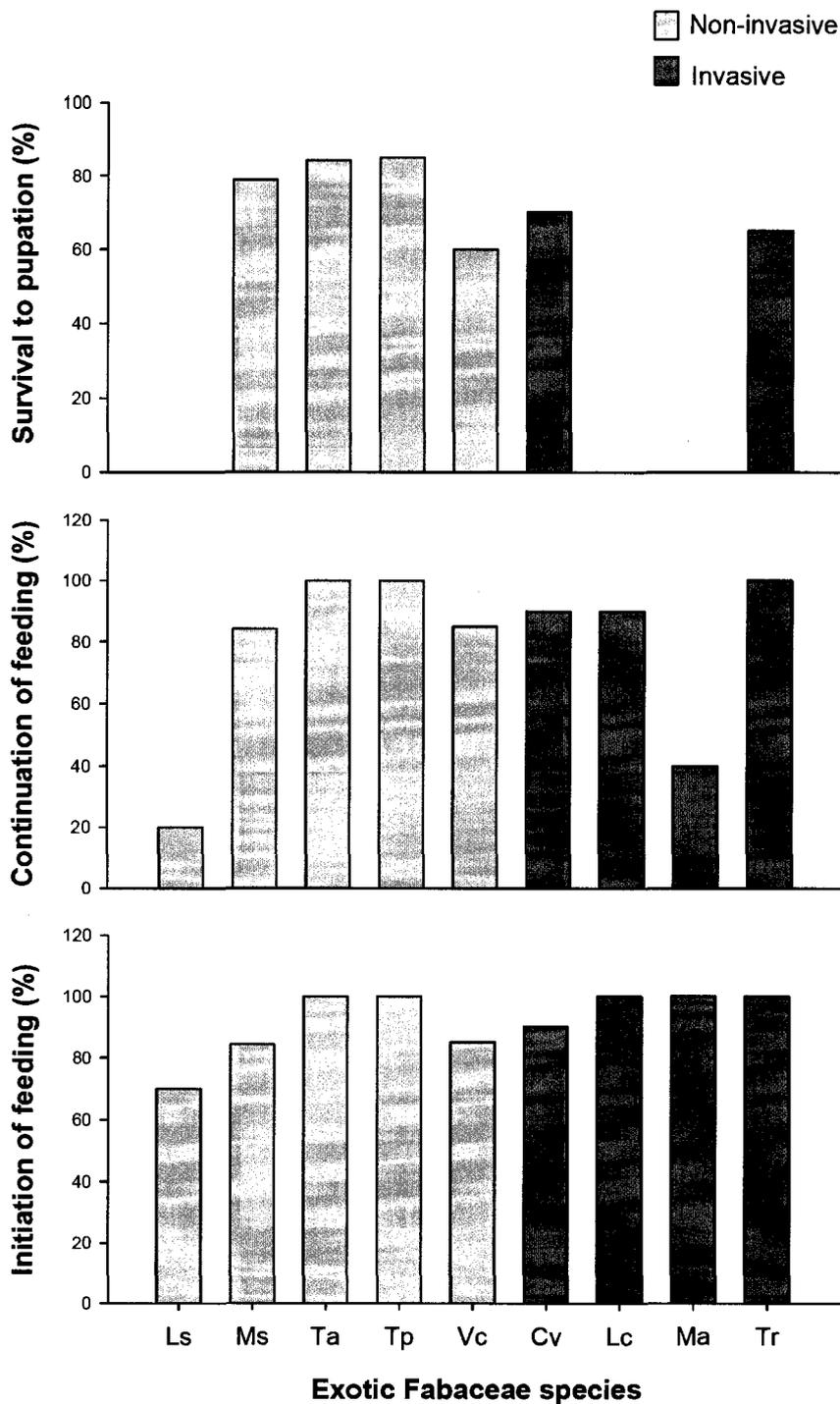


Figure 11: Percentage of *C. philodice* larvae that initiated feeding, continued feeding and survived to pupation on each exotic Fabaceae species. 20 larval replicates were reared on each exotic species. (Ls = *Lathyrus sylvestris*, Ms = *Medicago sativa*, Ta = *Trifolium aureum*, Tp = *Trifolium pratense*, Vc = *Vicia cracca*, Cv = *Coronilla varia*, Lc = *Lotus corniculatus*, Ma = *Melilotus alba*, Tr = *Trifolium repens*)

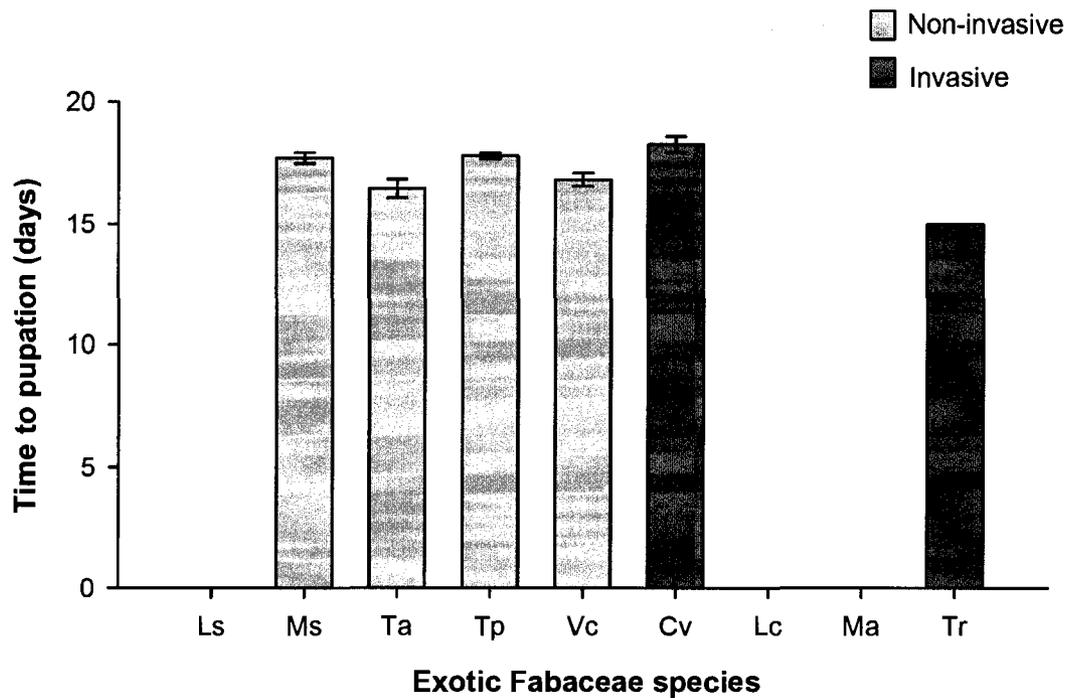


Figure 12: Average time taken for *C. philodice* larvae to develop from egg to pupation (in days) on each plant. Error bars are \pm Standard Error. 20 larval replicates were reared on each exotic species. (Ls = *Lathyrus sylvestris*, Ms = *Medicago sativa*, Ta = *Trifolium aureum*, Tp = *Trifolium pratense*, Vc = *Vicia cracca*, Cv = *Coronilla varia*, Lc = *Lotus corniculatus*, Ma = *Melilotus alba*, Tr = *Trifolium repens*)

Table 2: Exotic invasive and non-invasive plant species that supported > 50% survival to pupation, initiation of feeding and continuation of feeding of oligophagous specialist herbivores. Relationships are analyzed using a G-test of independence.

		Invasiveness			G-value	df	P-value
		Non-invasive	Invasive	Total			
Survival to Pupation(>50%)	No	5	3	8	0.18506	1	0.667
	Yes	10	4	14			
Total		15	7	22			
Initiation of Feeding (>50%)	No	3	1	4	1.623754	1	0.202
	Yes	12	6	18			
Total		15	7	22			
Continuation of Feeding (>50%)	No	2	0	2	0.108429	1	0.741
	Yes	13	7	20			
Total		15	7	22			

Table 3: No-choice oviposition by *P. polyxenes* females on introduced Apiaceae plant species. Eggs counts indicate the average number of eggs laid by over the lifetime of one female.

Species	Invasiveness Rank	Average egg count over female lifetime
<i>Aegopodium podagraria</i>	3	0
<i>Angelica sylvestris</i>	0	3
<i>Daucus carota</i>	3	113.2
<i>Heracleum mantegazzium</i>	4	0
<i>Pastinaca sativa</i>	2	8

Table 4: Choice oviposition by *P. rapae* females on introduced Brassicaceae plant species. Eggs counts indicate total number of eggs found on each plant species.

Species	Invasiveness Ranking	Total egg count
<i>Alliaria petiolata</i>	5	40
<i>Barbarea vulgaris</i>	2	292
<i>Berteroa incana</i>	2	8
<i>Sinapis arvensis</i>	2	137
<i>Capsella bursa-pastoris</i>	1	11
<i>Erysimum cheiranthoides</i>	0	2
<i>Hesperis matronalis</i>	4	0
<i>Thlaspi arvensis</i>	2	23
<i>Brassica oleraceae</i>	0	206

Defensive Chemistry

Defensive phytochemicals that have been reported for each of the exotic species along with the activity and distribution of the phytochemical compound in other plants, whenever known, are outlined in Appendix 1.

The highest concentration of furanocoumarin compounds were detected in *Pastinaca sativa* and *Heracleum mantegazzianum*, with *P. sativa* having slightly higher concentrations (Table 5). *P. sativa* leaves were predominantly defended by Imperatorin, a linear furanocoumarin while *H. mantegazzianum* contained a large concentration of Angelicin, an angular furanocoumarin (Table 5). Comparatively low furanocoumarin concentrations were detected in *Daucus carota*, *Aegopodium podagraria* and *Angelica sylvestris* (Table 5).

Taxonomic Isolation

Invasive plants in this study did not have fewer native congeners compared to non-invasive plants (Figure 13, Spearman's Rho = -0.16, P-value = 0.23).

Table 5: Distribution and concentration of furanocoumarin compounds in five exotic Apiaceae plants. Concentrations are measured as $\mu\text{g} / \text{mg}$ of dry leaf weight. Furanocoumarin compounds detected and compared to known standards via HPLC methods (Appendix 2)

	Angelicin	Trimethoxy coumarin	Imperatorin	Bergapten	Isopimpinellin	Psoralen	Total
<i>Aegopodium podagraria</i>		0.028	0.183	0.126			0.339
<i>Angelica sylvestris</i>	0.204	0.051		0.079	0.001		0.337
<i>Daucus carota</i>			0.040			0.171	0.212
<i>Heracleum mantegazzianum</i>	4.408		0.053	2.029		3.08	9.573
<i>Pastinaca sativa</i>	2.217		5.925	1.216		1.065	10.426

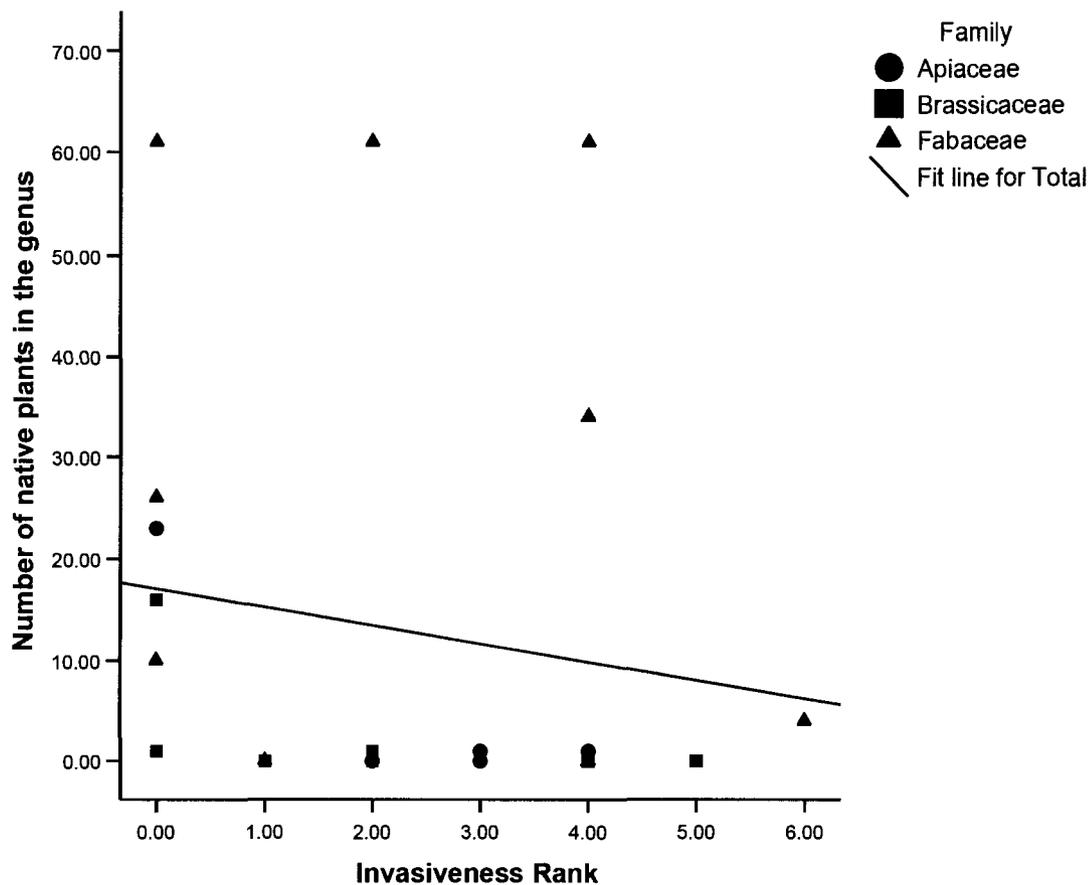


Figure 13: Relationship between the relatedness of an introduced plant species to North American taxa and the numerical invasiveness ranking, obtained from the NatureServe I-Rank (www.natureserve.com). Relatedness for each species is calculated as the number of native congeneric plants occurring in North America. Correlation between relatedness and invasiveness is not significant $R^2 = 0.024$, Spearman's Rho = -0.249, $P = 0.126$

DISCUSSION

Observed leaf damage strongly suggests that the highly invasive plants, in each family, suffer minimal amounts of damage in the field (Figure 1). These findings are consistent with previous comparisons of enemy release on invasive and non-invasive exotic plants (Carpenter and Cappuccino, 2005; Cappuccino and Carpenter, 2005; Mitchell and Power, 2002), implying that invasion potential could in part be ascribed to enemy escape. Nevertheless, there are a few recent studies that suggest otherwise. Dawson *et al.* (2008) found no correlation between leaf damage and invasiveness in introduced tropical plants. Invasive and non-invasive *Eugenia* spp. did not differ in their levels of leaf damage (Liu *et al.*, 2007). Invasive *Trifolium* and *Medicago* spp. did not host more pathogens or incur high levels of herbivory in comparison to non-invasive species in these genera (Parker and Gilbert, 2007). ‘Invasive’ and ‘Non-Invasive’ are not well-defined terms and this ambiguity might account for the discrepancy between studies. Additionally, enemy release might be important drivers of invasion success for only some plant species (Maron and Vilà, 2001).

A fundamental assumption of the ERH is that natural enemies negatively influence plant fitness. The success of some biological control agents, in reducing invasive plant abundance, provides evidence that invertebrate herbivores can adversely impact plant populations. Moreover, several effective bio-control agents have been foliar feeders including *Gallerucella* spp on *Lythum salicaria* (Landis *et al.*, 2003), *Chrysolina quadrigemina* on *Hypericum perforatum* (Coombs *et al.*, 2004) and *Tyria jacobaeae* on *Senecio jacobaeae* (McEvoy *et al.*, 1993), indicating that defoliation can effectively decrease plant fitness. Nonetheless, certain feeding guilds, such as seed predators and

root feeders, are likely to have a greater impact (Maron and Vilà, 2000; Liu and Stiling, 2006). Assessing herbivory using leaf damage overlooks the role of these feeding guilds. Our study suggests that highly invasive plants do escape foliar herbivores but whether this escape translates into a competitive benefit for the plants still needs to be tested.

Several other factors have the potential to confound comparisons of leaf damage between invasive and non-invasive plants. Herbivory might be disproportionately detrimental to some species and have little impact on others. Leaf damage is more debilitating for short-lived annual and biennial species than perennials (Southwood *et al.*, 1986). Plants with limited seed sets are also more likely to be negatively affected by herbivory (Maron and Vilà, 2000). Likewise, plants growing under high resource conditions can compensate for tissue loss and should be less affected by herbivores (Coley, 1988). Further, the ERH does not take into consideration tolerance to herbivory, which might be an important coping strategy for several plants (Agrawal and Strauss, 1999). By definition, tolerant plants are less affected by herbivores and this can be especially true for foliar herbivory where the loss of photosynthetic material might be compensated without fitness costs (Agrawal and Strauss, 1999). Tolerance to herbivory has been demonstrated for some invasive plants including *Sapium sebiferum* (Rogers and Siemman, 2004), *Senecio jacobea* (Stastny *et al.*, 2005) and *Spartina alterniflora* (Garcia-Rossi *et al.*, 2003).

Exotic plants are expected to accumulate herbivores over time (Strong *et al.*, 1984). While monophagous species-specialists are mostly left behind in the native range, generalists and oligophagous herbivores on closely related plants could potentially incorporate introduced plants into their diets (Keene and Crawley, 2002; Sheldon and

Creed, 1995; Bowers *et al.*, 1992). Exotic plants that escape herbivory might be unpalatable to these generalists and oligophagous herbivores. Further, deterrence might evince the presence of defenses that could facilitate enemy escape.

A few studies have looked at whether invasive exotic plants are deterrent to native generalist herbivores. Erhard *et al.* (2007) found that the generalist aquatic moth, *Acentria ephemerella* showed increased mortality on the invasive aquatic plant, *Elodea nuttallii* owing to its defensive chemistry. However, Buschmann *et al.* (2006) found that the generalist slugs, *Arion lusitanicus* and *Deroceras reticulatum*, did not avoid feeding on exotic Brassicaceae in Europe, compared to confamilial natives. In a previous study, I showed that invasive Asteraceae and Brassicaceae were not palatable to the native generalist grasshopper, *Schistocerca americana* (Jogesh *et al.*, 2008). Additionally, two invasive *Centaurea* spp., *C. diffusa* and *C. maculosa*, had low feeding damage by the generalist grasshopper, *Melanoplus femurrubrum* (Jogesh *et al.*, 2008). In this study, I found that highly invasive exotics were not palatable to the generalist herbivore, *Pseudaletia unipuncta*, but the generalist, *Heliothis zea* did not show any feeding preference based on the invasiveness of a plant (Figures 3 and 5) suggesting that highly invasive plants might be well defended against some generalists but not others.

H. zea has a larger diet breadth than *P. unipuncta* and is well known for its capacity to detoxify a wide range of plant chemicals as well as synthetic insecticides (Sasabe *et al.*, 2004), which might explain its ability to feed on plants that deterred *P. unipuncta*. Interestingly, these results show that *H. zea* had higher feeding damage on Apiaceae compared to other families (Figure 6) while *P. unipuncta* avoided feeding on all Apiaceae (Figure 4). *H. zea* larvae are able to detoxify some furanocoumarins present in

Apiaceae, which are usually toxic to most other generalists (Li *et al.*, 2003). Further, *H. zea* did not feed on most Brassicaceae while *P. unipuncta* fed substantially on these plants, suggesting that glucosinolate compounds present in the Brassicaceae are deterrent to *H. zea* but not to *P. unipuncta*. Interestingly, the most invasive Brassicaceae in this study, *Alliaria petiolata*, deterred feeding by both generalist herbivores. *A. petiolata* is defended by alliarinoside and isovitexin 6'-O- β -D-glucopyranoside, both of which are potent anti-herbivore defenses (Renwick, 2002). *A. petiolata* also produces high concentrations of cyanide in its leaves, which can be toxic to herbivores (Cipollini and Grunner, 2007). Aversion to *A. petiolata*, by both of these species, strongly supports the role of novel or unusual defenses in facilitating generalist enemy escape.

Family-specialist herbivores are capable of feeding on different members of a plant family, owing to their ability to metabolize defensive compounds that commonly occur in the family (Cates, 1980). There are several instances where native family- and genus- specialist herbivores have incorporated exotic food plants into their diet. Native and exotic Brassicaceae in Europe host similar numbers of oligophagous herbivores (Frenzel and Brandt, 2003). The North American weevil, *Euhrychiopsis lecontei*, which is a specialist on native *Myriophyllum* spp., also feeds on the exotic plant *Myriophyllum spicatum* (Sheldon and Creed, 1995). Similarly, the herbivores in this study, *P. polyxenes*, *P. rapae* and *C. philodice*, are known to include several exotic species in their host range. However, a majority of invasive exotic plants in this study have not typically been reported as hosts for these family-specialists herbivores and these invasive exotics suffer low levels of damage in the field, suggesting that invasive exotics might escape family-specialist herbivores. Contrary to these expectations, I found that several invasive plants

were not deterrent to family-specialists and supported larval survival, implying that if invasive plants do escape these herbivores, escape must occur via other means such as oviposition deterrence or the unapparency of invasive exotics.

The primary host plant utilized by the Fabaceae specialist, *C. philodice*, is the non-invasive exotic plant, *Medicago sativa* (Tabashnik, 1983), which supported high larval survivorship in this study (Figure 11). *C. philodice* has also been observed feeding on the invasive plant, *Melilotus alba*, as a secondary host (Karowe, 1989), but I found that *M. alba* did not support larval survival. *Lotus corniculatus*, another invasive Fabaceae, did not support *C. philodice* larval growth and has not been reported as a suitable host plant (Porter and Levin, 2007). The highly invasive plant, *Coronilla varia*, has not been reported as a host for *C. philodice*. However, this study demonstrates that *C. philodice* larvae are not averse to feeding on *C. varia* and survive fairly well on this plant (Figure 11) as has been previously documented (Karowe, 1990). The unwillingness of *C. philodice* to incorporate *C. varia* as a host might have more to do with behavioral constraints rather than deterrent plant chemistry (Karowe, 1989).

The primary hosts of the Apiaceae specialist, *P. polyxenes*, in Eastern North America are the non-invasive exotic plants, *Daucus carota* and *Pastinaca sativa* (Feeny *et al.*, 1985), both of which were found to support high larval survivorship (Figure 7). The invasive plant, *H. mantegazzianum* has not been previously reported as a host plant for *P. polyxenes* (Berenbaum, 1981). However, *H. mantegazzianum* was not deterrent to *P. polyxenes* and 75% of larvae survived to pupation (Figure 7). For this herbivore as well, behavioral constraints to utilization of an invasive exotic plant seem more plausible than deterrence.

Unlike, *P. polyxenes* and *C. philodice*, the family-specialist, *Pieris rapae*, is not native to North America. *P. rapae* has a long association with several exotic host plants that are present in its native range and is expected to incorporate a number of these exotic species into its diet (Chew, 1980). *P. rapae* has been reported to feed on several non-invasive exotic Brassicaceae including *Barbarea vulgaris*, *Sisymbrium altissimum* and *Sinapis alba* (Richards, 1940). Additionally, *P. rapae* larvae reject a number of non-invasive Brassicaceae including *Capsella bursa-pastoris* and *Erysimum cheiranthoides* (Renwick, 2002), which is consistent with my findings (Figures 9 & 10). One of the two invasive Brassicaceae in this study, *Hesperis matronalis*, supported low larval survival and has not been reported as a *P. rapae* host (Figure 9). The other invasive exotic, *Alliaria petiolata*, supported over 90% larval survival and all larvae initiated and continued feeding on this plant (Figure 9). These findings do not support previous studies that document deterrence of *A. petiolata* to *P. rapae* feeding (Renwick, 2002). The chemical profile of *A. petiolata* is extremely variable over space and time (Cipollini, 2002) and several deterrent compounds in this plant are induced by herbivory (Cipollini *et al.*, 2005). These methods do not take into consideration inducible defenses in the plant, which might strongly reduce larvae survival. It is also probable that the life-stage at which leaves were collected or the populations I sampled had comparatively lower constitutive defenses. Interestingly, Keeler and Chew (2008) have recently shown that the Brassicaceae family-specialist, *P. napi oleraceae*, that are sympatric with *A. petiolata* populations oviposit and feed on this plant. It is plausible that *Pieris* butterflies are adapting to *A. petiolata* as a host plant. Nevertheless, leaf damage observed in this study suggests that *A. petiolata* effectively escapes foliar herbivory in the Ottawa region.

While three invasive plants, *Melilotus alba*, *Lotus corniculatus* and *Hesperis matronalis* deterred family-specialist herbivores, other invasive exotics including the two highly invasive plants, *Alliaria petiolata* and *Coronilla varia*, supported larval growth. Even though family-specialist herbivores have the capacity to incorporate several invasive exotics into their diets, these plants suffer low levels of leaf damage in the field. In the case of family-specialist Lepidoptera, female oviposition choice often determines the larval host (Renwick and Chew, 1994). Female butterflies often make oviposition mistakes and lay eggs on plants that do not support larval development (Renwick and Chew, 1994). For example, *P. napi oleraceae* frequently oviposits on *Barbarea vulgaris* which is toxic to the larvae (Chew, 1981). These oviposition mistakes over time can result in the incorporation of novel host plants in a native insect's diet. On the other hand, female butterflies reject some plants that are suitable for larval development (Renwick and Chew, 1994). This behavioral rejection can provide an escape opportunity for an exotic plant even if it is not well defended.

The preliminary oviposition experiments with *P. rapae* indicate that oviposition choice broadly coincided with larval survivorship on the plant. Female butterflies oviposited on the invasive plant *Alliaria petiolata*, which supported larval survival but did not oviposit on *H. matronalis*, on which larval mortality was high (Table 4). Oviposition on *A. petiolata* has been reported previously as an oviposition mistake by *P. rapae* females (Huang *et al.*, 1994). Females did not lay a large proportion of eggs on *E. cheiranthoides* or *C. bursa-pastoris*, both of which did not support larval survival (Table 4). The only exception was the non-invasive plant, *Berteroa incana*, which supported

larval survivorship but was not deemed suitable for oviposition (Table 4). I found limited evidence that invasive Brassicaceae escape *P. rapae* herbivory via oviposition deterrence.

The *P. polyxenes* oviposition experiments in this study were limited in their ability to predict oviposition choice. Low egg counts were observed on all plants that were tested with second-generation females. As the colony was initiated with a few wild-caught butterflies, inbreeding in the second generation of butterflies could have resulted in lower female fecundity. Oviposition choice in *P. polyxenes* depends on a combination of attractive and deterrent chemical cues which are unrelated to the chemical constituents that determine larval feeding (Heinz and Feeny, 2005). While I found no eggs on the invasive plant, *H. mantegazzianum*, it is not possible to ascertain that no eggs were laid as a result of oviposition deterrence on this plant.

I was unable to conduct oviposition experiments for *C. philodice*. However, prior studies indicate that *C. philodice* does not oviposit on the invasive plant, *Coronilla varia*, in spite of relatively high larval survivorship on this plant (Karowe, 1990). In this case, escape might occur owing to female behavioral constraints.

In this study, several non-invasive plants deterred family-specialist larval feeding and development. *P. rapae* did not feed on *Erysimum cheiranthoides* or *Capsella bursa-pastoris*, *P. polyxenes* did poorly on *Angelica sylvestris* and *Aegopodium podagraria* and *C. philodice* did not survive on *Lathyrus sylvestris*. These findings demonstrate that even though some exotic plants might escape family-specialist herbivores, they do not suffer low levels of damage in the field or become invasive, suggesting that escape from family-specialists might not be as important as escape from generalists. The relative impact of generalist and family-specialist herbivores on exotic plants is largely unknown (Maron

and Vilà, 2001). Parker *et al.* (2006) and Maron and Vilà (2001) insinuate that generalists alter plant community structure to a greater extent than specialists. Several studies also indicate that exotic plants accumulate a greater diversity of generalist herbivores compared to specialists (Keene and Crawley, 2002). The most common herbivores sampled on introduced populations of *Hieracium* spp. in New Zealand were generalists (Syrett and Smith, 1998). Similarly, 49 generalist herbivores occur on introduced *Lythrum salicaria* populations in North America compared to only 6 specialists (Keene and Crawley, 2002). *Solidago altissima* in Switzerland hosts 13 generalists but only 2 specialists (Jobin *et al.*, 1996). These generalist herbivores might simply be more damaging and have a larger impact on exotic plant species. While this has not been specifically tested with exotic plants, it is plausible that escape from generalist herbivores provides a greater invasion opportunity for some exotic species.

A literature search on the chemical defenses in the Apiaceae exotics revealed that furanocoumarins were the most commonly occurring compounds and were only absent from *Aegopodium podagraria* (Appendix 1). Further, on extracting furanocoumarin compounds from Ottawa populations, I found that the highest concentration of furanocoumarins occurred in the leaves of *Heracleum mantegazzianum* and *Pastinaca sativa*, with *P. sativa* having marginally higher concentrations in comparison to *H. mantegazzianum* (Table 5). However, *H. mantegazzianum* had double the amount of angelicin, an angular furanocoumarin, which is more deterrent to Apiaceae specialists (Berenbaum and Zangerl, 1993). In spite of this difference the percentage of *P. polyxenes* larvae that survived on *H. mantegazzianum* and *P. sativa* did not differ. *H. mantegazzianum* was the most invasive Apiaceae in this study and I found limited

evidence that this plant is better defended when compared to other non-invasive Apiaceae plants. However, I only screened for 6 furanocoumarin compounds in the HPLC analysis and it is possible that *H. mantegazzianum* contains a number of other furanocoumarin compounds. In a previous study, Berenbaum (1981) found that the seeds of *H. mantegazzianum* contained a greater diversity of furanocoumarin compounds compared to *P. sativa*, but this was not the case for the leaves. It is probable that *H. mantegazzianum* is better defended but its defenses are concentrated in plant parts such as umbels and seeds, which are more seriously impacted by herbivory. I also found no evidence from the literature that any of the exotic Apiaceae had novel or unusual defenses (Appendix 1). Nonetheless, all Apiaceae plants in the study, except for *Angelica sylvestris*, suffered low levels of leaf damage in the field, indicating that plants in this family are generally well defended.

As previously stated, the most invasive Brassicaceae in this study, *A. petiolata* is defended by a novel cyanoallyl glycoside, alliarinoside, which has not previously been reported in the North American flora (Renwick, 2002). Furthermore, this plant produces cyanide in concentrations that are higher than in any other Brassicaceae (Cipollini and Grunner, 2007). The other invasive Brassicaceae in this study, *Hesperis matronalis*, produces a glucosinolate compound, 3-O-Apiosylglucomatronalin that is unique to this species (Renwick, 2002). The role of this compound in herbivore deterrence is unknown but it has been implicated as an attractant to a monophagous herbivore that specializes on this plant (Fahey *et al.*, 2001). Most other Brassicaceae in this study typically contain a large diversity of glucosinolate compounds (Appendix 1). Additionally, the non-invasive plants, *Erysimum cheiranthoides* and *Capsella bursa-pastoris* are defended by cardiac

glycosides and alkaloid compounds, respectively (Renwick, 2002). Both *Erysimum cheiranthoides* and *Capsella bursa-pastoris* were deterrent to *P. rapae* suggesting that atypical compounds in the family might allow these plants to escape family-specialist herbivores.

The most invasive Fabaceae, *Coronilla varia*, was reported to contain psoralens and cardiac glycosides (Appendix 1). While these compounds are potent defenses, they are by no means novel to the introduced range. Two other invasive plants in the Fabaceae, *Lotus corniculatus* and *Trifolium repens* are widely known for their ability to produce hydrogen cyanide from cyanogenic glycosides in their leaves (Gleadow and Woodrow, 2002). These compounds are toxic in high concentrations, especially to generalists (Gleadow and Woodrow, 2002). Invasive exotics in this family appear to be well defended in general, but there is no evidence that their defenses are unique or that non-invasive Fabaceae are less well defended.

There appears to be no obvious differences between the defensive chemistry of invasive and non-invasive exotic plants in the three plant families studied. Invasives were not consistently better defended than non-invasives and only one plant in the study was reported to contain a novel herbivore defense. However, chemical defenses that have been reported for a plant in the literature might not necessarily occur in populations that were sampled for this study. Concentrations of defensive compounds can be extremely variable between populations and can even differ between the life-stages of a plant (Berenbaum, 1995). Several defenses increase in concentration only after being induced (Karban and Myers, 1989). A number of compounds reported for the plants in this study had an unspecified location and may not occur in leaf tissues. Also, some plants have not

been thoroughly examined in terms of their defensive chemistry and the information that is required to make an unbiased comparison might be missing. Nevertheless, there is evidence that a few highly invasive plants including *Centaurea maculosa*, *Centaurea diffusa* and *Vincetoxicum rossicum*, are equipped with novel defenses (Cappuccino and Arnason, 2006). On the other hand, novel defenses might not always guarantee enemy escape. The exotic Apiaceae plant, *Conium maculatum* contains toxic piperidine alkaloids, which rarely occur in native North American plants, and yet the Apiaceae specialist *P. polyxenes* utilizes this plant as a host and the generalist *Tricophsia ni* is capable of feeding on it (Castells and Berenbaum, 2008).

Taxonomic isolation has often been cited as an important predictor of invasion potential (Lockwood *et al.*, 2001). I found no evidence that invasive exotic plants had fewer congeneric relatives in North American compared to non-invasive exotics. Previous studies have also found limited evidence that invasive plants are taxonomically isolated at the genus level (Dawson *et al.*, 2008; Cappuccino and Carpenter, 2005). The three congeneric *Trifolium* spp., in this study, varied considerably in their invasiveness as well as in the amount of damage sustained in the field. Of the two *Heracleum* species that have been introduced, only *H. mantegazzianum* is reported as invasive (NatureServe: www.natureserve.org). Similarly, several invasive *Centaurea* spp. have been introduced into North America and only a few have become extremely invasive (Jogesh *et al.*, 2008). Species within the same genus can vary in a number of traits including their defensive chemistry. *Centaurea maculosa* has a novel compound (-)- catechin that has not been reported in other *Centaurea* spp (Callaway and Ridenour, 2004). The differential success of species within the same genus questions the importance of taxonomic isolation at the

genus level. Isolation at the family level might be a better predictor of invasion success for some exotic species (Cappuccino and Carpenter, 2005). Additionally, phylogenetic distance might provide a more comprehensive measurement of relatedness (Strauss *et al.*, 2006).

While enemy release can be an important factor in facilitating exotic plant invasions there are several other biotic interactions that may be just as vital or even more so, in conferring invasion potential. A few well studied invasive exotic plants including *Centaurea maculosa*, *Alliaria petiolata* and *Vincetoxicum rossicum*, demonstrate that multiple factors are responsible for their strong invasion capacity. The highly invasive *C. maculosa* effectively escapes herbivory in the introduced range (Jogesh *et al.*, 2008), is released from debilitating soil pathogens that occur in its native range, accumulates beneficial soil mutualists (Reinhart and Callaway, 2006) and also competitively excludes other species via allelopathy (Ridenour and Callaway, 2001). Another serious invader, *Alliaria petiolata*, is well defended, escapes native herbivores and produces allelopathic compounds that inhibit the formation of mycorrhizal associations in neighboring species (Stinson *et al.*, 2006). Similarly, *Vincetoxicum rossicum* has potent defenses that allow it to escape from native herbivores and pathogens (Mogg *et al.*, 2008) as well as strong seedling survival (Ladd and Cappuccino, 2005) and it also forms more arbuscular mycorrhizal associations than native Asclepiaceae (Smith *et al.*, 2008). Further, these multiple factors may interact synergistically and exacerbate the impacts of enemy escape (Mitchell *et al.*, 2006).

CONCLUSIONS

In this study, I aimed to test whether invasive exotic plants were more likely to escape herbivory compared to confamilial non-invasive exotics and whether enemy escape could be attributed to generalists and/or family-specialist herbivores in the introduced range.

Invasive exotic plants were more likely to escape foliar herbivory compared to confamilial non-invasive exotics. While these results partially indicate that invasive plants are more deterrent to generalists, I found no evidence that family-specialist herbivores were deterred by, or had low survivability on, highly invasive plants. These results suggest that enemy escape is more likely to occur as a result of escape from generalist herbivores. I found little evidence that invasive exotic plants in the Apiaceae, Brassicaceae and Fabaceae contained novel defenses and no evidence that invasive exotics were more taxonomically isolated at the genus level. However, there are several caveats to the methods employed in this study to determine novel chemistry and taxonomic relatedness. A more detailed analysis of plant chemistry via HPLC methods might be more accurate in determining the diversity and concentration of defensive chemicals that occur in these plants. Further, phylogenetic distance might be a better alternative to measuring relatedness. Although I have shown that invasive exotic plants suffer lower levels of leaf damage compared to non-invasive exotics, whether enemy escape translates to a competitive advantage for the plant, still needs to be determined.

CHAPTER THREE: POLYPLOIDY AND THE INVASIVENESS OF EXOTIC PLANTS

INTRODUCTION

Polyploidy is frequently cited as a recurrent trait in invasive plants (Bennett *et al.*, 1998; Lee, 2002; Rejmánek, 1996). Eighteen of the world's worst weeds described by Holm *et al.* (1977) are polyploid (Hollingsworth and Bailey, 2000). Several highly invasive plants in North America, including *Lythrum salicaria* (Kubatova *et al.*, 2008), *Centaurea maculosa* (Muller, 1989) and *Spartina alterniflora* (Daehler and Strong, 1997), are polyploid. Additionally, Pundit (2006) suggests that invasive plants tend to be polyploid while rare and endangered plants are more often diploid. The common occurrence of polyploidy in aggressive invaders suggests that it might play an important role in facilitating exotic plant invasions.

Exotic plants might benefit from polyploidy in several different ways. High genetic diversity and heterozygosity, imparted by multiple chromosome copies, can overcome the detrimental effects of inbreeding and selfing that often occur in small founding populations (Soltis and Soltis, 2000). The octaploid exotic plant *Fallopia japonica* is extremely successful and invasive, even though it only undergoes clonal propagation throughout its entire introduced range (Hollingsworth and Bailey, 2000). Further, the formation of novel genotypes via chromosome reorganization and substitution can enhance the phenotypic variability of a polyploid plant, allowing it to adapt to a broad range of conditions (Soltis *et al.*, 2003). Polyploids often occupy larger and more extreme niches compared to their progenitors and are more likely to colonize and succeed in a novel habitat (Hegarty and Hiscock, 2008). The ubiquity of recently

formed polyploid karyotypes in the Arctic, illustrates the propensity of polyploids to colonize and succeed in novel habits (Brochmann *et al.*, 2004). A few studies also indicate that polyploid karyotypes have greater fitness than their diploid counterparts. Polyploid *Carpobrotus* hybrids, derived from exotic and native *Carpobrotus* spp. have greater vegetative growth, are less susceptible to mammalian herbivory and occur more frequently than their non-hybrid progenitors (Vilà and D'Antonio, 1998). Similarly, the hexaploid, *Rorripa sylvestris* and the pentaploid hybrid of *R. sylvestris* and *R. austriaca*, have greater seedling emergence rates and produce larger seed sets compared to the diploid *Rorripa austriaca* (Bleeker and Matthies, 2005).

Given the frequency of polyploidy in invasive plants and the apparent success of polyploids, it is plausible that exotic plants with high levels of polyploidy are likely to become more invasive than diploid exotics. In this study, I examine the relationship between polyploidy and invasiveness for 23 plant species in the families Apiaceae, Brassicaceae and Fabaceae. I predict that invasive exotic plants should more frequently be polyploid compared to non-invasive exotics.

MATERIALS AND METHODS

I consulted the Missouri Botanical Garden's Index to Plant Chromosome Number database (<http://mobot.mobot.org/W3T/Search/ipcn.html>) and Darlington and Wylie (1955) to obtain chromosome counts in each of the plant species. I classified a plant as 'polyploid' if chromosome counts were greater than twice the basal chromosome number. Plants were classified as 'invasive' or 'non-invasive' based on the methods employed for the herbivory study. I used a ranking system compiled by NatureServe (www.natureserve.org), a non-governmental organization, to assess the invasiveness of all plant (Table 1). Introduced plants with a low numerical ranking (0-3) were categorized as Non-invasive and plants with a high ranking (4-6) were categorized as Invasive. I used Fisher's Exact test to determine the relationship between polyploidy and invasiveness.

RESULTS

Highly invasive exotic plants in this study were more likely to be polyploid than non-invasive exotics (Fisher's Exact significance = 0.027) (Table 6).

Table 6: Exotic invasive and non-invasive plant species that are diploid and polyploidy. Relationships are analyzed using Fisher's Exact test.

		Invasiveness		Total	Fisher's Exact significance
		Non-invasive	Invasive		
Ploidy level	Diploid	11	1	12	0.027
	Polyploid	5	6	11	
Total		16	7	23	

DISCUSSION

Our results suggest that invasive exotic plants have a greater tendency to be polyploid (Table 6). Higher incidences of polyploidy in invasive populations can emanate from two mechanisms. Either 1. Polyploids and diploids are prevalent in native populations of the plant but only polyploid karyotypes become successful invaders or 2. Hybridization events between an exotic species and closely related native kin result in the formation of allopolyploids, which are more invasive than their progenitors (Prentis *et al.*, 2008).

There are several instances where two or more ploidy levels exist in native populations but only one polyploid karyotype is invasive (Bossdorf *et al.*, 2005). *Centaurea maculosa* is entirely tetraploid in the introduced range while both diploid and tetraploid forms occur in the native range (Muller, 1989). Only tetraploid *Lythrum salicaria* is invasive in North America, while diploids, triploids and hexaploids occur in the plant's native range (Kubatova *et al.*, 2008). Similarly, tetraploid *Solidago gigantea* is invasive in Europe, while multiple ploidy levels are reported in the native range (Schlaepfer *et al.*, 2008). These studies broadly suggest that certain polyploid karyotypes might be disproportionately successful compared to diploids, in the introduced range.

Alternatively, invasive exotics might form allopolyploids after introduction, as a result of hybridization with congeneric native plants. Allopolyploids are typically derived from the hybridization of two closely related species (Soltis *et al.*, 2003). There is considerable evidence to suggest that recently formed hybrid allopolyploids are more abundant and invasive than their progenitors. Allopolyploid hybrids derived from the exotic *Spartina alterniflora* and *S. foliosa* are more vigorous than either *S. alterniflora* or

S. foliosa (Daehler and Strong, 1998). Invasive biotypes of *Rhododendron ponticum* are all hybrids (Hafling and Kollmann, 2002). Likewise, *Fallopia japonica* hybrids spread more rapidly and have a higher regeneration capacity in their introduced range (Baily *et al.*, 2007).

In addition to the fitness benefits associated with polyploidy, recent studies also indicate that plant-animal interactions vary between diploid and polyploid karyotypes (Soltis *et al.*, 2003). For example, sympatric populations of diploid and tetraploid *Heuchera grossulariifolia* host different insect assemblages (Thompson and Merg, 2008). The seed head weevil, *Larinus minutus*, prefers feeding on diploid *Centaurea maculosa* plants that occur in the native range over tetraploid plants that occur in the invasive range (Blair *et al.*, 2008). A recent study also suggests that neo-polyploids have the potential to be more pathogen resistant (Oswald and Nuismer, 2007). Altered biotic interactions in invasive polyploids might increase their chances of enemy-escape in the introduced range.

CONCLUSIONS

In this study, I present preliminary evidence that polyploidy is associated with increased invasion capacity. However, I do not specifically determine whether polyploid individuals are prevalent in invasive populations or whether polyploidy confers invasion potential. Nonetheless, the disproportionate representation of polyploid individuals in the introduced range, of some invasive plants, and the success of recently formed polyploids over their diploid counterparts, illustrates that polyploidy can play an important role in facilitating invasiveness. Further, future studies that compare biotic interactions between diploid and polyploid karyotypes of an invasive species might exemplify the interactive role of polyploidy and enemy-release in fostering exotic plants invasions.

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APPENDIX 1
List of defensive phytochemicals

Species	Family	Chemical	Class	Part	Activity	Distribution	Reference
<i>Aegopodium podagraria</i>	Apiaceae	Falcarindiol	polyactylene	leaves and flowers	anti-inflammatory, anti fungal		Prior et al. (2007)
						<i>Athamanta oeeoselinum</i> , <i>Amni visnaga</i> , <i>Athamanta cretensis</i> , <i>Libanotis transcaucasica</i> , <i>Peucedanum spp.</i> <i>Seseli libanotis</i>	Murphy et al. (2004)
<i>Angelica sylvestris</i>	Apiaceae	Athamantin	angular furanocoumarin	roots and seeds	spasmolytic		Murphy et al. (2004)
		Bergapten	Linear furanocoumarin	unknown			Murphy et al. (2004)
						Umbelifers (<i>Pimpinella spp.</i> , <i>Angelica spp.</i> , <i>Heracleum spp.</i> , <i>Pastinaca spp.</i> and <i>Seseli spp.</i>), Rutaceae(<i>Citrus aurantifolia</i> , <i>Skimmia laureola</i> <i>Luvunga spp.</i> , <i>Flindersia bennettiana</i>) Compositae (<i>Trichocline incana</i>)	Murphy et al. (2004)
		Isopimpinellin	linear furanocoumarin	roots and seeds	antibacterial, antifungal and anti piscidal		
		Aviprin	Linear furanocoumarin	unknown			Murphy et al. (2004)

		Byakangelicin	Linear furanocoumarin	unknown			Murphy et al. (2004)
		Imperatorin	Linear furanocoumarin	unknown			Murphy et al. (2004)
		Xanthotoxin	Linear furanocoumarin	unknown			Murphy et al. (2004)
		umbelliprenin	sequiterpinylicoumarin	unknown			Murphy et al. (2004)
		Imperatorin	linear furanocoumarin	roots and seeds	HeLa cell proliferation, antimutagenic, toxic to toads	<i>Angelica Heracleum and Pastinaca</i> spp., Rutaceae (<i>Citrus meyeri</i> , <i>Aegle marmelos</i>), Rosaceae (<i>Fragaria</i> spp.)	Harborne et al. (1999)
<i>Daucus carota</i>	Apiaceae	Carotol	Sequesterpinoic acid	seeds		none	Harborne et al. (1999)
		Daucol	Sequesterpinoic acid	seeds		none	Harborne et al. (1999)
		Elemicin	Phenylpropanoids	unknown	DNA binding, invitro inhibition of platelet aggregation	<i>Cinnamomum glanduliferum</i> , <i>Cybopogon procerus</i> , <i>Boronia pinnata</i> , <i>Zieria smithii</i> , <i>Melaleuca bracteata</i> , <i>Blachousia myrtifolia</i> , <i>Aniba</i> spp. <i>Croton nepetaefolius</i> ,	Harborne et al. (1999)

					<i>Dalbergia spruceata</i> , <i>Monoteryx uauca</i>	
Falcarindiol	Acetylene (phytoalexin)	roots	antifungal, analgesic, toxic	Leaves of tomato infected with <i>Cladosporium fulvum</i>	Harborne et al. (1999)	
Luteolin	Flavone	Leaves	anti-inflammatory, anti-bacterial	Widespread	Harborne et al. (1999)	
Luteolin 7-o-glucoside	Flavone	Leaves	oviposition stimulant for <i>P.polyxenes</i>	Widespread	Harborne et al. (1999)	
6-methoxymellein	Phenolic	unknown	fungal metabolite, produced on fungal attack		Harborne et al. (1999)	
			expectorant, spasmolytic, antihistaminic		Harborne et al. (1999)	
Methylisoeugenol	Phenylpropanoids	Leaf wax	antibacterial, moderate zoo-phyto-toxic	<i>Asarum europaeum</i> , <i>Acorus calamus</i>		
			inhibits monoamine oxidase, synergistic activity to insecticides (eg. Xanthotoxin), spasmolytic	<i>Myristica fragrans</i> , <i>Cinnamomum glanduliferum</i> , <i>Apium graveolens</i> , <i>Petroselinum crispum</i> , <i>Levisticum</i>	Harborne et al. (1999)	
Myristicin	Phenylpropanoids	unknown				

				effects	<i>scoticum</i> , <i>Pastinaca sativa</i>		
		Peucedanin	Chromones and Chromenes	rhizome and fruit	antineoplastic	Mainly Peucedanum officinale, Prangos pabularia Also, <i>Anthriscus cerefolium</i> , <i>Meum athamanticum</i> , <i>Myrrhis odorata</i> , <i>Pastinaca sylvestris</i>)	Harborne et al. (1999)
		Psoralen	Linear furanocoumarin	unknown			Harborne et al. (1999)
		Bergapten	Linear furanocoumarin	unknown			Harborne et al. (1999)
		Xanthotoxin	Linear furanocoumarin	unknown			Harborne et al. (1999)
<i>Heracleum mantegazzianum</i>	Apiaceae (<i>Heracleum</i> spp.)	Angelicin	angular furanocoumarin	roots	Photosensitizi ng (slight), spasmolytic	Umbellifers(incl. <i>Angelica archangelica</i> , <i>Selinum vaginatum</i>), Fabaceae (<i>Psoralea corylifolia</i>), Fagaceae (<i>Castanopsis indica</i>),	Harborne et al. (1999)

					Moraceae (<i>Ficus nitida</i>)		
		Bergapten	linear furanocoumarin	unknown			Harborne et al. (1999)
		Bykangelicin	linear furanocoumarin	seeds	inhibits human chorionic gonadotrophin	<i>Angelica glabra</i> and <i>Citrus</i> spp	Harborne et al. (1999)
		Imperatorin	linear furanocoumarin	unknown			Harborne et al. (1999)
		Isopimpinellin	linear furanocoumarin	unknown			Harborne et al. (1999)
						Umbellifers(<i>Pimpinella saxifraga</i> , <i>Angelica genuflexa</i>) Cyperaceae (<i>Cyperus papyrus</i>) Compositae (<i>Artemisia canariensis</i>)	Harborne et al. (1999)
		Pimpenellin	angular furanocoumarin	fruits	tuberculostatic activity(myobacterium tuberculosis)		
		Umbelliferone	hydroxycoumarin	resin	antifungal, antibacterial	Widespread	Harborne et al. (1999)
<i>Pastinaca sativa</i>	Apiaceae	Myristicin		unknown			Dukes Phytochemical Database

Xanthotoxin	linear furanocoumarin	unknown	dermetitis, piscidal, antibacterial, impairment of DNA synthesis	Apiaceae (<i>Apium graveolens</i> , <i>Ammi majus</i> , <i>Angelica archangelica</i> , <i>A. officinalis</i> , <i>Heracleum sphondylium</i>) Rutaceae (<i>Ruta and Fagara</i> spp)	Harborne et al. (1999), Dukes Phytochem ical Database
Xanthotoxol	Linear furanocoumarin	seeds	HeLa cell proliferation	<i>Angelica archangelica</i> , <i>Heracleum lantanum</i> , <i>Cnidium monnieri</i> , Rutaceae (<i>Poncirus trifoliata</i>)	Harborne et al. (1999), Dukes Phytochem ical Database
Imperatorin	linear furanocoumarin	unknown			Dukes Phytochem ical Database
Isopimpinellin	linear furanocoumarin	unknown			Dukes Phytochem ical Database
Alpha- Terpinene		unknown	insectifuge		Dukes Phytochem ical Database
Apterin		unknown			Dukes Phytochem ical

					Database	
				unknown	insectifuge	Dukes Phytochem ical Database
	Bergapten			unknown	insectifuge	Dukes Phytochem ical Database
	Camphene			unknown	insectifuge	Dukes Phytochem ical Database
	Cis-allo- ocimine	monoterpene		unknown		Dukes Phytochem ical Database
	Cis-beta- ocimene	monoterpene		unknown		Dukes Phytochem ical Database
	Gamma- Terepene			unknown	insectifuge	Dukes Phytochem ical Database
	Isobergapten	angular furanocoumarin		unknown	insectifuge	Dukes Phytochem ical Database
	Isorhamnetin	flavenol		unknown	insectifuge	Dukes Phytochem ical Database
	Isorhamnetin- 3-glucoside-4- rhamnoside	flavenol		unknown	insectifuge	Dukes Phytochem ical Database

Kaempferol	flavenol	unknown		Dukes Phytochem ical Database
Limonene		unknown	insectifuge	Dukes Phytochem ical Database
Linoleic- Acid		unknown	insectifuge	Dukes Phytochem ical Database
Myrcene		unknown	insectifuge	Dukes Phytochem ical Database
Octyl-butyrate	fatty acid	unknown		Dukes Phytochem ical Database
Octyl-Propionate		unknown		Dukes Phytochem ical Database
Oleic-acid	fatty acid	unknown	insectifuge	Dukes Phytochem ical Database
Oxalic-acid		unknown	insectifuge	Dukes Phytochem ical Database
P-cymene		unknown		Dukes Phytochem

					Dukes Phytochem ical Database
	Palmetic-acid		unknown		Dukes Phytochem ical Database
	Petroselinic- acid		unknown		Dukes Phytochem ical Database
	Pimpinellin	angular furanocoumarin	unknown	insectifuge	Dukes Phytochem ical Database
	Psoralen	Linear furanocoumarin	unknown	insectifuge	Dukes Phytochem ical Database
	Quercetin	Flavone	unknown		Dukes Phytochem ical Database
	Rutin		unknown		Dukes Phytochem ical Database
	Sphondin	angular furanocoumarin	unknown	insectifuge	Dukes Phytochem ical Database
	Suberin		unknown		Dukes Phytochem ical Database

		Terpinolene		unknown		Dukes Phytochem ical Database
		Trans-beta-ocimene		unknown		Dukes Phytochem ical Database
		Umbelliferone	hydroxy coumarin	unknown		Dukes Phytochem ical Database
<i>Alliaria petiolata</i>	Brassicaceae	Allyl, Sinigrin	Glucosinolate	unknown		Harborne et al. (1999)
		Glucotropeolin	Glucosinolate	unknown		Harborne et al. (1999)
			flavone glycoside	unknown	inhibits 4th instar feeding in <i>P. rapae</i>	Renwick (2002)
		Alliarinoside	flavone glycoside	unknown	inhibits neonate feeding in <i>P. rapae</i>	Renwick (2002)
<i>Barbarea vulgaris</i>	Brassicaceae	Glucobarbarin	Glucosinolate	unknown		Harborne et al. (1999)
		Glucobrassicin	Glucosinolate	unknown		Harborne et al. (1999)
		Neoglucobrassicin	Glucosinolate	unknown		Harborne et al. (1999)

		Glucoberverin	Glucosinolate	unknown	Harborne et al. (1999)
		Gluconasturtiin; phenethyl	Glucosinolate	unknown	Harborne et al. (1999)
<i>Berteroa incana</i>	Brassicaceae	Glucoberteroin	Glucosinolate	unknown	Harborne et al. (1999)
		Glucobrassicinapin	Glucosinolate	unknown	Harborne et al. (1999)
		glucoalyssin		unknown	Harborne et al. (1999)
		rhamnocitrin	flavonoid	unknown	Harborne et al. (1999)
		kaempferol	flavonoid	unknown	Harborne et al. (1999)
		quercetin	flavonoid	unknown	Harborne et al. (1999)
<i>Sinapis alba</i>	Brassicaceae	Sinalbin		unknown	Harborne et al. (1999)
		Gluconapin		unknown	Harborne et al. (1999)
		Progoitrin		unknown	Harborne et al. (1999)

				Fabaceae (<i>Lathyrus</i> , <i>Medicago</i> , <i>Trifolium</i> , <i>Trigonella</i> spp)	(1999)
				<i>Dalbergia</i> <i>varibialis</i> (heartwo od), <i>Len culinaris</i> , <i>L.nigricans</i> , <i>Caragana</i> and <i>Lathyrus</i> spp.	Harborne et al. (1999)
	[Gluco]sinalbi n	Glucosinolate	unknown		
				Malvanaceae(<i>Hibiscus</i> <i>tiliaceus</i>) Asteraceae (<i>Chrysanthemum</i> <i>segetum</i>)	Harborne et al. (1999)
	Glucocamelini n	Glucosinolate	unknown		
				Linaceae, Compositae, Euphorbiaceae, Passifloareaceae , tribes Loteae and Phaseoleae	Harborne et al. (1999)
	Glucocarabin	Glucosinolate	unknown		
				Leaves of <i>Derris</i> <i>amazonica</i> , leaves of <i>Lotus</i> , <i>Medicago</i> , <i>Trifolium</i> and <i>Trigonella</i> spp.	Harborne et al. (1999)
	Glucoerucin	Glucosinolate	unknown		
				(-)- induced as phytoalexin in <i>Lotus</i> , <i>Medicago</i> , <i>Trifolium</i> and <i>Onobrychis</i> spp,	Harborne et al. (1999)
	Glucoberverin	Glucosinolate	unknown		

					(+)-trunk wood of <i>Machaerium vestitum</i> and <i>Dalbergia variabilis</i>	
		Glucobrassica napin	Glucosinolate	unknown	found in free form in asparagus, Medicago spp. and fenugreek	Harborne et al. (1999)
		Allyl, Sinigrin	Glucosinolate	unknown	apple peel, fruits of <i>Citrus</i> spp	Harborne et al. (1999)
			Alkaloids	unknown		Renwick (2002)
<i>Erysimum cheiranthoides</i>	Brassicaceae	Helveticoside		unknown	<i>Achillea millifolium</i> (Asteraceae)	Harborne et al. (1999)
		Glucoerucin		unknown	Many Fabaceae	Harborne et al. (1999)
					11 groups of this compound in Alfalfa <i>Ononis</i> spp, <i>Vigna catjang</i> , <i>Leucaena glauca</i> (Fabaceae), <i>Kiggelaria africana</i> (Flacourtiaceae)	Harborne et al. (1999)
		Glucoberverin		unknown		
			Cardenolides	unknown		Renwick (2002)
<i>Hesperis matronalis</i>	Brassicaceae	Gluconapin		unknown	Spinach, alfalfa, senega root and	Harborne et al.

				bitter apple	(1999)
				<i>Triticum dicoccum</i> , rice, Widespread in the <i>Cyperaceae</i>	Harborne et al. (1999)
	Progoitrin	unknown			
	[Gluco]sinalbin	unknown		Fenugreek, alfalfa, coffee, <i>Strophanthus</i> spp. <i>Cannabis</i> spp. and yarrow	Harborne et al. (1999)
	Glucomatronalin	unknown			Harborne et al. (1999)
	Glucocochlearin, glucojiabutin, sec-Butyl, 2-Butyl	unknown	induced as phytoalexins	<i>Trifolium</i> and <i>Medicago</i> spp.	Harborne et al. (1999)
	Glucohesperin	unknown			Harborne et al. (1999)
	Glucoalyssin	unknown			Harborne et al. (1999)
	Glucoerucin	unknown			Harborne et al. (1999)
	Glucoberteroin	unknown			Harborne et al. (1999)
	Glucoiberberin	unknown		Cinnamon, <i>Melilotus alba</i> and <i>M. caspius</i>	Harborne et al. (1999)

		Gluconasturtiin; phenethyl	unknown	<i>Anthoxanthum</i> and <i>Melilotus</i> spp	Harborne et al. (1999)
		3-O- Apiosylglucom atronalin	unknown	feeding stimulants for monophagous specialists in europe	Rewick (2002)
		3-O- Apiosylglucom atronalin 3,4- dimethoxyben zoyl ester	unknown		Renwick (2002)
<i>Sisymbrium altissimum</i>	Brassicaceae	Gluconapin	unknown		Harborne et al. (1999)
		Progoitrin	unknown	widespread in legumes	Harborne et al. (1999)
		[Gluco]sinalbin	unknown	<i>Prunus</i> spp, <i>Genista</i> spp, clovers and many other legumes	Harborne et al. (1999)
		[Gluco]napoleiferin	unknown	heartwood of <i>Maackia amurensis</i> and other woody legumes, <i>Cicer arietinum</i> , <i>Pisum</i> , <i>Trifolium</i> and <i>Trigonella</i> spp.	Harborne et al. (1999)
		Glucoputranjivin, isopropyl	unknown		Harborne et al. (1999)

				unknown		<i>Onionis spinosa</i> , <i>Baptisia</i> <i>thermopsis</i> and <i>Trifolium</i> spp.	Harborne et al. (1999)
		Glucosisymbri n		unknown			Harborne et al. (1999)
		Glucocochlear in, glucojiabutin, sec-Butyl, 2- Butyl		unknown		<i>Ciecer arietinum</i> and <i>Trifolium</i> spp.	Harborne et al. (1999)
				unknown			Harborne et al. (1999)
		Glucoibererin		unknown			Harborne et al. (1999)
		Glucouasturtii n; phenethyl		unknown			Harborne et al. (1999)
<i>Thlaspi arvense</i>	Brassicaceae	Glucotropaeoli n		unknown			Harborne et al. (1999)
				unknown			Harborne et al. (1999)
		Glucoiberin		unknown		<i>Glycine max</i> , <i>Trifolium</i> <i>pratense</i> , <i>Pueraria</i> spp and <i>Baptisia</i> spp.	Harborne et al. (1999)
		Allyl, Sinigrin		unknown			Harborne et al. (1999)
<i>Coronilla varia</i>	Fabaceae	Daphnoretin	Chromones and Chromenes	unknown		widespread	Harborne et al. (1999)
				unknown			Harborne et al. (1999)
<i>Lathyrus sylvestris</i>	Fabaceae	Psoralen Diaminobutyri c acid	Coumarin Amino acid	unknown seeds	insect antifeedant to		Harborne et al.

				armyworms, chronic ammonia toxicity in rats, inhibits ornithine carbamoyltra nsferase		(1999)
alpha-amino- beta- oxalylaminopr opionic acid	Amino acid	all parts	neurolathyris m	root of <i>Baptisia australis</i> , <i>Euchresta japonica</i> , <i>Onionis spinosa</i> and <i>Sophora subprostrata</i>	Harborne et al. (1999)	
L-Bornestitol	Sugar alcohols and cyclitols	unknown			Harborne et al. (1999)	
L- Homoarginine	Amino acid	seeds	toxic to rats and insects, competitive inhibitor of arginine, microbial growth inhibitor, germination inhibitor	widespread in beans <i>Vicia</i> , <i>Pisium</i> and <i>Phaseolus</i> spp.	Harborne et al. (1999)	
Lathyrine	amino acid	seeds		free amino acid in coffee, asparagus, soybeans	Harborne et al. (1999)	
(-)-Medicarpin	isoflavinoid and neoflavinoid	induced as phytoalexin	antifungal	only <i>Vicia</i> spp.	Harborne et al.	

							(1999)
		(-)-Variabilin	isoflavonoid and neoflavonoid	induced as phytoalexin	antifungal	at least in 17 <i>Vicia</i> spp.	Harborne et al. (1999)
<i>Lotus corniculatus</i>	Fabaceae	Gossypetin	Flavones and Flavanols	flowers	antibacterial, yellow coloring		Harborne et al. (1999)
		Linamarin	Amines	seedlings	toxic and sequestered	<i>Vicia</i> spp and <i>Lens culinaris</i>	Harborne et al. (1999)
		(-)-Sativan	isoflavonoid and neoflavonoid	induced as phytoalexin	antifungal		Harborne et al. (1999)
		Vestitol	isoflavonoid and neoflavonoid	unknown	antifungal		Harborne et al. (1999)
<i>Medicago sativa</i>	Fabaceae	L-arginine		unknown			Harborne et al. (1999)
		Citramalic acid	Organic acids	unknown			Harborne et al. (1999)
		alpha-Cryptoxanthin		unknown	yellow food coloring		Harborne et al. (1999)
		Homostachydrine	Amino acids	seeds			Harborne et al. (1999)
		Liquiritigenin	Minor flavinoids	unknown	weak antifungal, acts on nervous system		Harborne et al. (1999)

Medicagenic acid-3-O-glucoside	triterpenoid saponins	unknown	Anti-nutritional , wide range of biological activities	Harborne et al. (1999)
Ononitol	Sugar alcohols and cyclitols	unknown		Harborne et al. (1999)
alpha-spinasterol	Phytosterols	unknown		Harborne et al. (1999)
tricin	flavones and flavinols	unknown	allelopathic to grass	Harborne et al. (1999)
trigonelline	nitrogen compounds	seeds	hypoglycaemic in animals	Harborne et al. (1999)
Vit K		unknown		Harborne et al. (1999)
Coumasterol	isoflavoid and neoflavonoid	unknown	oestrogenic, antifungal, non-competitive inhibitor of peroxidase	Harborne et al. (1999)
(-)-Medicarpin		unknown		Harborne et al. (1999)
(-)-Sativan		unknown		Harborne et al. (1999)
Vestitol		unknown		Harborne et al.

						(1999)
<i>Melilotus alba</i>	Fabaceae	O-Coumaric acid	phenylpropanoid	unknown		Harborne et al. (1999)
		Melilotic acids	phenylpropanoid	stem	antiulcerogenic activity	Harborne et al. (1999)
					Hemorrhagic, anti coagulant, inhibitor of various enzymes (Warfarin in rat poison is a related compound)	Harborne et al. (1999)
		Dicoumarol	coumarins	precursor to coumaric acid		
<i>Trifolium spp.</i>	Fabaceae	Biochanin A	Isoflavonoids and neoflavonoids	unknown	hypolipidemic activity, oestrogenic activity	Harborne et al. (1999)
		Coumesterol		unknown		Harborne et al. (1999)
		Formononetin	isoflavonoid and neoflavonoid	unknown	hypolipidemic and antifungal, infertility in ewes	Harborne et al. (1999)
		Genistein	isoflavonoid and neoflavonoid	unknown	oestrogenic and antifungal, inhibits soybean	Harborne et al. (1999)

					lipase and comp inhibits peroxidase	
		(-)-Maackiain	isoflavonoid and neoflavonoid	phytoalexin	antifungal	Harborne et al. (1999)
		(-)-Medicarpin		unknown		Harborne et al. (1999)
		Ononin	isoflavonoid and neoflavonoid	unknown		Harborne et al. (1999)
		Prantesein	isoflavonoid and neoflavonoid	unknown	hypolipidaemic	Harborne et al. (1999)
		(-)-Sativan		unknown		Harborne et al. (1999)
		Vestitol		unknown		Harborne et al. (1999)
<i>Trifolium pratense</i>	Fabaceae	Daidzin	isoflavonoid and neoflavonoid	unknown		Harborne et al. (1999)
		Irilone	isoflavonoid and neoflavonoid	unknown	supresses growth of wheat coleoptiles	Harborne et al. (1999)
		kaempferol	flavone and flavanol	leaves	anti-inflammatory, antibacterial and mutagenic	Harborne et al. (1999)

		Phaseolic acid		unknown		Harborne et al. (1999)
		Prantensein		unknown		Harborne et al. (1999)
		Trifolirhizin	isoflavonoid and neoflavonoid	root and stem	inhibits seed germination	Harborne et al. (1999)
<i>Vicia cracca</i>	Fabaceae	Vicia cracca lectins	proteins and peptides	unknown		Harborne et al. (1999)
		aminobutyric acid	amino acid	seeds	inhibits transmitter at neuromuscular junction in CNS	Harborne et al. (1999)
		asparagine	amino acid	unknown	dietary supplement	Harborne et al. (1999)
		cyanoalanine	amino acid	unknown	neurotoxic - neuroleptin in birds and other animals	Harborne et al. (1999)
		hydroxy-L-arginine	amino acid	unknown	phytotoxic, germination inhibitor	Harborne et al. (1999)
		(+)-Hydroxy-L-homoarginine		unknown		Harborne et al. (1999)
		Wyerone		phytoalexin	antifungal	Harborne et al. (1999)