HOST PLANT RELATIONSHIPS AND CHEMICAL COMMUNICATION IN THE CERAMBYCIDAE

BY

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DISSERTATION

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Abstract

The beetle family Cerambycidae is one of the largest groups of insects. Commonly referred to as longhorned beetles, the larvae of cerambycids usually feed on the tissues of woody plants and can be important insect pests, damaging and even killing trees in managed and natural landscapes. In this dissertation, I revise a historical database on associations between the adult beetles and the plant species whose flowers they visited, and determine that beetles were commonly found on plants in the Asteraceae. However, the umbellifer *Pastinaca sativa* L. and the rose *Aruncus dioicus* (Walter) Fernald var. *vulgaris* (Maxim) were visited by the greatest number of beetle species. I conducted an experiment to explore the relationship between environmental stress of woody host plants and susceptibility to attack by cerambycid beetles, and found that the number of beetles completing development was positively associated with growth rate of the larval host tree. I also studied cross-attraction between beetles of different species and discovered that live male beetles in traps produced an aggregation pheromone that attracted adults of both sexes of a different cerambycid species. Finally, I conducted a field study that showed that the efficiency with which pheromone traps captured cerambycid beetles was greatly improved by treating trap surfaces with the polymer Fluon®. This information can be applied to improve methods for determining the geographic distribution and local abundance of species.

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Chapter 1: Introduction

The beetles (Coleoptera) comprise one of the largest and most diverse groups of insect. These stunning organisms occupy nearly every terrestrial habitat (Arnett and Thomas 2000). Beetles are incredibly variable both in their morphology and ecology, drawing the attention of collectors and ecologists for centuraries.

The beetle family Cerambycidae is one of the largest groups of insects with more than 35,000 species worldwide (Lawrence 1982). Commonly referred to as longhorned beetles, they vary greatly in body size, morphology, coloration, and natural history (see volumes indexed in Linsley and Chemsak 1997). Cerambycids inhabit nearly every terrestrial habitat and can be ecologically important by recycling dead plants (e.g., Solomon 1995).

The larvae of cerambycids usually feed on the tissues of woody plants, but different species may require hosts that are healthy, moribund, dead, or even in various stages of decomposition (Linsley 1961). Some species are important insect pests, damaging and even killing trees in managed and natural landscapes (Solomon 1995). For example, *Enaphalodes rufulus* (Haldeman), the red oak borer, is native to the eastern United States and was implicated as the causal agent of extensive oak mortality in Arkansas, where oak trees were experiencing between 50 and 75% mortality (Stephen et al. 2001). Because the larvae are concealed in wood, many species are easily transported through international commerce (e.g., see Haack and Cavey 1997; Brockerhoff and Bain 2000, Lingafelter and Hoebeke 2002, Sweeney et al. 2004). Cerambycid beetles are among the most commonly intercepted insects in quarantine at ports of entry, and a number of exotic species have become significant pests in the United States (Haack 2006). *Tetropium fuscum* (F.), the brown spruce borer, was recently introduced in Nova Scotia, Canada (Smith and Hurley 2000). *T. fuscum* is generally a secondary pest in its native range; however it has been found attacking healthy, vigorous trees in Canada (Sweeney et al. 2006). *Anoplophora glabripennis* (Motschulsky), the Asian longhorned beetle, was first found in New York City in 1996 (Cavey et al. 1998) and since then has caused extensive tree mortality in Chicago, New York, New Jersey, Ontario Canada, and most recently in Massachusetts. Approximately $170 million has been invested to eradicate this species, which is estimated to cause $670 billion dollars in damage if it is left unmanaged (USDA 2005). Traps that are efficient in capturing and containing cerambycid beetles are critical for monitoring these potential invasive species.

Reproductive strategies of cerambycids vary with the condition of the host that is required by the larvae (Hanks 1999). In some species, the sexes are brought together by their mutual attraction to a host plant; however in other species mate location is mediated by volatile pheromones (Millar et al. 2009). Males of several species in the diverse subfamily Cerambycinae are known to produce volatile sex or aggregation pheromones (Lacey et al. 2004, 2007, 2009; Ray et al. 2006; Hanks 2007). These pheromones are comprised of one to three compounds that share a similar structural motif consisting of 2,3-hexanediols and/or hydroxyhexanones (reviewed by Lacey et al. 2004, 2007). Similarity among sympatric species in the composition of their pheromones results in multiple species responding to synthetic pheromone in traps, suggesting that some species are cross attractive. Cross-attraction could facilitate location of larval hosts by species that compete for the same host species. Once on the host plant, however, males may avoid making mistakes by choosing females of the wrong species by using species-specific contact pheromones in the cuticular wax layer of females (Hanks et al. 1996, Fukaya et al. 1996, Ginzel et al. 2003).

Although much is know about the geographic distribution and host range of cerambycid species, little is known of the behavior of the adults, especially their chemical ecology (e.g., Linsley 1961, Solomon 1995, Hanks 1999). As a result, it can be difficult to develop effective management strategies for cerambycid species that are pests. The goal of my dissertation research has been to improve our understanding of the ecology and behavior of cerambycid species that are native to Illinois, by documenting associations between the adult beetles and the plant species that they visit to feed on pollen and nectar, by exploring the relationship between environmental stress of woody host plants and susceptibility to attack, by studying cross-attraction between beetles of different species, and finally by improving the efficiency of pheromone traps that can be used to determine the geographic distribution and local abundance of species.

In Chapter 2, I tabulated plant species that served as floral hosts of adult beetles as reported by Charles Robertson in his 33-year data set of flower-visiting insects of central Illinois at the start of the 20th century. This information may serve as a reference to compare to current populations of species, such as for studying the influence of invasive plant species on beetle communities. Of course, I was particularly interested in the species of cerambycid beetles that Robertson recorded to compare with the species that I capture in field bioassays today.

In Chapter 3, I tested the hypothesis that environmental stress renders trees susceptible to attack by longhorned beetle. I measured the width of xylem growth rings to characterize the history of environmental stress that trees experience and analyzed the number of beetles that emerged per tree to determine if there was a relationship. I found that the average width of growth rings was not significantly correlated with the number of beetle that emerged for one study set, but was significantly correlated when I increased the sample number in the next study set.

In Chapter 4 I investigated cross-attraction in longhorned beetles of the Cerambycinae. I conducted field experiments that compared the response of wild beetles of two species to traps that were separately baited with live males of the same species. I found that, although wild beetles showed the strongest response to males of the same species, there was a significant response of beetles of both species to heterospecific males. The experiment therefore supports the notion that adult cerambycid beetles will respond to calling males of the wrong species if they produce pheromones that share components with the pheromone of their species.

Finally, in Chapter 5, I compared the efficacies of Rain-X®, a polysiloxane liquid, and Fluon®, a PTFE fluoropolymer dispersion, as surface treatments for panel traps that are deployed to capture cerambycid beetles. Rain-X is often used to condition intercept traps to render their surfaces more slippery and Fluon is commonly applied to the upper walls of containers used to house insects in insectaries. Treating panel traps with Fluon dramatically enhances their efficiency in capturing cerambycid beetles.

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Chapter 2: Floral Host Plants of Adult Beetles of Central Illinois

Abstract In this chapter, I tabulate plant species that served as floral hosts of adult beetles as reported by Charles Robertson in his 33-year data set of flower-visiting insects of central Illinois. He recorded host plants of 153 beetle species, most of the plants were in the Asteraceae. The umbellifer *Pastinaca sativa* L. and the rose *Aruncus dioicus* (Walter) Fernald var. *vulgaris* (Maxim) were visited by the greatest number of beetle species. The most common beetle species were the cantharid *Chauliognathus pennsylvanicus* DeGeer, the chrysomelid *Diabrotica undecimpunctata* Mannerheim, and the scarab *Trichiotinus piger* F. Most of the beetle species (81%) visited four or fewer plant species. These findings may have important implications for choosing native plant species for ornamental landscapes to foster populations of endemic beetles, to encourage natural enemies of plant-feeding pests, and to improve pollination services for crop plants.

KEY WORDS: Charles Robertson, floral resources, Coleoptera, pollinator

Introduction

POLLINATING INSECTS PLAY a critical role in reproduction of many plant species, including important species of crop plants (Faegri and van der Pijl 1979). Populations of hymenopterous pollinators apparently are declining world wide for as yet unknown reasons, which undoubtedly will have disastrous implications for agriculture (NRC 2006, vanEngelsdorp et al 2007). It therefore may be necessary in the future to develop methods for encouraging other types of pollinators, such as beetles. Beetles of many species commonly visit flowers where they feed on nectar and pollen (Faegri and van der Pijl 1979, Evans and Bellamy 1997). They are considered "mess-and-soil" pollinators, not particularly efficient in transferring pollen between plants, but communities of beetles nevertheless may be important for plant reproduction due to their species diversity and general abundance (Kevan and Baker 1983, Dieringer et al. 1999, Goldblatt et al. 2009, Thien et al. 2009). Plant species that have co-evolved with beetle pollinators usually have flowers that are pale in color and offer nectar and pollen that are readily accessible to insects with generalized mouthparts, a combination of traits that defines the cantharophily syndrome (Faegri and van der Pijl 1979).

In this chapter, I summarize information on associations between beetle species of central Illinois and their floral host plants from data collected at the turn of the 20th century by Charles Robertson (1929). Over a 33-year period, Robertson recorded 15,172 observations of insects that were visiting flowers of 453 plant species in the vicinity of Carlinville, Illinois "... for the purpose of ascertaining the different kinds of insect visitors." (For summaries of data on the hymenopteran parasitoids, lepidopterans, and syrphid and tachinid flies, see Tooker and Hanks 2000, Tooker et al. 2002, 2006). Robertson's publication is limited in its utility for studying the host range of individual insect species because his collection records were categorized by plant species, and he provides no index for insect species. I corrected this omission here by listing host plant species for each of the beetle species, and updating all scientific names. I also rank plant families and species by the abundance and diversity of beetles that visited them, and assess levels of polyphagy among beetle taxa.

Materials and Methods

Robertson (1929) described in general his methods of collecting data, and other details have been provided in a biography (Parks 1936) and a more recent review (Marlin and LaBerge 2001). From early spring to late fall, every year from 1884 to 1916, Robertson was in the field collecting insects from flowers. On any given day he may have collected insects from only a few species of plants, but he nevertheless made note of all floral visitors that he observed, and indicated which species were “abundant” and “frequent” on particular plant species (a qualitative assessment of relative abundance). Robertson made a special effort to collect insect species that were rare, or of uncertain taxonomy.

I have updated species names and taxonomy of beetles with Nomina Insecta Neartica (Entomological Information Services 1996), and more recent taxonomic references for some species (see footnotes in Table 2). Plant species names were updated with the most recent edition (Fernald 1978) of Robertson’s original reference (Robinson and Fernald 1908) and confirmed with more current publications (Kartesz 1994; USDA 2009). I ranked the plant species and families by the number of beetle species that visited them, and beetle species by their level of floral polyphagy. I tested differences among percentages and ranks using the nonparametric Kruskal-Wallis test, and tested linear relationships with Pearson’s correlation coefficient (PROC NPAR1WAY and PROC CORR, respectively; SAS Institute 2001).

In discussing our results, I use the words "preference" and "preferred" only for convenience. I acknowledge that these terms are inaccurate because Robertson (1929) provided no indication of relative abundance of plant species.

Results and Discussion

The Robertson (1929) data set included 141 species of plants (44 families; Table 2.1) that were visited by beetles, with the dominant plant families being the Asteraceae (48 species, or 34% of the total) and the Rosacae (10 species; 7%), followed by the Asclepiadaceae, Lamiaceae, Liliaceae, and Fabaceae (all with six species; 4%). Species of these plant families that were in the data set all had flowers that were pale or white in color, and were either solitary and large, or small and clustered (Gleason and Cronquist 1991), consistent with the floral preferences of beetles (Faegri and van der Pijl 1979).

The data set includes 153 species of beetles in 28 familes (Tables 2.2 and 2.4). The greatest number of beetle species visited plants of the Apiaceae (Table 2.2), with a mean of 11.2 ± 10.3 (SD) beetles species per plant species, followed by the Rosaceae (6.0 ± 9.3), Asclepiadaceae (3.0 ± 2.1), Asteraceae (2.9 ± 2.4), Lamiaceae (2.7 ± 3.1), Salicaceae (2.6 ± 1.1), and Fabaceae (2.5 ± 1.8). Plant species in the remaining families were visited by fewer than two species of beetle, on average.

Among plant species that were preferred by beetles (i.e., those visited by ≥ 13 beetle species; Table 2.3), the umbellifer *Pastinaca sativa* L. and the rose *Aruncus dioicus* (Walter) Fernald var. *vulgaris* (Maxim.) H. Hara were visited by the greatest number of beetle species. Again, these species have small, clustered flowers that are pale in color (Gleason and Cronquist 1991).

The number of beetle species that Robertson recorded from a given plant species could have been influenced by its relative abundance in the plant community. In fact, ten of the eleven plant species that had the greatest diversity of beetles have long been relatively common species in central Illinois, including *P. sativa*, *A. dioicus* var. *vulgaris*, and *Cryptotaenia canadensis* (L.) (Tables 2.1, 2.3; Illinois Natural History Survey 1936, Jones 1945, Mohlenbrock 1986). Nevertheless, one plant species that had a great diversity of beetle visitors, *Viburnum dentatum* var. *dentatum* L., is currently uncommon in Illinois (Mohlenbrock 1986). Moreover, Robertson recorded few beetle visitors for other plant species that probably were abundant at the time, including *Silphium integrifolium* Michaux, *Solidago gigantea* Aiton, and *Helianthus tuberosus* L. (Table 2.2; INHS 1936, Jones 1945). Foraging preferences of beetles, rather than relative abundance of plant species, may at least partly account for these patterns of floral visitation across plant species.

Familes of beetles were similar in the percentage of their species that visited the most preferred plant species (Table 2.3; Kruskal-Wallis $X^2 = 0.48$; df = 4; $P = 0.98$) and ranked preferences also were similar (Kruskal-Wallis $X^2 = 5.50$; df = 4; $P = 0.24$). Preference rankings for mordellids and cerambycids were significantly correlated ($r = 0.60$, $P = 0.05$), and the same was true for coccinellids and cantharids ($r = 0.59$, $P = 0.05$). These findings indicate that, in general, beetles in different families nevertheless tended to prefer the same host plant species, especially for species in these pairs of families. Preference ranks of other beetles families were not significantly correlated with one another ($P > 0.05$).

The plant species on which beetles were most abundant (based on the number of beetle species that were listed as “abundant” or “frequent”) included *A. dioicus* var. *vulgaris* (12 beetle species were abundant), followed by *V. dentatum* var. *dentantum* (7 species), *Solidago* *canadensis* L. (6 species), and *Salix cordata* Michaux. (four species). Some of the plant species, however, were visited in great number by only one beetle species (from Table 2.2). For example, the mustard *Cardamine concatenata* (Michaux) Sw. was commonly visited by only *Boreades abdominalis* (Erichson) (Table 2.1), suggesting that this plant species is important to the nutritional ecology of this brachypterid. On the other hand, *B. abdominalis* is not necessarily vital to reproduction of *C. concatenata* because that plant also is visited by many other types of insects, including a diversity of bee species (Robertson 1929).

Chrysomelids visited the greatest number of plant species (N = 61; Table 2.4), but most of the species visted only one or two host species (Table 2.2). Of all of the beetles, 124 species (81% of the total) visited five or fewer plant species, with 73 species (59%) recorded from a single plant species (from Table 2.2). These data indicate that many beetle species visit surprisingly few plant species, and that some plant species play important roles in biology and/or nutrition of these insects. On the other hand, scarabs were the most polyphagous, averaging 5.63 plant species per beetle species (Table 2.4). The most polyphagous beetle species in the entire data set were the scarab *Trichiotinus piger* F. (28 plant species), the cantharid *Chauliognathus pennsylvanicus* (DeGeer) (41species), and the chrysomelid *Diabrotica undecimpunctata* Mannerheim (33 species). *T. piger* and *C. pennsylvanicus* also were among the most abundant beetle species, with *T. piger* listed as abundant on eight plant species in six families and *C. pennsylvanicus* abundant on 17 plant species in four families (Table 2.2). These findings are consistent with other reports of polyphagy in *T. piger* (Hoffman 1935), and the general abundance of *C. pennsylvanicus* (Borrer et al. 1989). It is likely that *C. pennsylvanicus* was common on flowers of many plant species not only because of floral polyphagy, but because it preys on adults of *Diabrotica* species (Clausen 1940) and adult *D. undecimpunctata* are polyphagous (Campbell and Meinke 2006). Such interactions between beetle species could be responsible for some of the patterns in abundance on plant species that are reported by Robertson (1929), and suggest that his findings should be interpreted with caution.

The beetle species that visited the greatest number of plants tended to be relatively large in body size, such as *C. pennsylvanicus, Coleomegilla maculata* (DeGeer), *Epicauta pennsylvanica* (DeGeer), and *T. piger*, or brightly colored, such as *D. undecimpunctata* (Table 2.2), suggesting that their designation as polyphagous could be due merely to their being the most conspicuous. Consistent with that hypothesis, beetle species that are represented by only one record in the data set tend to be small in body size, including e.g., *Apion nigrum* Herbst, *Agrilus* spp., *Acanthoscelides submuticus* (Sharp), and *Rhabdopterus picipes* (Olivier) (Table 2.2).

The relative abundance of the beetles *T. piger* and *C. pennsylvanicus*, and their high levels of polyphagy (see above), also suggests that our assessment of polyphagy is an artifact of sample size (see Jervis et al. 1993). There is a positive linear relationship between the host range of beetle species (as assessed from Table 2.1) and the number of plant species on which they were listed as abundant or frequent (Fig. 2.1). It nevertheless is possible that polyphagous species simply were more abundant than species with narrower host ranges.

The associations between beetle species and their floral host plants that I summarize above may be used to guide research on improving pollination services for crop plants, for studying insect ecology and behavior, and for selecting plant species to include in ornamental landscapes that will foster populations of endemic beetle species. Plant species such as *P. sativa* or *A. pilosus*, whose flowers apparently appeal to a great diversity of beetle species, may be used to encourage predaceous beetles to better regulate plant-feeding pests. For example floral resources for hymenopterous parasitoids can help regulate populations of herbivorous pests (Ellis et al.

2005). On the other hand, some beetle species may rely on only a few plant species as sources of nectar and pollen, but more research is required to confirm these relationships. Robertson's (1929) data set also provides an early assessment of the relative abundance of beetle species that could now be used in studying how beetle communities, and associations with host plants, have changed over time. In fact, Robertson's data has been used for just this purpose for species of endemic bees (Marlin and LaBerge 2001).

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Tables

Table 2.1 Plant species (listed alphabetically) in the Robertson (1929) data set. Plant species codes are the first three letters of genus and species names, except where duplication necessitated different letter combinations.

Current plant species name	Species name cited (if different from current)	Species code	Family	Native or Introduced	No. of beetle species
Abutilon theophrasti Medicus	-	*Abuthe*	Malvaceae	Introduced	1
Achillea millefolium L.	-	*Achmil*	Asteraceae	Native	1
Agalinis tenuifolia (Vahl) Rafinesque-Schmaltz	*Gerardia tenuifolia*	*Agaten*	Scrophulariaceae	Native	1
Amorpha canescens Pursh	-	*Amocan*	Fabaceae	Native	3
Anethum graveolens L.	-	*Anegra*	Apiaceae	Introduced	3
Antennaria plantaginifolia (L.) Richardson	-	*Antpla*	Asteraceae	Native	2
Apocynum cannabinum L.	-	*Apocan*	Apocynaceae	Native	1
Aristolochia tomentosa Sims	-	*Aritom*	Aristolochiaceae	Native	1
Aruncus dioicus (Walter) Fernald var. *vulgaris* (Maxim) H. Hara	*Aruncus sylvester*	*Arudio*	Rosaceae	Native	32
Asclepias incarnata L.	-	*Ascinc*	Asclepiadaceae	Native	6
Asclepias longifolia Michaux	*Acerates floridana*	*Asclon*	Asclepiadaceae	Introduced	1

Table 2.1 (cont.)

Current plant species name	Species name cited (if different from current)	Species code	Family	Native or Introduced	No. of beetle species
Asclepias purpurascens L.	-	*Ascpur*	Asclepiadaceae	Native	1
Asclepias sullivantii Engelmann ex Gray	-	*Ascsul*	Asclepiadaceae	Introduced	2
Asclepias syriaca L.	-	*Ascsyr*	Asclepiadaceae	Native	5
Asclepias verticillata L.	-	*Ascver*	Asclepiadaceae	Native	3
Bidens aristosa (Michaux) Britton	-	*Bidari*	Asteraceae	Native	6
Bidens laevis (L.) Britton, Sterns, Poggenberg	-	*Bidlae*	Asteraceae	Native	2
Blephilia ciliata (L.) Bentham	-	*Blecil*	Lamiaceae	Native	2
Boltonia asteroides (L.) L'Heritier de Brutelle	-	*Bolast*	Asteraceae	Native	4
Calystegia sepium ssp. *sepium* (L.) R. Brown	*Convolvulus sepium*	*Calsep*	Convolvulaceae	Introduced	1
Camassia scilloides (Rafinesque-Schmaltz) Cory	*Camassia esculenta*	*Melvir*	Liliaceae	Native	1

Table 2.1 (cont.)

Current plant species name	Species name cited (if different from current)	Species code	Family	Native or Introduced	No. of beetle species
Cardamine concatenata (Michaux.) Sw.	*Dentaria laciniata*	*Carcon*	Brassicaceae	Native	1
Caulophyllum thalictroides (L.) Michaux	-	*Cautha*	Berberidaceae	Native	3
Ceanothus americanus L.	-	*Ceaame*	Rhamnaceae	Native	14
Cephalanthus occidentalis L.	-	*Cepocc*	Rubiaceae	Native	2
Cercis canadensis L.	-	*Cercan*	Fabaceae	Native	1
Chaerophyllum procumbens (L.) Crantz	-	*Chapro*	Apiaceae	Native	4
Cicuta maculata L.	-	*Cicmac*	Apiaceae	Native	14
Cirsium discolor (Muhlenberg ex Willdenow) Sprengel	-	*Cirdis*	Asteraceae	Native	1
Cirsium pumilum (Nuttall) Sprengel	-	*Cirpum*	Asteraceae	Native	2
Claytonia virginica L.	-	*Clavir*	Portulacaceae	Native	1
Conoclinium coelestinum (L.) DC.	*Eupatorium coelestinum* L.	*Concoe*	Asteraceae	Native	1

Table 2.1 (cont.)

Current plant species name	Species name cited (if different from current)	Species code	Family	Native or Introduced	No. of beetle species
Comandra umbellata L.	-	*Comumb*	Santalaceae	Native	2
Coreopsis tripteris L.	-	*Cortri*	Asteraceae	Native	1
Cornus amomum P. Miller	-	*Coramo*	Cornaceae	Native	2
Cornus florida L.	-	*Corflo*	Cornaceae	Native	1
Cornus racemosa Lamarck	*Cornus paniculata*	*Corrac*	Cornaceae	Native	8
Crataegus chrysocarpa Ashe	*Crataegus coccinea*	*Crachr*	Rosaceae	Native	6
Crataegus crus-galli L.	-	*Cracru*	Rosaceae	Native	4
Crataegus mollis Scheele	-	*Cramol*	Rosaceae	Native	6
Cryptotaenia canadensis (L.) DeCandolle	-	*Crycan*	Apiaceae	Native	19
Dalea purpurea Ventenat	*Petalostemum purpureum*	*Dalpur*	Fabaceae	Native	4
Datura stramonium L.	*Datura tatula*	*Datstr*	Solanaceae	Introduced	1
Echinacea pallida (Nutt.) Nutt.	-	*Echpal*	Asteraceae	Native	1
Enemion biternatum Rafinesque-Schmaltz	*Isopyrum biternatum*	*Enebit*	Ranunculaceae	Native	4

Table 2.1 (cont.)

Current plant species name	Species name cited (if different from current)	Species code	Family	Native or Introduced	No. of beetle species
Erigenia bulbosa (Michaux) Nuttall	-	*Eribul*	Apiaceae	Native	2
Erigeron philadelphicus L.	-	*Eriphi*	Asteraceae	Native	3
Erigeron strigosus Muhlenberg ex Willdenow	*Erigeron ramosus*	*Eristr*	Asteraceae	Native	2
Eryngium yuccifolium Michaux	-	*Eryyuc*	Apiaceae	Native	8
Euonymus atropurpurea Jacquin	-	*Euoatr*	Celastraceae	Native	2
Eupatorium altissimum L.	-	*Eupalt*	Asteraceae	Native	1
Eupatorium perfoliatum L.	-	*Eupper*	Asteraceae	Native	6
Eupatorium serotinum Michaux	-	*Eupser*	Asteraceae	Native	6
Euthamia graminifolia var. *graminifolia* (L.) Nutt.	*Solidago graminifolia*	*Eutgra*	Asteraceae	Native	2
Galium trifidum L.	-	*Galtri*	Rubiaceae	Native	3
Gentiana andrewsii Grisebach	-	*Genand*	Gentianaceae	Native	1
Geum canadense Jacquin	-	*Geucan*	Rosaceae	Native	2
Helenium autumnale L.	-	*Helaut*	Asteraceae	Native	2

Table 2.1 (cont.)

Current plant species name	Species name cited (if different from current)	Species code	Family	Native or Introduced	No. of beetle species
Helianthus annuus L.	-	*Helann*	Asteraceae	Native	4
Helianthus divaricatus L.	-	*Heldiv*	Asteraceae	Native	1
Helianthus grosseserratus Martens	*Helianthus grosse-serratus*	*Helgro*	Asteraceae	Native	3
Helianthus x *laetiflorus* Pers. (pro sp.) [pauciflorus x tuberosus]	*Helianthus scaberrimus*	*Hellae*	Asteraceae	Native	1
Helianthus tuberosus L.	-	*Heltub*	Asteraceae	Native	4
Heliopsis helianthoides (L.) Sweet	-	*Helhel*	Asteraceae	Native	1
Heracleum maximum Bartram	*Heracleum lanatum*	*Hermax*	Apiaceae	Native	16
Hydrangea arborescens L.	-	*Hydarb*	Hydrangeaceae	Native	5
Hypoxis hirsuta (L.) Coville	-	*Hyphir*	Liliaceae	Native	1
Impatiens capensis Meerburgh	*Impatiens biflora*	*Impcap*	Balsaminaceae	Native	1
Iris hexagona Walter	-	*Irihex*	Iridaceae	Native	1
Krigia biflora var. *biflora* (Walter) S. F. Blake	*Krigia amplexicaulis*[b]	*Kriamp*	Asteraceae	Native	3
Lactuca canadensis L.	-	*Laccan*	Asteraceae	Native	1
Liatris scariosa (L.) Willdenow	-	*Liasca*	Asteraceae	Native	6

Table 2.1 (cont.)

Current plant species name	Species name cited (if different from current)	Species code	Family	Native or Introduced	No. of beetle species
Leucanthemum vulgare Lam.	*Chrysanthemum leucanthemum* L.	*Leuvul*	Asteraceae	Native	1
Lycopus americanus Muhlenberg	-	*Lycame*	Lamiaceae	Native	1
Maianthemum racemosum ssp. *racemosum* L.	*Smilacina racemosa*	*Mairac*	Liliaceae	Native	5
Malva pusilla Sm.	*Malva rotundifolia L.*	*Malrot*	Malvaceae	Introduced	1
Melanthium virginicum L.	-	*Camsci*	Liliaceae	Native	6
Melilotus officinalis (L.) Lamarck	*Melilotus alba*	*Meloff*	Fabaceae	Introduced	5
Mentha arvensis L.	-	*Menarv*	Lamiaceae	Native	1
Mollugo verticillata L.	-	*Molver*	Molluginaceae	Native	1
Nelumbo lutea Willdenow	-	*Nellut*	Nelumbonaceae	Native	4
Oenothera fruticosa L.	-	*Oenfru*	Onagraceae	Native	2
Osmorhiza longistylis (Torrey) DeCandolle	-	*Osmlon*	Apiaceae	Native	5
Oxalis violacea L.	-	*Oxavio*	Oxalidaceae	Native	1

Table 2.1 (cont.)

Current plant species name	Species name cited (if different from current)	Species code	Family	Native or Introduced	No. of beetle species
Oxypolis rigidior (L.) Rafinesque-Schmaltz	-	*Oxyrig*	Apiaceae	Native	16
Pastinaca sativa L.	-	*Passat*	Apiaceae	Introduced	42
Penstemon laevigatus Aiton	-	*Penlae*	Scrophulariaceae	Native	1
Perideridia americana (Nuttall) Reichenbach	*Eulophus americanus*	*Perame*	Apiaceae	Native	7
Persicaria pensylvanica L.	*Polygonum pennsylvanicum L.*	*Polpen*	Polygonaceae	Native	1
Polemonium reptans L.	-	*Polrep*	Polemoniaceae	Native	2
Polygonum hydropiperoides Michaux	-	*Polhyds*	Polygonaceae	Native	4
Polygonum scandens L.	-	*Polsca*	Polygonaceae	Native	1
Polytaenia nuttallii DeCandolle	-	*Polnut*	Apiaceae	Native	1
Portulaca oleracea L.	-	*Porole*	Portulacaceae	Introduced	1
Prenanthes crepidinea Michaux	-	*Precre*	Asteraceae	Native	2
Prunus americana Marshall	-	*Pruame*	Rosaceae	Native	3

Table 2.1 (cont.)

Current plant species name	Species name cited (if different from current)	Species code	Family	Native or Introduced	No. of beetle species
Prunus serotina Ehrhart	-	*Pruser*	Rosaceae	Native	1
Pseudognaphalium obtusifolium ssp. *obtusifolium* (L.) Hilliard & B. L. Burtt	*Gnaphalium polycephalum*	*Gnaobt*	Asteraceae	Native	1
Pycnanthemum flexuosum (Walter) Britton, Sterns, Poggenberg	-	*Pycfle*	Lamiaceae	Native	9
Pycnanthemum verticillatum var. *pilosum* (Nuttall) Cooperrider	*Pycnanthemum pilosum*	*Pycver*	Lamiaceae	Native	2
Pycnanthemum virginianum (L.) Durand, Jackson	-	*Pycvir*	Lamiaceae	Native	1
Ranunculus abortivus L.	-	*Ranabo*	Ranunculaceae	Native	2
Ranunculus fascicularis Muhlenberg ex Bigelow	-	*Ranfas*	Ranunculaceae	Native	1
Ranunculus hispidus var. *nitidus* (Chapman) T. Duncan	*Ranunculus septentrionalis*	*Ranhis*	Ranunculaceae	Native	7

Table 2.1 (cont.)

Current plant species name	Species name cited (if different from current)	Species code	Family	Native or Introduced	No. of beetle species
Ratibida pinnata (Ventenat) Barnhart	*Lepachys pinnata*	*Ratpin*	Asteraceae	Native	2
Rhus glabra L.	-	*Rhugla*	Anacardiaceae	Native	1
Rosa humilis[b]	-	*Roshum*	Rosaceae	Native	2
Rosa setigera Michaux	-	*Rosset*	Rosaceae	Native	1
Rubus flagellaris Willd.	*Rubus villosus*	*Rubfla*	Rosaceae	Native	3
Rudbeckia hirta L.	-	*Rudhir*	Asteraceae	Native	6
Rudbeckia subtomentosa Pursh	-	*Rudsub*	Asteraceae	Native	3
Rudbeckia triloba L.	-	*Rudtri*	Asteraceae	Native	3
Sagittaria latifolia Willdenow	-	*Saglat*	Alismaceae	Native	3
Salix amygdaloides Andersson	-	*Salamy*	Salicaceae	Native	1
Salix cordata Michaux	*Salix cordata*	*Salcor*	Salicaceae	Native	4
Salix exigua Nuttall	*Salix longifolia*	*Salexi*	Salicaceae	Native	2
Salix humilis Marshall	-	*Salhum*	Salicaceae	Native	3
Salix nigra Marshall	-	*Salnig*	Salicaceae	Native	3

Table 2.1 (cont.)

Current plant species name	Species name cited (if different from current)	Species code	Family	Native or Introduced	No. of beetle species
Sambucus nigra L. ssp. *canadensis* (L.) R. Bolli	*Sambucus canadensis* (L.)	*Samnig*	Caprifoliaceae	Native	5
Sanguinaria canadensis L.	-	*Sangcan*	Papaveraceae	Native	1
Sassafras albidum (Nuttall) Nees Von Esenbeck	*Sassafras variifolium*	*Sasalb*	Lauraceae	Native	3
Senna marilandica (L.) Link	*Cassia marilandica*	*Senmar*	Fabaceae	Native	1
Sium suave Walter	*Sium cicutaefolium*	*Siusua*	Apiaceae	Native	18
Smilax herbacea L.	-	*Smiher*	Smilacaceae	Native	2
Solidago canadensis L.[a]	-	*Solcan*	Asteraceae	Native	14
Solidago gigantea Aiton	*Solidago serotina*	*Solgig*	Asteraceae	Native	1
Solidago missouriensis Nuttall	-	*Solmis*	Asteraceae	Native	4
Solidago nemoralis Aiton	-	*Solnem*	Asteraceae	Native	5
Solidago rigida L.	-	*Solrig*	Asteraceae	Native	4
Solidago speciosa Nuttall	-	*Solspe*	Asteraceae	Native	1
Staphylea trifolia L.	-	*Statri*	Staphyleaceae	Native	2
Stenanthium angustifolium[b]	-	*Steang*	Liliaceae	Native	1

Table 2.1 (cont.)

Current plant species name	Species name cited (if different from current)	Species code	Family	Native or Introduced	No. of beetle species
Strophostyles helvola (L.) Elliott	-	*Strhel*	Fabaceae	Native	1
Symphoricarpos orbiculatus Moench	-	*Symorb*	Caprifoliaceae	Native	2
Symphyotrichum anomalum Engelmann	*Aster anomalus*	*Symano*	Asteraceae	Native	1
Symphyotrichum cordifolium (L.) G. L. Nesom	*Aster sagittifolius*	*Symcor*	Asteraceae	Native	4
Symphyotrichum ericoides var. *ericoides* (L.) G. L. Nesom	*Aster multiflorus*	*Symeri*	Asteraceae	Native	1
Symphyotrichum lanceolatum ssp. *lanceolatum* var. *lanceolatum* (Willd.) G. L. Nesom	*Aster paniculatus*	*Symlan*	Asteraceae	Native	3
Symphyotrichum pilosum var. *pilosum* (Willd.) G. L. Nesom	*Aster ericoides villosus*	*Sympil*	Asteraceae	Native	6
Symphyotrichum turbinellum (Lindl.) G.L. Nesom	*Aster turbinellus*	*Symtur*	Asteraceae	Native	2

Table 2.1 (cont.)

Current plant species name	Species name cited (if different from current)	Species code	Family	Native or Introduced	No. of beetle species
Taenidia integerrima (L.) Drude	-	*Taeint*	Apiaceae	Native	9
Thalictrum thalictroides (L.) Eames & Boivin	*Anemonella thalictroides*	*Thatha*	Ranunculaceae	Native	1
Thaspium trifoliatum (L.) Gray	*Thaspium aureum trifoliatum*	*Thatri*	Apiaceae	Native	2
Tilia americana L.	-	*Tilame*	Tiliaceae	Native	1
Tradescantia virginiana L.	-	*Travir*	Commelinaceae	Native	1
Verbena hastata L.	*Verbena hastata*	*Verhas*	Verbenaceae	Native	1
Verbesina alternifolia (L.) Britton	*Actinomeris alternifolia*	*Veralt*	Asteraceae	Native	1
Viburnum dentatum var. *dentatum* L.	*Viburnum pubescens*	*Vibden*	Caprifoliaceae	Native	17
Zanthoxylum americanum Miller	-	*Zaname*	Rutaceae	Native	1
Zizia aurea (L.) Koch	-	*Zizaur*	Apiaceae	Native	13

[a] Often confused with other *Solidago* species; possibly *S. altissima* L. (Jones 1945).

[b] Species name not in Fernald (1978) or Kartesz (1994)

Table 2.2 Associations between beetle and plant species as reported by C. Robertson (1929). Beetle families are listed in alphabetical order. Plant families are abbreviated to three or four letters, and most plant species names are abbreviated to the first three letters of genus and species names (see Table 1).

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Apionidae	*Apion nigrum* Herbst	-	**Api:** *Crycan*
Brachypteridae	*Boreades abdominalis* (Erichson)	*Cercus abdominalis*	**Bra:** *Carcon*[a]*;* **Ran:** *Thatha*[a]
Buprestidae	*Acmaeodera pulchella* (Herbst)	-	**Asc:** *Ascinc;* **Ast:** *Ratpin*[a], *Rudhir;*
Buprestidae	*Acmaeodera tubulus* (F.)	*Acmaeodera culta*	**Lil:** *Hyphir*; **Oxa:** *Oxavio*; **Ros:** *Cracru*
Buprestidae	*Agrilus difficilis* Gory	-	**Api:** *Passat*
Buprestidae	*Agrilus egenus* Gory	-	**Api:** *Passat*
Cantharidae	*Atalantycha bilineata* (Say)[bc]	*Telephorus bilineatus*	**Lau:** *Sasalb*[a]; **Api:** *Zizaur*; **San:** *Comumb*
Cantharidae	*Atalantycha dentigera* (LeConte)[bc]	*Telephorus dentiger*	**Cap:** *Vibden*
Cantharidae	*Cantharis flavipes* LeConte[b]	*Telephorus flavipes*	**Ast:** *Eriphi*; **Cor:** *Corrac*[a]; **Api:** *Hermax*, *Passat*, *Zizaur*
Cantharidae	*Chauliognathus marginatus* (F.)[b]	-	**Api:** *Passat*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Cantharidae	*Chauliognathus pennsylvanicus* (De Geer)[b]	-	**Ali:** *Saglat*; **Asc:** *Ascinc*[d]; **Ast:** *Astpil, Veralt*, *Sympil*[a], *Symcor*, *Symlan*, *Symtur*, *Bidari*[d], *Bidlae*[d], *Bolast*[a], *Cortri*, *Concoe*, *Eupper*, *Eupser*, *Eutgra*[d], *Gnaobt*, *Helaut*[d], *Helann*, *Heldiv*[a], *Helgro*, *Hellae*, *Heltub*, *Helhel*, *Laccan*[a], *Precre*[a], *Rubsub*, *Rubtri*[d], *Solcan*[d], *Solmis*, *Solnem*, *Solrig*[d], *Solspe*[a]; **Lam:** *Lycame*[d], *Menarv*[d]; **Pol:** *Polhyd*, *Polpen*, *Polsca*; **Api:** *Oxyrig*, *Siusua*; **Ver:** *Verhas*[a]
Cantharidae	*Podabrus brunnicollis* F.[b]	-	**Api:** *Crycan*
Cantharidae	*Podabrus rugulosus* LeConte[b]	-	**Api:** *Passat*
Cantharidae	*Podabrus tomentosus* (Say)[b]	-	**Api:** *Perame*, *Passat*; **Cor:** *Corrac*[a]
Cantharidae	*Rhagonycha scitulus* (Say)[b]	*Telephorus scitulus*	**Rha:** *Ceaame*
Cantharidae	*Silis bidentatus* Say[b]	*Ditemnus bidentatus*	**Api:** *Siusua*
Carabidae	*Calleida punctata* LeConte[b]	-	**Ast:** *Solcan*
Carabidae	*Lebia viridis* Say[b]	-	**Ran:** *Ranhis*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Cerambycidae	*Anoplodera pubera* (Say)[e]	*Leptura pubera*	**Ros:** *Arudio*
Cerambycidae	*Batyle suturalis suturalis* (Say)	*Batyle suturalis*	**Ast:** *Rudsub*; **Api:** *Cicmac*
Cerambycidae	*Brachysomida bivittata* (Say)	*Acmaeops nigripennis*	**Api:** *Zizaur*
Cerambycidae	*Callimoxys sanguinicollis* (Olivier)	-	**Cap:** *Vibden*; **Api:** *Passat*
Cerambycidae	*Callimoxys sanguinicollis* subsp. *fuscipennis* (LeConte)	*Callimoxys fuscipennis*	**Api:** *Passat*
Cerambycidae	*Euderces picipes* (F.)	-	**Cap:** *Samnig*, *Vibden*; **Lil:** *Smiher*; **Ros:** *Arudio*[d], *Geucan*; **Sax:** *Hydarb*; **Api:** *Cicmac*, *Crycan*, *Perame*, *Hermax*, *Passat*, *Thatri*
Cerambycidae	*Grammoptera exigua* (Newman)	*Leptura exigua*	**Ros:** *Arudio*
Cerambycidae	*Megacyllene decora* (Olivier)	*Cyllene decorus*	**Ast:** *Eupser*, *Solcan*
Cerambycidae	*Megacyllene robiniae* (Forster)	*Cyllene robiniae*	**Ast:** *Astpil*, *Sympil*, *Symlan*, *Eupser*, *Solcan*[a], *Solnem*, *Solgig*
Cerambycidae	*Metacmaeops vittata* (Swederus)	*Acmaeops directa*	**Api:** *Passat*; **Ros:** *Arudio*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Cerambycidae	*Molorchus bimaculatus* Say	-	**Cap:** *Vibden*[d]; **Cor:** *Corflo*; **Fab:** *Cercan*; **Ros:** *Crachr*[a], *Cracru*, *Cramol*, *Pruame*, *Pruser*; **Sal:** *Salnig*; **Sta:** *Statri*
Cerambycidae	*Strangalepta abbreviata* (Germar)	*Leptura vittata*	**Ros:** *Arudio*
Cerambycidae	*Strangalia famelica famelica* Newman	-	**Cor:** *Corrac*
Cerambycidae	*Tetraopes tetrophthalmus* (Forster)	-	**Asc:** *Ascinc*, *Ascpur*, *Ascsyr*
Cerambycidae	*Typocerus badius* (Newman)	-	**Nym:** *Nellut*; **Ros:** *Arudio*
Cerambycidae	*Typocerus lugubris* (Say)	-	**Api:** *Crycan*; **Ros:** *Arudio*
Cerambycidae	*Typocerus sinuatus* (Newman)	-	**Asc:** *Ascver*; **Ast:** *Echpal*, *Cirpum*, *Corpal*, *Ratpin*, *Liasca*[a], *Rudhir*[a]; **Lam:** *Pycfle*[a]; **Fab:** *Meloff*, *Dalpur*; **Rha:** *Ceaame*; **Api:** *Passat*
Cerambycidae	*Typocerus velutinus velutinus* (Olivier)	*Typocerus velutinus*	**Sax:** *Hydarb*; **Api:** *Passat*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Chrysomelidae[f]	*Acalymma vittatum* F.	*Diabrotica vittata*	**Cap:** *Vibden*; **Ast:** *Sympil*, *Symcor*, *Helann*, *Solcan*; **Ran:** *Enebit*, *Ranhis*; **Ros:** *Crachr*, *Cramol*; **Sal:** *Salexi*[a], *Comumb*; **Api:** *Chapro*, *Eribul*, *Hermax*, *Passat*, *Siusua*, *Zizaur*
Chrysomelidae	*Acanthoscelides obsoletus* (Say)	*Bruchus obsoletus*	**Ast:** *Solcan*; **Api:** *Siusua*
Chrysomelidae	*Acanthoscelides submuticus*(Sharp)	*Bruchus eixguus*	**Api:** *Crycan*
Chrysomelidae	*Althaeus hibisci* (Olivier)	*Bruchus hibisci*	**Cap:** *Vibden*; **Ros:** *Arudio*; **Api:** *Siusua*, *Taeint*
Chrysomelidae	*Altica carinata* Germar	*Haltica carinata*	**Api:** *Perame*
Chrysomelidae	*Anomoea laticlavia* (Forster)	-	**Api:** *Passat*
Chrysomelidae	*Babia quadriguttata* (Olivier)	*Babia 4-guttata*	**Api:** *Taeint*
Chrysomelidae	*Bruchus bivulneratus* Horn	-	**Api:** *Cicmac*, *Crycan*, *Taeint*
Chrysomelidae	*Gibbobruchus mimus* (Say)	*Bruchus mimus*	**Lil:** *Mairac*; **Api:** *Crycan*[a], *Osmlon*
Chrysomelidae	*Calligrapha bidenticola* Brown	*Chrysomela similis*	**Ast:** *Bidari*
Chrysomelidae	*Cerotoma trifurcata* (Forster)	*Cerotoma caminea*	**Ast:** *Eupper*[a], *Zizaur*
Chrysomelidae	*Chrysomela lapponica* L.	*Lina lapponica*	**Sal:** *Salcor*[d]

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Chrysomelidae	*Cryptocephalus insertus* Haldeman	-	**Api:** *Eryyuc*
Chrysomelidae	*Diabrotica cristata* (Harris)	*Diabrotica atripennis*	**Ast:** *Liasca*; **Fab:** *Amocan*; **Lil:** *Camsci*; **Rha:** *Ceaame*; **Api:** *Cicmac*, *Oxyrig*
Chrysomelidae	*Diabrotica undecimpunctata* Mannerheim	*Diabrotica 12-punctata*	**Ali:** *Saglat*; **Bal:** *Impcap*; **Ast:** *Astpil, Sympil*, *Symeri*, *Symcor*, *Symtur*, *Bidari*, *Bidlae*[a], *Bolast*, *Eriphi*, *Eupser*, *Helann*, *Helgro*, *Kriamp*[a], *Liasca*, *Rudhir*, *Solcan*[d], *Solmis*, *Solrig*; **Fab:** *Amocan*, *Dalpur*; **Nym:** *Nellut*[d]; **Ona:** *Oenfru*; **Rha:** *Ceaame*; **Ros:** *Roshum*; **Sol:** *Datstr*; **Api:** *Cicmac*, *Crycan*, *Hermax*, *Oxyrig*, *Siusua*, *Zizaur*
Chrysomelidae	*Diabrotica longicornis* (Say)	-	**Ast:** *Astpil, Sympil*, *Symcor*, *Bolast*, *Cirdis*, *Helann*, *Helgro*, *Heltub*, *Precre*[a], *Solcan*[a], *Solnem*, *Solrig*[d]; **Api:** *Siusua*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Chrysomelidae	*Diabrotica vittata* F.	*Acalymma vittata*	**Api:** *Chapro, Eribul, Hermax, Passat, Siusua, Zizaur* **Ast:** *Astcor, Astpil, Helann, Solcan*; **Cap:** *Vibpru* **Ran:** *Enebit, Ranhis*; **Ros:** *Crachr, Cramol*; **Sal:** *Salexi*; **San:** *Comumb*
Chrysomelidae	*Disonycha limbicollis* LeConte	-	**Cap:** *Vibden*; **Pol:** *Polhyds*; **Ros:** *Arudio*, *Cramol*
Chrysomelidae	*Glyptina spuria* LeConte	-	**Api:** *Chapro*
Chrysomelidae	*Luperaltica nigripalpis* LeConte	*Luperaltica fuscula*	**Api:** *Oxyrig*
Chrysomelidae	*Mantura chrysanthemi* (Koch)	*Mantura floridana*	**Api:** *Chapro*
Chrysomelidae	*Megacerus discoidus* (Say)	*Bruchus discoideus*	**Api:** *Siusua*
Chrysomelidae	*Meibomeus musculus* (Say)	*Bruchus musculus*	**Api:** *Crycan*
Chrysomelidae	*Orsodacne atra* (Ahrens)	-	**Ros:** *Pruame*; **Sal:** *Salamy*, *Salcor*[d], *Salhum*[d]
Chrysomelidae	*Pachybrachis atomarius* (Melsheimer)	-	**Rha:** *Ceaame*; **Api:** *Passat*
Chrysomelidae	*Pyrrhalta tuberculata* Say	*Galeruca tuberculata*	**Sal:** *Salcor*[a]
Chrysomelidae	*Rhabdopterus picipes* (Olivier)	-	**Cel:** *Euoatr*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Chrysomelidae	*Sennius cruentatus* (Horn)	*Bruchus cruentatus*	**Api:** *Thatri*, *Passat*
Chrysomelidae	*Trirhabda tomentosa* (L.)	-	**Api:** *Passat*
Cleridae	*Pelonides quadripunctatus* (Say)[b]	*Enoplium 4-punctatum*	**Ros:** *Cracru*, *Cramol*
Coccinellidae	*Coccinella novemnotata* Herbst[b]	*Coccinella 9-notata*	**Ast:** *Solcan*, *Solnem*; **Fab:** *Senmar*, *Strhel*; **Pol:** *Polhyd*; **Ran:** *Ranabo*; **Api:** *Cicmac*, *Passat*
Coccinellidae	*Coleomegilla maculata* (DeGeer)[b]	*Megilla fuscilabris*	**Ali:** *Saglat*; **Ast:** *Kriamp*, *Solcan*; **Lau:** *Sasalb*; **Nym:** *Nymodo*; **Pol:** *Polrep*; **Por:** *Clavir*; **Ran:** *Enebit*, *Ranabo*, *Ranhis*; **Sal:** *Salexi*[a], *Salnig*; **Api:** *Passat*, *Siusua*, *Zizaur*
Coccinellidae	*Cycloneda sanguinea* (L.)[b]	*Coccinella sanguinea*	**Ros:** *Crachr*; **Api:** *Oxyrig*, *Passat*, *Siusua*, *Zizaur*
Coccinellidae	*Diomus terminatus* (Say)[b]	*Scymnus terminatus*	**Api:** *Crycan*
Coccinellidae	*Hippodamia convergens* Guérin-Méneville[b]	-	**Api:** *Oxyrig*, *Passat*
Coccinellidae	*Hippodamia glacialis* (F.)[b]	-	**Ast:** *Solcan*[a]
Coccinellidae	*Hippodamia parenthesis* (Say)[b]	-	**Ast:** *Bolast*; **Sal:** *Salhum*; **Api:** *Passat*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Coccinellidae	*Hippodamia quindecimmaculata* Mulsant[b]	*Hippodamea 15-maculata*	**Lil:** *Melvir*; **Ros:** *Crachr*; **Rub:** *Cepocc*
Coccinellidae	*Hippodamia tredecimpunctata* (L.)[b]	*Hippodamea 13-punctata*	**Nym:** *Nellut*
Coccinellidae	*Scymnus consobrinus* LeConte[b]	-	**Api:** *Cicmac*
Curculionidae	*Centrinites strigicollis* Casey	-	**Com:** *Travir*; **Lil:** *Melvir*[a], *Steang*; **Rha:** *Ceaame*; **Rub:** G*altri*; **Api:** *Perame*, *Hermax*, *Polnut*, *Taeint*, *Zizaur*
Curculionidae	*Centrinus perscillus* Gyllenhal	-	**Ran:** *Ranhis*, **Fab:** C*eaame*; **Ros:** A*rudio*[d]; **Api:** C*icmac*, *Crycan*, *Oxyrig*, *Siusua*, *Zizaur*
Curculionidae	*Centrinus scutellum-album* Say, T. ed. Leconte	-	**Asc:** *Ascsul*[a]; **Ast:** *Eupper*, *Rudhir*, *Rudsub*; **Cor:** *Coramo*; **Lam:** *Pycfle*[a]; **Fab:** *Meloff*[a]; **Ona:** *Oenfru*[d]; **Rha:** *Ceaame*; **Rub:** *Galtri*; **Api:** *Cicmac*, *Eryyuc*
Curculionidae	*Idiostethus subcalvus* Casey	-	**Ber:** *Cautha*; **Ran:** *Ranhis*
Curculionidae	*Idiostethus tubulatus* Say	-	**Api:** *Osmlon*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Curculionidae	*Limnobaris prolixus* Casey	*Limnobaris prolixa*	**Api:** *Taeint*
Curculionidae	*Listronotus caudatus* Say	-	**Pol:** *Polhyd*
Curculionidae	*Rhodobaenus tredecimpunctatus* Blatchley and Leng	*Rhodobaenus 13-punctatus*	**Ast:** *Bidari*
Dermestidae	*Anthrenus castaneae* Melsheimer	*Anthrenus musaeorum*	**Api:** *Hermax, Passat;* **Cap:** *Vibden*[a]*;* **Ros:** *Arudio*[d]
Dermestidae	*Anthrenus scrophulariae* (L.)	-	**Ast:** *Antpla*
Dermestidae	*Attagenus piceus* Olivier	-	**Cap:** *Samnig*[a]; **Api:** *Passat*[a], *Siusua*
Dermestidae	*Cryptorhopalum haemorrhoidalis* LeConte	*Cryptorhopalum haemorrhoidale*	**Rha:** *Ceaame*; **Ros:** *Arudio*[a]; **Api:** *Hermax*, *Passat*
Dermestidae	*Cryptorhopalum triste* (LeConte)	-	**Cap:** *Vibden*; **Ros:** *Arudio*[d]; **Api:** *Crycan*
Dermestidae	*Orphilus glabratus* F.	-	**Cap:** *Vibden*[d]; **Ros:** *Arudio*[d]; **Api:** *Hermax*
Elateridae	*Agriotes insanus* Candeze	-	**Api:** *Passat*
Elateridae	*Limonius griseus* (Beauvois)	-	**Rha:** *Ceaame*
Elateridae	*Melanotus communis* (Gyllenhal)	-	**Asc:** *Ascsyr*
Elateridae	*Sericus silaceus* (Say)	*Seracosomus silaceus*	**Ros:** *Arudio*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Histeridae	*Atholus americanus* (Paykull)[b]	*Hister americanus*	**Api:** *Zizaur*
Histeridae	*Phelister subrotundatus* (Say)[b]	*Hister subrotundus*	**Api:** *Perame*, *Taeint*
Lampyridae	*Ellychnia corrusca* (L.)[b]	-	**Sal:** *Salhum*; **San:** *Salnig*
Lampyridae	*Photinus pyralis* (L.)[b]	-	**Asc:** *Ascsyr*; **Lil:** *Melvir*; **Api:** *Passat*, *Siusua*
Lampyridae	*Pyractomena angulata* (Say)[b]	-	**Api:** *Passat*
Languriidae	*Languria mozardi* Latreille	-	**Ast:** *Kriamp*[a]; **Api:** *Zizaur*
Latridiidae	*Melanopthalma americana* Mannerheim	*Corticaria distinguenda*	**Api:** *Oxyrig*
Lycidae	*Calopteron reticulatum* (F.)	-	**Api:** *Passat*
Melandryidae	*Osphya varians* (LeConte)	*Nothus varians*	**Api:** *Passat*
Meloidae	*Epicauta atrata* (F.)[b]	*Epicauta trichrus*	**Fab:** *Dalpur*; **Api:** *Cicmac*
Meloidae	*Epicauta cinereus* (Förster)[b]	*Epicauta cinerea*	**Ast:** *Bidari*, *Corpal*; **Api:** *Oxyrig*, *Passat*
Meloidae	*Epicauta maculata* (Say)[b]	*Macrobasis unicolor*	**Ast:** *Rudhir*; **Fab:** *Amocan*; **Api:** *Hermax*, *Passat*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Meloidae	*Epicauta pennsylvanica* (DeGeer)[b]	-	**Ast:** *Astpil, Symano*, *Sympil*, *Symcor*, *Bidari*, *Eutgra*[d], *Eupper*, *Helaut*, *Heltub*, *Rudtri*, *Solcan*[d], *Solmis*[d], *Solnem*[d], *Solrig*[d]; **Gen:** *Genand*; **Fab:** *Dalpu*; **Api:** *Oxyrig*, *Siusua*
Meloidae	*Epicauta vittata* (F.)[b]	-	**Asc:** *Ascinc*[d]
Meloidae	*Pyrota germari* Haldeman[b]	-	**Api:** *Oxyrig*
Meloidae	*Pyrota mylabrina* (Chevrolat)[b]	-	**Scr:** *Agaten*
Meloidae	*Pyrota terminalis* LeConte[b]	*Pyrota terminata*	**Api:** *Eryyuc*
Meloidae	*Zonitis vittigera* (LeConte)[b]	*Nemognatha vittigera*	**Api:** *Eryyuc*
Melyridae	*Anthocomus erichsoni* LeConte[b]	-	**Cap:** *Samnig*; **Ros:** *Arudio*; **Til**: *Tilame*; **Api:** *Crycan*, *Hermax*, *Passat*, *Taeint*
Melyridae	*Attalus scincetus* (Say)[b]	-	**Rha:** *Ceaame*; **Ros:** *Arudio*[a]; **Api:** *Passat*
Melyridae	*Collops quadrimaculatus* (F.)[b]	*Collops 4-maculatus*	**Mol:** *Molver*; **Ast:** *Eristr*, *Solcan*; **Mal:** *Malrot*; **Por:** *Porole*; **Api:** *Siusua*
Melyridae	*Melyrodes cribratus* (LeConte)[b]	*Melyris cribrata*	**Ros:** *Arudio*[a]

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Mordellidae	*Hoshihananomia octopunctata* F.	*Mordella 8-punctata*	**Lam:** *Pycfle*; **Api:** *Passat*, *Siusua*
Mordellidae	*Mordella atrata atrata* Melsheimer	*Mordella scutellaris*	**Ast:** *Corpal*, *Heltub*, *Rudhir*; **Api:** *Cicmac*
Mordellidae	*Mordella capillosa* Liljeblad	*Mordella pubescens*	**Api:** *Crycan*
Mordellidae	*Mordella marginata* Melsheimer	-	**Cap:** *Symorb*; **Ast:** *Corpal*, *Rudtri*; **Cor:** *Coramo*, *Corrac*[a]; **Lam:** *Pycfle*; **Fab:** *Meloff*; **Lil:** *Melvir*; **Rha:** *Ceaame*; **Ros:** *Arudio*[d], *Geucan*; **Sax:** *Hydarb*[d]; **Api:** *Cicmac*, *Crycan*, *Perame*[a], *Hermax*, *Passat*, *Siusua*, *Taeint*
Mordellidae	*Mordella melaena* Germar	-	**Ana:** *Rhugla*; **Ast:** *Achmil*; **Lil:** *Melvir*[a]; **Api:** *Cicmac*, *Oxyrig*, *Passat*, *Siusua*
Mordellidae	*Mordellistena andreae* LeConte	*Mordellistena grammica*	**Cap:** *Vibden*[a]
Mordellidae	*Mordellistena aspersa* (Melsheimer)	-	**Cap:** *Cibpru*, **Ros:** *Arudio*[a]; **Api:** *Taeint*
Mordellidae	*Mordellistena comata* (LeConte)	-	**Ast:** *Eristr*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Mordellidae	*Mordellistena limbalis*(Melsheimer)	-	**Api:** *Crycan*, *Perame*, *Oxyrig*
Mordellidae	*Mordellistena lutea* (Melsheimer)	-	**Ros:** *Arudio*
Mordellidae	*Mordellistena ornata* (Melsheimer)	-	**Cel:** *Euoatr*; **Ros:** *Arudio*; **Sax:** *Hydarb*; **Api:** *Passat*
Mordellidae	*Mordellistena pubescens* (F.)	-	**Cap:** *Symorb*; **Ros:** *Arudio*; **Sax:** *Hydarb*[d]
Mordellidae	*Mordellistena scapularis* (Say)	*Mordellistena biplagiata*	**Ber:** *Cautha*; **Cap:** *Vibden*[a]; **Lil:** *Mairac*; **Ros:** *Arudio*[a]; **Api:** *Hermax*[a], *Osmlon*
Mordellidae	*Mordellistena tosta* LeConte	-	**Ros:** *Arudio*
Mordellidae	*Paramordellaria triloba* (Say)	*Mordella triloba*	**Api:** *Crycan*
Nitidulidae	*Carpophilus brachypterus* Say	-	**Api:** *Passat*
Nitidulidae	*Epuraea labilis* Erichson	*Epurea labilis*	**Ros:** *Arudio*
Nitidulidae	*Epuraea truncatella* Mannerheim	*Epurea truncatella*	**Ros:** *Arudio*
Oedemeridae	*Asclera puncticollis* (Say)	-	**Lau:** *Sasalb*; **Ros:** *Arudio*, *Crachr*, *Cramol*; **Rut:** *Zaname*; **Sal:** *Salcor*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Oedemeridae	*Asclera ruficollis* (Say)	-	**Cap:** *Vibden*; **Ast:** *Antpla*; **Pap:** *Sancan*[a]; **Ran:** *Enebit*, *Ranfas*, *Ranhis*; **Api:** *Eribul*
Oedemeridae	*Oxycopis thoracica* F.	*Oxacis thoracica*	**Rha:** *Ceaame*
Pyrochroidae	*Pedilus labiatus* (Say)	*Corphyra labiata*	**Api:** *Hermax*
Pyrochroidae	*Pedilus terminalis* (Say)	*Corphyra terminalis*	**Ber:** *Cautha*; **Lil:** *Mairac*; **Pol:** *Polrep*; **Ran:** *Enebit*, *Ranhis*; **Api:** *Chapro*, *Osmlon*
Rhipiphoridae	*Macrosiagon flavipennis* (LeConte)	*Rhipiphorus flavipennis*	**Lam:** *Pycfle*
Rhipiphoridae	*Rhipiphorus dimidiatus* F.[bg]	-	**Lam:** *Pycfle*, *Pycver*
Rhipiphoridae	*Rhipiphorus fasciata* Say[bg]	*Myodites fasciatus*	**Ast:** *Solmis*; **Api:** *Cicmac*, *Eryyuc*
Rhipiphoridae	*Rhipiphorus limbatus* F.[bg]	-	**Asc:** *Ascver*; **Ast:** *Eupper*, *Eupser*, *Liasca*; **Lam:** *Pycfle*[d], *Pycver*[d], *Pycvir*; **Nym:** *Nellut*; **Api:** *Eryyuc*, *Oxyrig*
Rhynchitidae	*Eugnamptus angustatus* Schoenerr	-	**Api:** *Crycan*
Scarabaeidae	*Euphoria fulgida* (F.)	-	**Cap:** *Samnig*, *Vibden*; **Cor:** *Corrac*; **Lil:** *Smiher*; **Ros:** *Crachr*, *Cracru*, *Cramol*, *Rubfla*; **Api:** *Passat*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Scarabaeidae	*Euphoria sepulcralis* F.	-	**Asc:** *Ascinc*[d]; **Ast:** *Symlan*, *Eupalt*, *Eupper*, *Eupser*, *Solcan*; **Mal:** *Abuthe*; **Ros:** *Rubfla*; **Sta:** *Statri*; **Api:** *Eryyuc*, *Hermax*, *Oxyrig*, *Passat*, *Siusua*
Scarabaeidae	*Hoplia trifasciata* Say	-	**Cap:** *Vibden*[a]
Scarabaeidae	*Macrodactylus angustatus* (Beauvois)	-	**Asc:** *Ascsyr*
Scarabaeidae	*Onthophagus pennsylvanicus* Harold	-	**Api:** *Zizaur*
Scarabaeidae	*Trichiotinus piger* (F.)[h]	*Trichius piger*	**Apo:** *Apocan*; **Asc:** *Asclon*, *Ascinc*, *Ascsul*, *Ascsyr*, *Ascver*; **Ast:** *Leuvul*, *Cirpum*[d], *Eriphi*[d], *Liasca*[a]; **Con**: *Calsep*; **Cor:** *Corrac*[a]; **Iri**: *Irihex*; **Lam:** *Blecil*[a], *Pycfle*; **Fab:** *Meloff*; **Lil:** *Melvir*; **Rha:** *Ceaame*; **Ros:** *Arudio*, *Roshum*[d], *Rosset*, *Rubfla*; **Rub:** *Cepocc*, *Galtri*[d]; **Scro:** *Penlae*; **Api:** *Eryyuc*, *Hermax*, *Passat*

Table 2.2 (cont.)

Coleopteran family	Current species name	Species name cited (if different from current)	**Plant family:** species code
Scarabaeidae	*Valgus canaliculatus* (Olivier)	-	**Cap:** *Vibden*; **Lil:** *Mairac*; **Ros:** *Arudio*, *Pruame*
Scraptiidae	*Canifa pallipes* (Melsheimer)	-	**Ari**: *Aritom*
Scraptiidae	*Pentaria trifasciata* (Melsheimer)	-	**Cap:** *Samnig*; **Ast:** *Liasca*; **Cor:** *Corrac*; **Ros:** *Arudio*[a]; **Api:** *Crycan*, *Passat*

[a] beetle species listed as "frequent" on this host (Robertson 1929)
[b] beetle species has a predaceous life stage
[c] species name confirmed with Kazantsev (2005)
[d] beetle species listed as "abundant" on this host (Robertson 1929)
[e] species name confirmed with Lingafelter (2007)
[f] species names for this family confirmed with Riley (2003)
[g] species name could not be confirmed in current literature
[h] species name confirmed with Smith (2009)

Table2.3 The eleven plant species that were most preferred (i.e., visited by ≥ 13 beetle species; from Table 2) and the percentage of beetle species of the dominant beetle families that visited them. Plant species are ordered by the total number of beetle species that visited them.

Plant species	Family	No. of beetle species	Percentage of beetle species within family (rank within family) Chrysomelidae	Cerambycidae	Mordellidae	Cantharidae	Coccinellidae	(mean rank)
Pastinaca sativa	Apiaceae	42	10.8 (3)	23.1 (2)	13.8 (2)	28.6 (1)	29.4 (1)	(1.8)
Aruncus dioicus	Rosaceae	32	5.4 (5)	30.7 (1)	24.1 (1)	0 (4)	0 (5)	(3.2)
Cryptotaenia canadensis	Apiaceae	19	13.5 (2)	7.6 (4)	13.8 (2)	7.1 (3)	5.9 (4)	(3)
Sium suave	Apiaceae	18	16.2 (1)	0 (6)	10.3 (3)	14.3 (2)	11.8 (3)	(3)
Viburnum dentatum	Caprifoliaceae	17	5.4 (5)	11.5 (3)	10.3 (3)	7.1 (3)	0 (5)	(3.8)
Oxypolis rigidior	Apiaceae	16	10.8 (3)	3.8 (6)	6.9 (4)	7.1 (3)	11.8 (3)	(3.8)
Heracleum maximum	Apiaceae	16	5.4 (5)	3.8 (5)	6.9 (4)	7.1 (3)	0 (5)	(4.4)
Ceanothus americanus	Rhamnaceae	14	8.1 (4)	7.6 (5)	3.4 (5)	7.1 (3)	0 (5)	(4.4)
Cicuta maculata	Apiaceae	14	8.1 (4)	7.6 (4)	10.3 (3)	0 (4)	11.8 (3)	(3.6)
Solidago canadensis	Asteraceae	14	8.1 (4)	7.6 (4)	0 (6)	7.1 (3)	17.6 (2)	(3.8)
Zizia aurea	Apiaceae	13	8.1 (4)	3.8 (5)	0 (6)	14.3 (2)	11.8 (3)	(4)

Table 2.4 Familes of beetles, ranked in descending order by the number of their species in the Robertson (1929) dataset, and taxonomic diversity of their floral host plants.

Family	No. of beetle species	No. of beetle genera	No. of plant species visited	No. of plant genera	No. of plant families	Avg. no. of plant species visited per beetle species
Chrysomelidae	28	16	61	47	16	2.18
Cerambycidae	18	13	47	35	14	2.61
Mordellidae	16	3	31	26	13	1.94
Cantharidae	10	6	49	34	12	4.90
Coccinellidae	10	5	28	24	15	2.80
Meloidae	9	3	26	19	6	2.89
Curculionidae	8	5	29	27	15	3.63
Scarabaeidae	8	6	45	37	17	5.63
Dermestidae	7	4	9	9	4	1.29
Buprestidae	4	2	8	7	6	2.00
Elateridae	4	4	4	4	4	1.00
Melyridae	4	4	14	14	9	3.50
Rhipiphoridae	4	1	15	9	5	3.75

Table 2.4 (cont.)

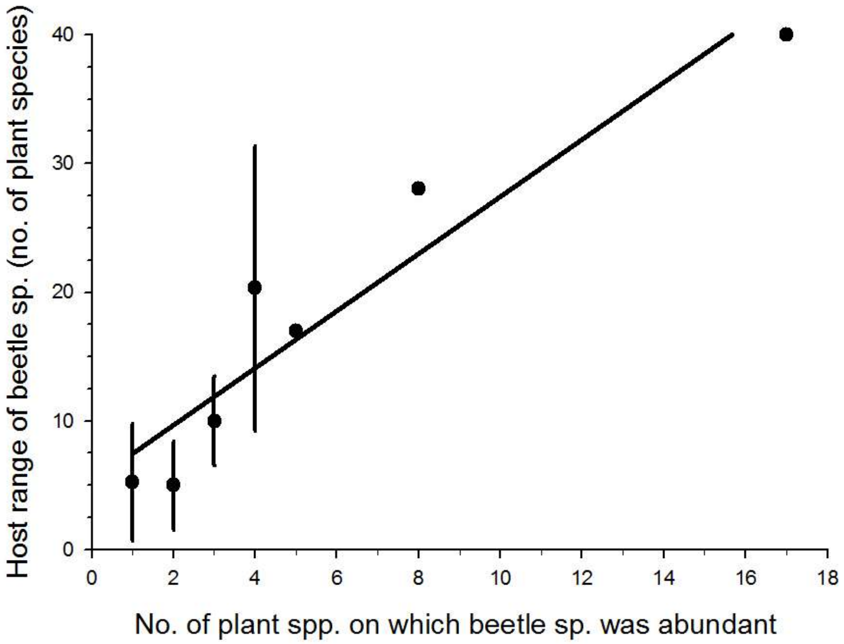
Family	No. of beetle species	No. of beetle genera	No. of plant species visited	No. of plant genera	No. of plant families	Avg. no. of plant species visited per beetle species
Lampyridae	3	3	6	6	4	2.00
Nitidulidae	3	2	2	2	2	0.67
Oedemeridae	3	2	14	12	9	4.67
Carabidae	2	2	2	2	2	1.00
Histeridae	2	2	3	3	1	1.50
Pyrochroidae	2	1	8	8	5	4.00
Scraptiidae	2	1	7	7	6	3.50
Apionidae	1	1	1	1	1	1.00
Attelabidae	1	1	1	1	1	1.00
Brachypteridae	1	1	2	2	2	2.00
Calandryidae	1	1	1	1	1	1.00
Cleridae	1	1	2	1	1	2.00
Languriidae	1	1	2	2	2	2.00

Table 2.4 (cont.)

Family	No. of beetle species	No. of beetle genera	No. of plant species visited	No. of plant genera	No. of plant families	Avg. no. of plant species visited per beetle species
Latridiidae	1	1	1	1	1	1.00
Lycidae	1	1	1	1	1	1.00
Melandryidae	1	1	1	1	1	1.00
Mean:	5.4	3.3	14.4	11.7	6.0	2.3
Standard deviation:	7.0	4.8	12.7	8.9	3.4	1.3

Figures

Figure 2.1 Relationship between number of plant species on which a beetle species was common (i.e., listed as abundant or frequent; Table 2) and the mean (± SE) number of host range of that beetle species (i.e., the number plant species listed; N = 28, 8, 3, 3, 1, 1, and 1, left to right). Best fit regression equation: $Y = 2.2X + 5.3$, $r^2 = 0.90$; $P < 0.001$.



Chapter 3: Environmental stress and resistance of black locust trees to attack by the locust borer, *Megacyllene robiniae* Förster (Coleoptera: Cerambycidae)

Abstract

Trees are subject to many abiotic and biotic stressors that may reduce growth rate. In this chapter, I tested the hypothesis that environmental stress renders trees susceptible to attack by longhorned borers. I used the width of xylem growth rings to characterize the history of environmental stress that trees experience. I also measured leaf asymmetry of study trees to evaluate that method as an indicator of environmental stress. The study species was the locust borer, *Megacyllene robiniae* Förster (Coleoptera: Cerambycidae), the larvae of which feed exclusively in black locust trees, *Robinia pseudoacacia* L. The adult beetles emerge by chewing through the bark, leaving scars that provide a record of their year of emergence. Average width of growth rings was not significantly correlated with the number of beetle that emerged during the 2007 project. Leaf asymmetry was not correlated with average width of growth rings nor the number of beetles that emerged, and thus was not a good predictor of either variable. However, the number of beetles emerging per year was positively associated with the width of the growth rings in the 2008 study. This positive relationship was the opposite trend that was predicted by our hypothesis, suggesting that the adult females preferred to oviposit on relatively vigorous trees, and/or the larvae performed better in those trees.

Key Words- *Megacyllene robiniae*, dendrochronology, leaf asymmetry

Introduction

Trees are subject to many abiotic and biotic stressors, such as drought, flooding, extreme temperatures, and insect attack (Kozlowski and Pallardy 1997). Environmental stress has been correlated with slow growth of trees and leaf asymmetry (Fritts and Swetnam 1989, Handy et al. 2004). Earlier reviews of the literature have suggested that wood–boring insects in general preferentially attack hosts that are under environmental stress (Haack and Slansky 1987, Larsson 1989, Waring and Cobb 1992, Koricheva et al. 1998). However, most of this literature concerns bark beetles (Curculionidae: Scolytinae), which have a unique system for overwhelming the defenses of host trees with concerted attack mediated by pheromones (Wood 1982). There have been few studies of the influence of environmental stress on resistance of trees to other types of wood-boring insects that have very different strategies for host location and colonization.

In this study, I tested hypothesis that environmental stress renders trees susceptible to attack by cerambycid beetles. Many species of cerambycid beetles develop in trees that are stressed or dying, so the adult beetles must quickly find and colonize these ephemeral hosts (Hanks 1999). Volatile chemicals released by damaged or dying host plants may provide signals that beetles use to locate larval hosts (Ginzel and Hanks 2005). Nevertheless, males of several species of the subfamily Cerambycinae produce volatile aggregation pheromones that also play an important role in mate location and colonization of larval hosts (e.g., Lacey et al. 2004, 2007, 2008, 2009).

Our study species was the locust borer, *Megacyllene robiniae* Förster (Coleoptera: Cerambycidae), the larvae of which feed exclusively in black locust trees, *Robinia pseudoacacia* L. (Galford, 1984; Solomon 1995; Yanega 1996). *M. robiniae* is univoltine, and diurnal adults emerge in late summer through early fall and are common on inflorescences of goldenrod

(*Solidago* spp.) where they feed on pollen (Garman 1916). The females oviposit in bark fissures of locust trees and around wounds in the bark. This species is usually associated with trees that are stressed, such as by poor soil quality, drought, and competition (Wollerman 1970, Galford 1984, Harmon et al. 1985). Nevertheless, the larvae are one of the few species of Clytini which require hosts that are alive, and sometime infest trees that appear to be healthy (Galford 1984). The larvae feed throughout the heartwood of the tree, leaving behind a gallery filled with frass (Sanborn and Painter 1917, Harman and Dixon 1984).

The relationship between plant stress and resistance to wood-boring insects can be difficult to study because it is difficult to assess the level of tree resistance prior to attack. The width of xylem growth rings in the woody tissues of trees provides a simple and efficient way to characterize their history of environmental stress (Weber 1997). For example, radial growth is reduced (and growth rings are thinner) after trees have been defoliated by caterpillars (Weber 1997, Muzika and Liebhold 1999), attacked by bark beetles (Ehle and Baker 2003, Rolland and Lemperiere 2004), or stressed by water deficit (reviewed by Fritts and Swetnam 1989). *M. robiniae* is a suitable species for our study because it is the only species of wood borer known to infest black locust (Huntley 1990). The adult beetles emerge from trees by chewing through the bark, and the resulting scar in the cambium will eventually heal over a period of several years (Harmon and Dixon 1984). Emergence holes of adults therefore provide a record of emergence year, determined simply by counting the number of growth rings that have developed to distal to the emergence scar (see Fig. 3.1).

I also assessed the stress level of our study trees by measuring leaf asymmetry (Palmer and Strobeck 1986, Freeman et al. 1993). Environmental stress may result in development instability in trees, with the result that physiological processes that normally govern symmetry in leaf production are compromised: the greater the degrees of stress, the more asymmetrical are the leaves (Leary and Allendorf 1989). Variation in leaf asymmetry has been correlated with many of the same environmental stressors that reduce xylem ring growth in trees, including soil contamination with heavy metals, serpentine soils, moisture deficit, and climatic extremes (Kozlov et al. 1996, Fair and Breshears 2005). To our knowledge, there has been no attempt to correlate xylem ring growth increment with leaf asymmetry, despite the fact that both methods are commonly used to assess environmental stress. Leaf asymmetry may provide a convenient method for assessing tree stress by arborists and forest managers because it requires no special equipment, is easily estimated, and does not harm the tree.

Materials and Methods

I conducted our research at Mazonia State Fish and Wildlife area (Grundy Co., IL), a 412-ha park that was heavily surface mined to create a cooling lake for the nearby Commonwealth Edison power plant and to create additional smaller lakes for fisheries (IDNR 2010). Between 1975 – 1980, the site was planted with black locust trees to stabilize the soil (M. Smith, pers. comm.). Goldenrod is now also abundant at the site and locust borer adults are common on the inflorescences during summer (pers. obs.). Trees for the study were selected to represent a range in level of attack by *M. robiniae* based on the density of the tree canopy (trees with heavy infestations of beetles tend to have thin canopies; from Schomaker 2003).

I conducted a preliminary study in 2007 to determine the best methodology for associating tree growth ring increment with attack density of the beetle. I felled six black locust trees (mean ± SD DBH = 14.8 ± 2. 82 cm; 18 ± 0.5 years old). Trunks were cut into ~30 cm-long bolts (4 to 8 per tree) on 27 September 2007 at the end of the growing season and after adult

M. robiniae were no longer active. Each bolt then was sectioned into disks (~2-3 cm) with a band saw (total N = 127 disks), the top surface of each disk was smoothed with a belt sander and treated with glycerol to make the rings easier to discern (R. Muzika, pers. comm.). Disks were digitally photographed and the images on a computer screen were used to measure the width of growth rings to the nearest mm with computer graphics software (Greer 2000). I measured the width of each growth ring per disk at each of three points that were approximately equally spaced (to account for uneven radial growth), and averaged the three values for each growth year. Beetle emergence scars were examined to determine the year of emergence.

The number of adult *M. robiniae* that emerged from a tree could be influenced by environmental stress of the host during the year that females oviposit (e.g., if females seek hosts that are stressed, and/or larvae are better able to colonize stressed hosts), but also by stress during the following year (during which time the larvae are developing). Thus, our measure of ring growth increment was an average of ring width for the year a beetle emerged and the previous year. I included in the analysis only data for the years that had the greatest number of beetles emerging (2004, 2005, and 2007; see Results).

The 2007 study revealed that growth ring increment per tree could be estimated with much fewer sections of the trunk, that emergence scars of beetles could only be discerned for tree rings of the previous ten years (because scars eventually were obscured by callous tissue during the healing process and could not be distinguished from branch scars) and that our study trees did have high enough densities of beetle larvae to test our hypothesis (see Results). I therefore repeated the experiment with a greater number of trees that showed a wider range in beetle densities (again, as estimated by canopy condition), and by sectioning trunks into wider disks. I felled eleven black locust trees on 10 October 2008 (14.1 ± 4.4 cm DBH, 18.6 ± 4.9

years old). Trunks were cut into ~30 cm-long bolts (2 to 5 per tree) that then were sectioned into disks (~3-5 cm) with a chainsaw (total N = 41 disks). I sanded disks and treated them with glycerol, and measured growth rings and estimated years of emergence for beetles, as described above. Only data for the last five years of growth rings (with the greatest number of emergence scars; see Results) were used in testing the relationship between ring width and beetle emergence.

I estimated leaf asymmetry for the 2008 study trees by collecting five mature leaves (selected arbitrarily from around the lower canopy) from each tree on 11 August 2008, and digitally imaging them using a flatbed scanner with a computer (Hewlett-Packard 2002). Printed images of leaves then were measured with a ruler to calculate the degree of asymmetry = (length of longest leaflet – length of shortest leaflet)/summed lengths of both leaflets (Cowart and Graham 1999, Hodar 2002, Samuelsson and Andersson 2003). A leaf with perfect symmetry therefore would have a value of zero, while asymmetrical leaves would have increasingly greater values.

Linear relationships between variables were tested either by regression analysis (PROC REG, SAS Institute 2001), or by analysis of covariance when categorical terms were included in statistical models (PROC GLM, SAS Insitute 2001). The relationship between growth ring width and number of beetles emerging per year included a “year” term (to account for differences between years in conditions that influenced development of beetles that were independent of their effect on tree growth rate) and a tree “term" (to account for differences between trees as hosts for larvae, independent of growth rate).

Results and Discussion

The 2007 study revealed that growth ring width, averaged per tree and then across trees, declined significantly over time (Fig. 3.2A; overall anova $F_{6,113} = 12.9$, $P < 0.0001$; year covariate $F_{1,113} = 24.2$, $P < 0.0001$; tree term $F_{5,113} = 13.2$, $P < 0.0001$). This finding is consistent with other studies that have shown a decline in width of growth rings with increasing tree age (Fritts 1969).

A total of 40 adult beetles had emerged from trunks of the 2007 study trees, as evidenced by the emergence scars. The sudden increase in numbers of emerging beetles, beginning in 1997 (Fig. 3.3), probably was due to the fact that the stand of black locust trees at the study site was established *de novo*, and *M. robiniae* must have colonized the area sometime after goldenrod had established. Moreover, this species prefers to attack trees that are older than 10 years (Galford 1984).

The hypothesis was not supported by the 2007 study: Average width of growth rings was not significantly correlated with the number of beetle that emerged (Fig. 3.4A: overall anova $F_{6,11} = 2.61$, $P = 0.08$; growth ring covariate $F_{6,11} = 0.12$, $P = 0.73$).

As in the previous study, the average width of xylem growth rings of trees in the 2008 study declined over years (Figure 2B: overall anova $F_{11,180} = 19.6$, $P < 0.0001$). Leaf asymmetry was moderately variable across trees, ranging from 0.16 to 0.67 and averaging 0.36 ± 0.17 (STD), but it was not correlated with average width of growth rings ($r^2 = 0.03$, df = 10, $P = 0.59$), nor with the number of beetles that had emerged ($r^2 = 0.001$, df = 10, $P = 0.92$). Thus, leaf asymmetry shows no promise as an indicator of either tree growth rate or resistance to attack by *M. robiniae*.

In the 2008 study, however, the number of beetles emerging per year was significantly associated with treatment effects (overall anova $F_{6,48} = 4.8$, $P = 0.0006$), including the year effect ($F_{4,48} = 4.88$, $P = 0.0022$) and the growth ring covariate $F_{1,48} = 7.53$, $P = 0.0085$). There was a positive relationship between the number of beetles emerging per tree and year (Fig. 3.5), and also with average ring width (Fig. 3.4B), the opposite trend from that predicted from our hypothesis. When the data were summarized on a whole-tree basis (Fig. 3.6), the total number of beetles emerging from sections of trunk (during 2004 - 2008) again was positively correlated with average width of growth rings (overall anova $F_{1,10} = 7.13$ $P = 0.026$), again refuting the hypothesis.

The positive relationship between numbers of beetle emerging and xylem growth ring increment suggests that, over time, faster growing trees are more likely to be attacked by *M. robiniae*. This finding seems to contradict earlier research on this species (Wollerman 1970), and also on other species of wood borers (Hard 1985, Haavik et al. 2008). Although *M. robiniae* requires hosts that are stressed to some degree (Hall 1942), the adult females may nevertheless discriminate among available hosts and choose to oviposit on those that are the more vigorous, the plant vigor hypothesis (Price et al. 1991), or alternatively, performance of larvae may be greatest in those trees (Huberty and Denno 2004). Thus, poor quality of soil at the study site may have rendered most, if not all, of the black locust trees vulnerable to attack by *M. robiniae*, but differences between trees in general vigor have resulted in considerable variation in the densities of larvae. This study implies that maintaining healthy tree vigor may not be enough to prevent beetle attack, especially when beetle populations are high.

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Figure legends

Fig. 3.1) Scar in xylem of black locust tree from emergence of an adult *M. robiniae*. Arrow indicates xylem growth ring around the site of emergence for the year 2000.

Fig. 3.2) Relationship between the mean (± SE) width of growth rings of study trees and year, for: A) Six trees in 2007 (best fit regression equation: $Y = -0.05X + 101.1$, $r^2 = 0.05$, $P < 0.009$), and B) Eleven trees in 2008 (best fit regression equation: $Y = -0.07X + 137.6$, $r^2 = 0.54$, $P < 0.0001$).

Fig. 3.3) Relationship between the total number of adult *M. robiniae* that emerged from six study trees in the 2007 study and the year of the growth ring.

Fig. 3.4) Relationship between mean (± SE) number of adult *M. robiniae* that emerged by year and the average width of the growth ring for that year for: A) six trees felled in 2007 (correlation not significant; see text), and B) eleven trees felled in 2008 (best fit regression equation: $Y = 1.71X – 0.08$, $r^2 = 0.08$; $P = 0.036$).

Fig. 3.5) Relationship between the total number of adult *M. robiniae* that emerged across host trees in 2008 and year. Best fit regression equation: $Y = 1.4X – 2{,}766$, $r^2 = 0.14$; $P = 0.005$.

Fig.3.6) Relationship between total number of adult *M. robiniae* that emerged per tree and the average width of growth rings (previous five years) for study trees in 2008. Best fit regression equation: $Y = 17.8X – 17.8$, $r^2 = 0.44$; $P < 0.02$.

Fig. 3.1

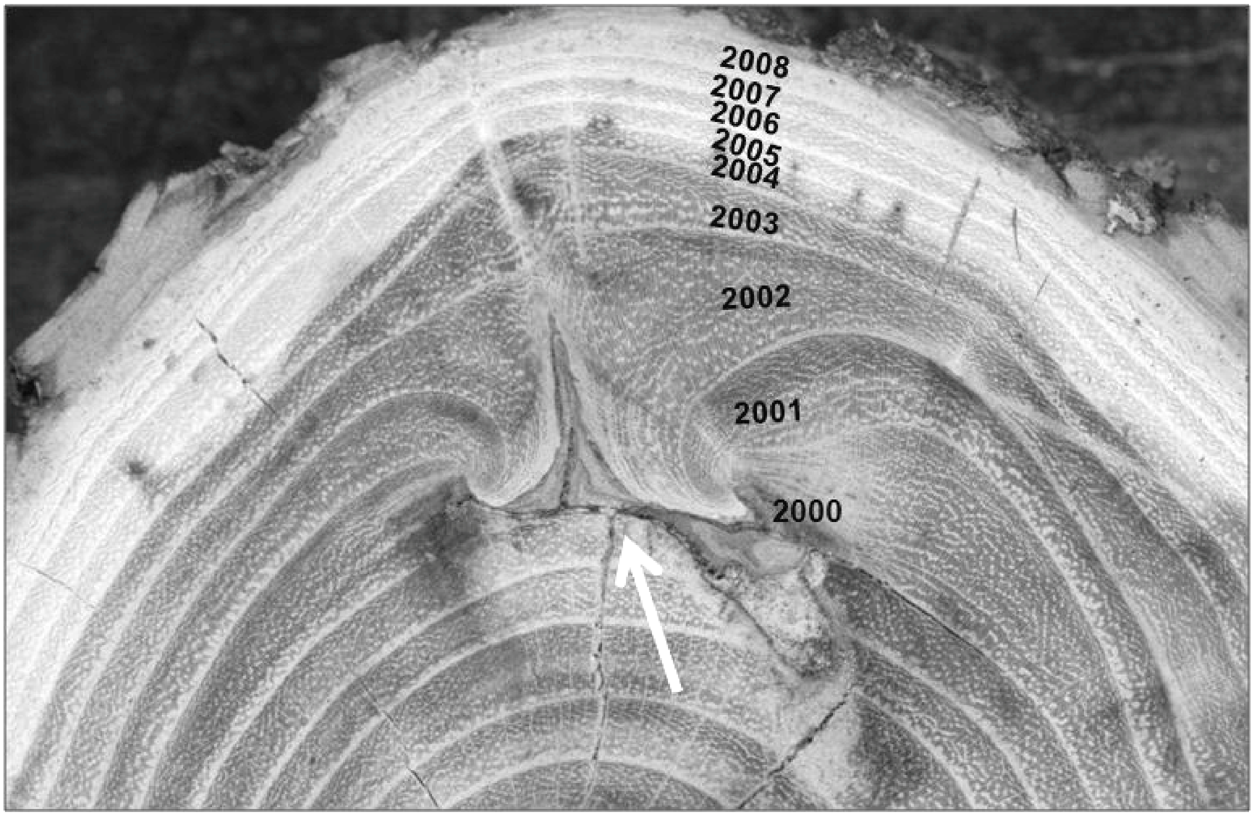


Fig. 3.2.

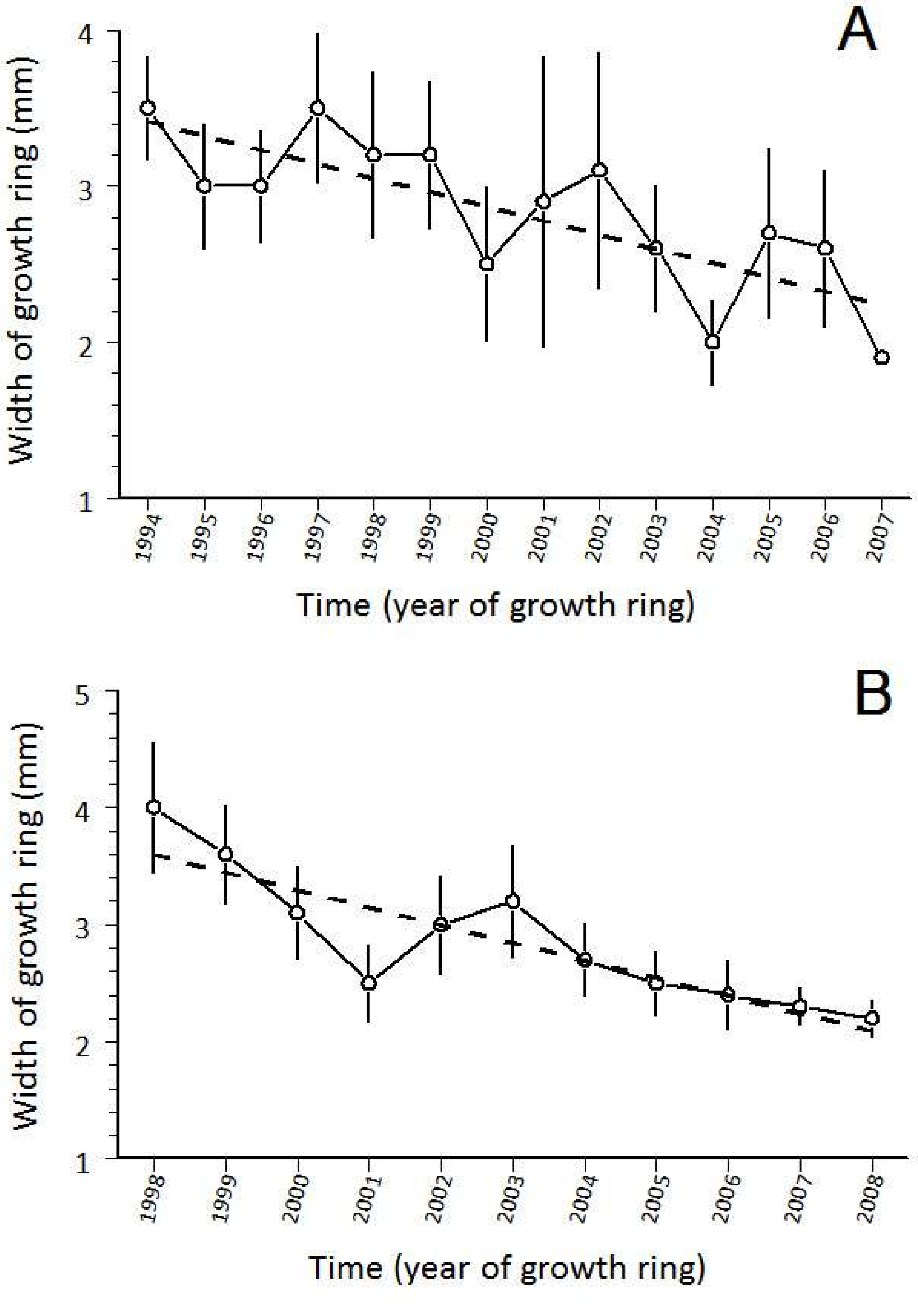

A
Width of growth ring (mm)
4
3
2
1
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
Time (year of growth ring)
B
Width of growth ring (mm)
5
4
3
2
1
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
Time (year of growth ring)

Fig. 3.3

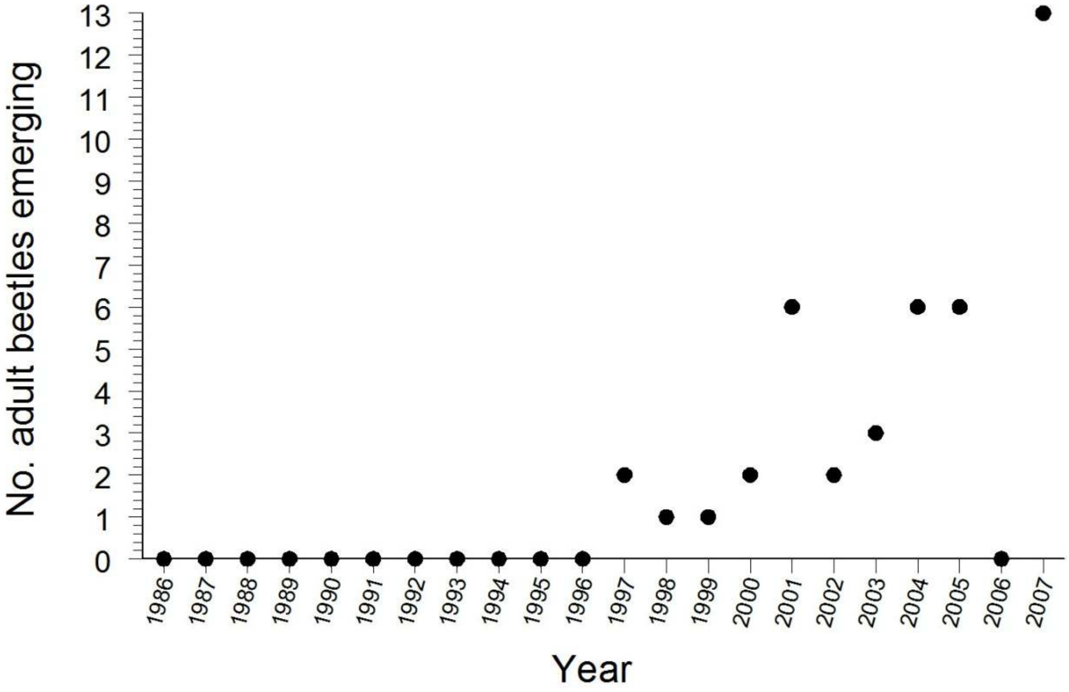

No. adult beetles emerging
0
1
2
3
4
5
6
7
8
9
10
11
12
13
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
Year

Fig. 3.4.

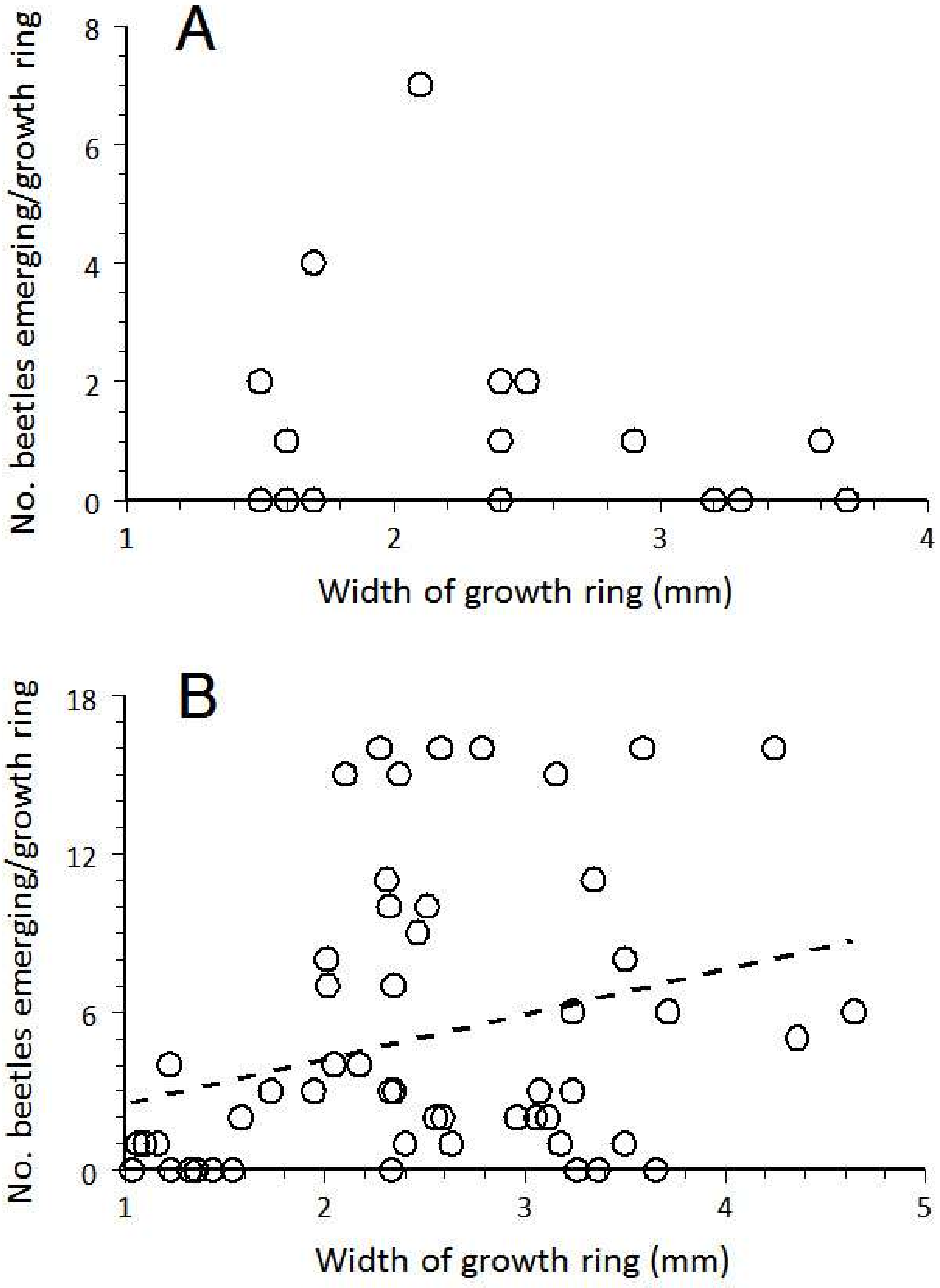

A
No. beetles emerging/growth ring
0
2
4
6
8
1
2
3
4
Width of growth ring (mm)
B
No. beetles emerging/growth ring
0
6
12
18
1
2
3
4
5
Width of growth ring (mm)

Fig. 3.5

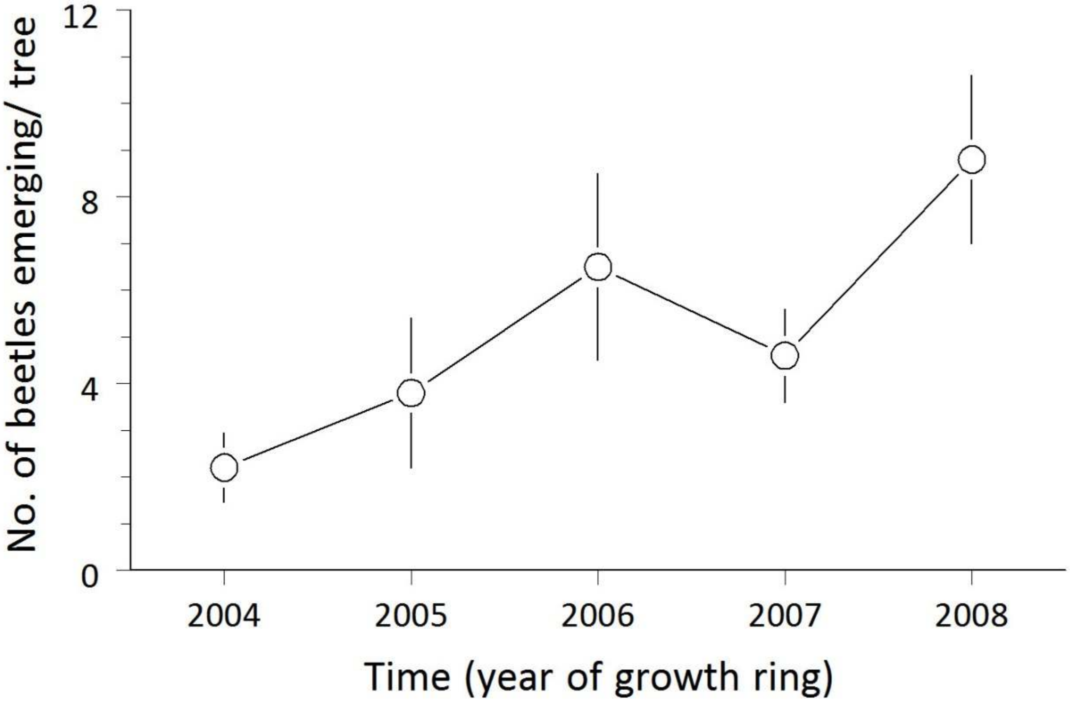
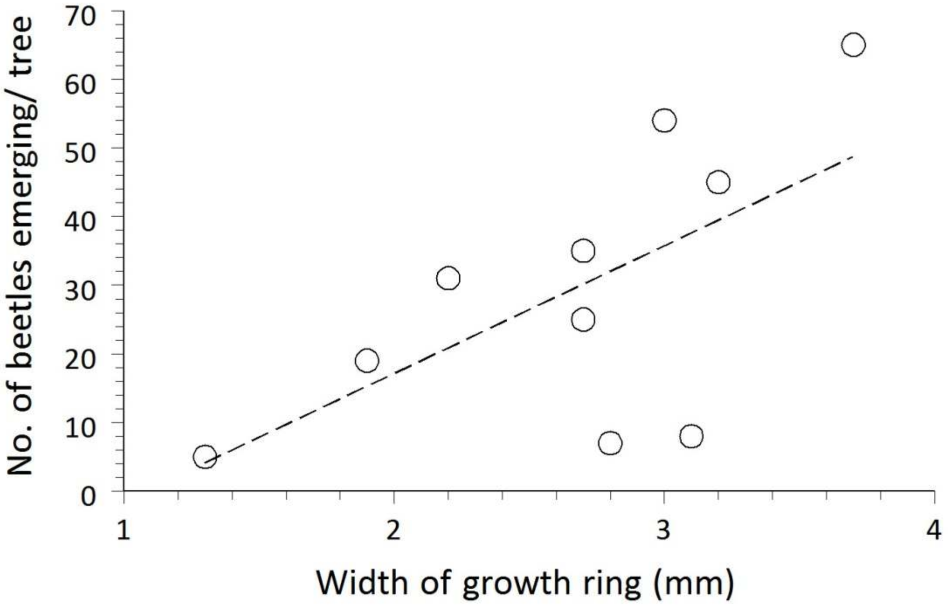

No. of beetles emerging/ tree
12
8
4
0
2004
2005
2006
2007
2008
Time (year of growth ring)

Fig. 3.6


No. of beetles emerging/ tree
0
10
20
30
40
50
60
70
1
2
3
4
Width of growth ring (mm)

Chapter 4: Cross-attraction to aggregation pheromones in the Cerambycinae

Abstract

Males of several species of longhorned beetle in the subfamily Cerambycinae are known to produce volatile aggregation pheromones composed of six-carbon chains with hydroxyl or carbonyl groups at C_2 and C_3. The similarity of pheromones among different cerambycine species that are sympatric and synchronic accounts for their mutual attraction to traps baited with individual synthetic pheromones. In this study I tested the hypothesis that cross-attraction of cerambycid species is a natural phenomenon. I conducted field experiments that compared the responses of beetles of the species *Neoclytus m. mucronatus* (F.) and *Xylotrechus colonus* (F.) (both Cerambycinae, tribe Clytini) to traps that were separately baited with live males of those species. Traps baited with male *N. m. mucronatus* captured ~3.5 time more conspecifics than male *X. colonus*, and conversely traps baited with male *X. colonus* captured ~6.5 time more conspecifics than *N. m. mucronatus*. Nevertheless, traps baited with live males captured significantly greater numbers of heterospecific beetles that did control traps that were not baited with beetles of either species. The experiment therefore provides evidence that cerambycid beetles may respond to calling heterospecific males in cases where males of the two species share one or more of the same pheromone components.

Key Words - *Neoclytus mucronatus, Xylotrechus colonus,* pheromones, field bioassay

Introduction

Chemical eavesdropping occurs when a different species responds to a chemical signal and modifies its own behavior because of it (Matthews and Matthews 2010). Several species of predators and parasitoids are known to eavesdrop on the pheromone signals of their prey species (e.g., Stowe et al. 1995, Haynes and Yeargan 1999). Insects of some species are able to detect and respond to pheromones of closely-related species (e.g., Pureswaran et al. 2008, Lacey et al. 2009). Interference of reproductive signals by other species can decrease the effectiveness of the signal (Gerhardt and Huber 2002). For example, individuals may waste time and energy attempting to mate with a heterospecific, which eventually can select for divergence in signals and responses (Pfennig 1998, Lemmon 2009).

Males of several species of longhorned beetle in the subfamily Cerambycinae are known to produce volatile aggregation pheromones composed of one or more compounds that are six-, eight-, or ten-carbon chains with hydroxyl or carbonyl groups at C_2 and C_3 (Lacey et al. 2004, 2007a; Hanks et al. 2007). Sympatric and synchronic cerambycine species that share larval hosts may have pheromone components in common, or even produce exactly the same compounds (Lacey et al. 2007b, 2009). In particular, (3*R*)-3-hydroxyhexan-2-one is the primary, and often sole component of the aggregation pheromones of many cerambycine species, including sympatric species (Hanks et al. 2007; Lacey et al. 2007b, 2009). The similarity of pheromones among different cerambycine species is demonstrated by the attraction of several species simultaneously to traps baited with individual synthetic compounds (Hanks et al. 2007). Nevertheless, the possibility remains that minor components that have not yet been identified, or not included in lures baited with synthetic pheromone, might impart species specificity to the natural pheromone blends, thus serving as prezygotic reproductive barriers (Fettköther et al.

1995, Reddy et al. 2005, Lacey et al. 2008). For instance, similar species that produce similar pheromones may limit their activity periods to times when heterospecifics are absent or not producing pheromone.

The cerambycine species *Neoclytus. m. mucronatus* (F.) and *Xylotrechus colonus* (F.) (both tribe Clytini) are sympatric throughout much of the eastern United States (Lingafelter 2007) and abundant in the area of our studies (east-central Illinois; pers. obs.). The larvae of both species are polyphagous on weakened or moribound hardwood hosts (Linsley 1959; Lingafelter 2007). Although adult *X. colonus* are active earlier in the season than *N. m. mucronatus*, the two species overlap broadly in flight period during late July and early August (pers. obs.). Adults of the two species also overlap in diel periodicity, both being crepuscular (pers. obs.), and in the composition of the aggregation pheromones produced by males when they are on the larval host: The pheromone of male *N. m. mucronatus* consists of only (3*R*)-3-hydroxyhexan-2-one, whereas male *X. colonus* produce primarily the same compound (~70%), but also the minor components (3*S*)-3-hydroxyhexan-2-one (10%), (2*S*,3*S*)-2,3-hexanediol (17%), and (2*R*,3*R*)-2,3-hexanediol (3%) (Lacey et al. 2004, 2007b, 2009). Adults of both sexes of *N. m. mucronatus* and *X. colonus* are attracted to synthetic racemic 3-hydroxyhexan-2-one in field bioassays (Lacey et al. 2009), suggesting that they also would respond to the (3*R*)-3-hydroxyhexan-2-one that is released by males of both species.

In this study I tested the hypothesis that cross-attraction of cerambycid species is a natural phenomenon and not an artifact that arises because trap lures release synthetic pheromones all day long. I conducted experiments that compared the responses of adult *N. m. mucronatus* and *X. colonus* to traps that were separately baited with live males of each species. Our hypothesis would be rejected if beetles were not significantly attracted to traps baited with heterospecific males compared to their response to control traps that were not baited with any beetles.

Materials and Methods

The study was conducted at Allerton Park (Piatt County, IL), a University of Illinois Natural Area that is a 600-ha mixed hardwood forest, during 9 August - 22 September 2009. Weather during the study was quite unfavorable for trapping, with 10 d of rain and a total rainfall of 9.9 cm (average ± SD maximum daily air temperature: 20.2 ± 2.6^{o}C; wind speed at dusk: 8.9 ± 2.7 kph; Weather Underground, Inc., Ann Arbor, MI). The beetles do not fly in the rain (pers. obs.)

The experimental unit was an individual flight intercept trap. I used cross-vane panel traps (black corrugated plastic, 1.2 m tall × 0.3 m wide; model PT Intercept™, APTIV, Portland, OR) that were modified to capture beetles alive as follows: A ~7.5 cm diameter hole was cut into the center of the threaded lid of a ~2-liter plastic jar and the supplied collection basin was replaced with the plastic jar (P.E.T.; model 55-650C, General Bottle Supply Company, Los Angeles, CA). The spout of a ~2-liter plastic funnel was cut to yield a 35-mm-diameter opening, and the funnel was glued into the lid such that its spout would be inside the jar when the lid was attached. The funnel and jar apparatus was wired in place to the bottom of each intercept trap. Traps were hung from L-shaped frames constructed of 1.27 cm i.d. PVC pipe (for details, see Graham et al. 2010) that were hung from 1.5-m sections of steel reinforcing bar (1.27-cm diameter) driven part way into the ground. I treated the interior surfaces of traps, funnels, and jars with Fluon® (Northern Products, Inc., Woonsocket, RI) a Teflon emulsion which dries to a slippery surface and greatly improves trap efficiency (Graham et al. 2010).

Preliminary research had revealed that males of the two species that were captured alive in panel traps would release pheromone, and the pheromone would be emitted from collection jars and attract conspecifics of both sexes into the trap (EEG, unpub. data). Therefore, I established our experimental treatments by stocking collection jars with males that had been live-trapped previously, and monitored the beetles in jars to determine the number and sex of wild beetles that had been attracted. Live males of the two species were captured using synthetic pheromone-baited traps in wooded areas in the vicinity of the study site. The synthetic pheromone was racemic 3-hydroxyhexan-2-one (to which both *N. m. mucronatus* and *X. colonus* respond; for chemical syntheses and bioassay results, see Hanks et al. 2007; Lacey et al. 2007b, 2009). Pheromone lures consisted of clear polyethylene sachets (press-seal bags, Bagette model 14770, 5.1 × 7.6 cm, Cousin Corp., Largo, FL) that were loaded with dilute pheromone (50 mg of racemic pheromone in 1 ml of 95% ethanol). Lures lasted ~5 d in the field (unpub. data).

I baited traps with live males of *N. m. mucronatus* or *X. colonus*, and control traps contained no beetles. The number of males that were used as bait varied with their availability, from 5-10 per trap (average ± SD: 8.9 ± 1.8 male *N. m. mucronatus*, 5.3 ± 3.1 male *X. colonus* per trap). Beetles were provided with 10% sucrose solution (8 ml glass vial plugged with a cotton dental roll) as food and a crumpled paper towel as a perch for releasing pheromone. I also added paper towels and vials containing sucrose solution to the containers of control traps to control for any effect these materials might have on response of beetles. Traps that were baited with live male beetles, as well as control traps, also had blank lures (sachets loaded with 1 ml of ethanol) to allow comparison of the data with earlier field bioassays of the same species (Lacey et al. 2004, 2007b, 2009). This small amount of ethanol has a negligible effect, if any, on response of adults of the two species to traps (Lacey et al. 2009).

Traps were set up in a linear transect through the woods in three blocks that each contained one trap of each treatment (20 m apart, position assigned randomly; blocks separated by at least 20 m). Each block also included one trap that was baited with synthetic pheromone which was used to monitor activity of the study species so as to optimize the timing of the experiment. One block of traps was destroyed by falling tree limbs during a thunderstorm on 17 August 2009. I checked traps for beetles every 1-2 d, removing beetles as necessary to maintain the treatments and recording the number and sex of beetles of the two target species (some beetles could not be sexed because they had been damaged in trap jars by other organisms or escaped during handling). Trap treatments were rotated within blocks and lures were replaced every 5 d.

I combined trap capture data for the two species, assigning captured beetles to categories based on the species of beetle that had been used as bait: beetles in the "conspecific" category had been captured by traps baited with males of the same species, those in the "heterospecific" category were in traps baited with males of the other species, and those in the "control" category were in the unbaited control traps. Differences between these categories in mean number of beetles captured per trap and day were tested with the nonparametric Friedman's test (blocked by set and day, PROC FREQ with CMH option; SAS Institute 2001) because data were heteroscedastic (Sokal and Rohlf 1995). Inclement weather accounted for the reduced number of sample days in the data set. I excluded from the analysis data for dates on which fewer than ten beetles (both species combined) were collected (final N = 15 replicates). Differences between pairs of means were tested with the Ryan–Einot–Gabriel–Welsch (REGWQ) means-separation test to control maximum experiment-wise error rates (SAS Institute 2001).

Results and Discussion

During the experiment, I captured a total of 201 *N. m. mucronatus* and 139 *X. colonus*. Both sexes of beetles were caught in baited traps, with a sex ratio of 0.87:1 (males:females) for *N. m. mucronatus* and 0.66:1 for *X. colonus*. The response of both sexes to natural pheromone of males of both species is consistent with their mutual response to pheromones in olfactometer studies and with their function as aggregation pheromones (Lacey et al. 2007, 2009), and to synthetic pheromone in field bioassays (Lacey et al. 2009).

Traps baited with male *N. m. mucronatus* captured ~3.5 time more conspecifics than heterospecifics, whereas those baited with male *X. colonus* captured ~6.5 time more conspecifics than heterospecifics (Fig. 4.1). Control traps captured very few beetles of either species (Fig. 4.1). The mean number of conspecific beetles that were captured (species combined) was significantly greater than that for heterospecifics, which in turn was greater than the mean for controls (Friedman's $Q_{2,42} = 31.4$, $P < 0.0001$). Thus, the experiment supports the hypothesis that adult cerambycid beetles respond to calling heterospecific males if pheromones of those males share components with the pheromone blend of conspecifics males.

This is the first study to confirm cross-attraction of cerambycid species to live heterospecific males. Many species of Cerambycidae require a stressed but living host (Linsley 1961), an ephemeral resource, resulting in interspecific competition among species that share hosts. Semiochemical-based interactions have been confirmed between cerambycids and bark beetles and share hosts (Scolytinae: Curculionidae; reviewed by Allison et al. 2004). Nevertheless, our study ignores a potentially important factor that influences the behavior of adult cerambycid beetles, the volatile chemicals released by host plants of the larvae. Adult males and females of both *N. m. mucronatus* and *X. colonus* were attracted to volatiles of freshly-cut hickory in olfactometer bioassays (Ginzel and Hanks 2005). It is possible that host plant volatiles could mediate the response of beetles to certain pheromone components, for example sensitizing adult *X. colonus* to the minor components of their pheromone blend, thus limiting cross-attraction to the pheromone of *N. m. mucronatus*. Even in the event that males of either species were to encounter females of the other species on a larval host, it is unlikely that mating will occur because of differences between the contact pheromones of the females of each species that present a second barrier to heterospecific mating (Ginzel and Hanks 2003; Ginzel et al. 2003).

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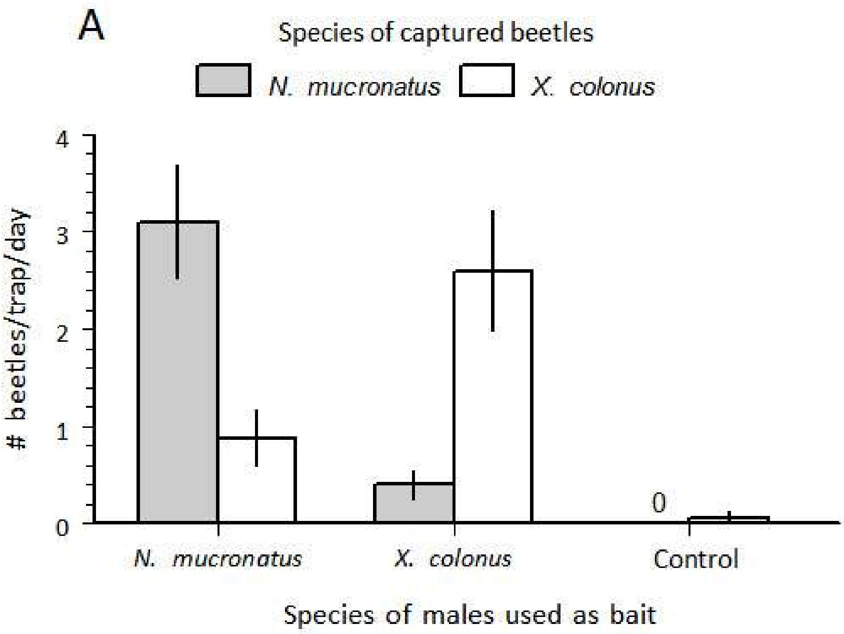
Figure legends

Fig. 4.1. Mean number (± SE) of *Neoclytus m. mucronatus* and *Xylotrechus colonus* that were captured by panel traps, per trap and day, and: A) The species of male beetles that were used as bait (no males in control traps), and B) the taxonomic relationship between the beetles that were used as bait and those that were captured by traps. Bars with different letters are significantly different (REGWQ test, $P < 0.05$).

Fig. 4.1.


A
Species of captured beetles
N. mucronatus
X. colonus
beetles/trap/day
4
3
2
1
0
0
N. mucronatus
X. colonus
Control
Species of males used as bait

Chapter 5: Treating panel traps with a fluoropolymer enhances their efficiency in capturing cerambycid beetles

Abstract

The most effective traps for capturing cerambycids and other saproxylic beetles are intercept designs such as funnel traps and cross-vane panel traps. I have observed that adult cerambycids of many species often alight and walk upon panel traps, and few are actually captured. In an effort to improve trap capture and retention, researchers have treated intercept traps with Rain-X®, a polysiloxane formulation that renders surfaces more slippery. Here, I summarize experiments that compared the efficacies of Rain-X® and Fluon®, a PTFE fluoropolymer dispersion, as surface treatments for panel traps that are deployed to capture cerambycid beetles, using untreated traps as controls. Fluon-treated traps captured on average more than fourteen times the total number of beetles, and many more cerambycid species, than were captured by Rain-X®-treated or control traps. Beetles captured by Fluon-treated traps ranged in body size by 350%. They could not walk on vertical panels treated with Fluon, but easily walked on those treated with Rain-X, and on untreated traps. Moreover, a single Fluon treatment remained effective for the entire field season, even in inclement weather. I conclude that treating panel traps with Fluon greatly improves their efficiency in capturing cerambycid beetles. This increased efficacy will be particularly important when traps are deployed to detect very low-density populations, such as incursions of exotic species, or remnant communities of rare and endangered species. The influence of Fluon on trap efficiency may vary with product formulation and its source, and also with climatic conditions.

Key Words – Wood-boring insect, Cerambycidae, monitoring, pheromone, trap, Fluon, Rain-X

Introduction

A variety of traps have been designed specifically to catch cerambycids and other saproxylic beetles (Southwood and Henderson 2000), and among the most effective are intercept designs such as funnel traps and cross-vane panel traps (McIntosh et al. 2001, Morewood et al. 2002, Sweeney et al. 2004, Nehme et al. 2009). Intercept traps are used for monitoring the spread of exotic and invasive species of cerambycids (e.g., Sweeney et al. 2004), estimating population densities of threatened species (e.g., Buse et al. 2008), and identifying geographic patterns in biodiversity, ecology, and behavior (e.g., Jacobs et al. 2007, Wermelinger et al. 2007). Some researchers condition intercept traps with Rain-X® (SOPUS Products, Houston, TX) to render their surfaces more slippery, with the goal of increasing trapping efficacy and retention of insects in traps (Czokajlo et al. 2003, de Groot and Nott 2003, Sweeney et al. 2004). Rain-X is a polysiloxane liquid that is marketed as a treatment for repelling water from glass, such as automobile windshields.

I have used cross-vane panel traps, conditioned with Rain-X, in our field research on volatile pheromones of cerambycid beetles of species that range in body size from ~4 – 50 mm in length (Hanks et al. 2007, Lacey et al. 2004, 2008, 2009; Ray et al. 2009; Barbour et al. 2010). However, during the course of these studies, I have observed that adult cerambycids of many species are attracted to traps in great numbers, but often alight and walk upon traps conditioned with Rain-X, and relatively few are actually captured (unpub. data). I therefore began to search for methods of improving the capture efficiency and retention of panel traps.

Here, I describe the results of experiments that tested the effect of the fluoropolymer Fluon® PTFE (AGC Chemicals Americas, Inc.), applied as a surface conditioner, on the efficiency with which panel traps capture and retain cerambycid beetles. Fluon is available as an aqueous dispersion that dries to leave a slippery film. It commonly is applied to the upper walls of containers used to house insects in insectaries, and to walls of behavioral arenas for studies of insect behavior, to prevent escape (e.g., Radinovsky and Krantz 1962, Suarez and Case 2002). To our knowledge, there has been little research to evaluate the effect of Fluon in enhancing the efficiency of insect traps for field research (but see Valles et al. 1991). Thus, I conditioned the panels and bases of pheromone-baited panel traps with Fluon or Rain-X, or left traps untreated, and compared the number of beetle species and individuals that they captured from a natural community of cerambycids. I also conducted studies to assess how trap conditioning influenced the mobility of beetles on trap surfaces, and the likelihood that beetles would escape from traps.

Materials and Methods

Experiment 1 tested the effect of trap conditioning on numbers of beetles captured, and was conducted at Allerton Park (Piatt County, IL), a University of Illinois Natural Area that is a 600-ha mixed hardwood forest, during 25 June - 27 July 2009. Weather during this period was often too inclement for the beetles to fly, with 13 d of rain and a total rainfall of 13.1 cm (average ± SD maximum daily air temperature: 25.9 ± 3.1^{o}C; wind speed at dusk: 10.9 ± 3.8 kph; www.wunderground.com). Inclement weather accounts for the reduced number of sample days in the data set.

I used cross-vane panel traps (black corrugated plastic, 1.2 m tall × 0.3 m wide; model PT Intercept™, APTIV, Portland, OR) that were modified to capture beetles alive by replacing the supplied collection basin with a plastic funnel that guided beetles into a plastic jar. The funnel-and- jar apparatus was constructed as follows: the spout of a ~2-liter plastic funnel was cut to yield a 35-mm-diameter opening; a ~7.5 cm diameter hole was cut into the center of the threaded lid of a ~2-liter plastic jar (P.E.T.; model 55-650C, General Bottle Supply Company, Los Angeles, CA). The funnel was glued into the lid such that the pointed end extended ~3 cm inside the jar when the lid was screwed on. The funnel and jar apparatus was wired to the bottom of the panel trap. Traps were hung from L-shaped frames constructed of 1.27 cm i.d. PVC irrigation pipe (SCH40, JM Eagle, Los Angeles, CA) with a 1.5-m-long upright connected with a T-fitting to a 20-cm long arm having a loop of wire at the end from which the trap was suspended. The frame upright was mounted on a 1.5-m section of steel reinforcing bar (1.27-cm diameter) that was driven part way into the ground.

I conditioned trap panels, the interior surfaces of their bases, and jar funnels with Fluon (Northern Products, Inc., Woonsocket, RI) or Rain-X. Untreated traps were used as controls. I applied Fluon with cotton pads, and it dried to a whitish, blotchy residue. Rain-X was applied from a spray bottle and spread evenly over the trap surface with a paper towel. Traps conditioned with Rain-X appeared shinier than control traps. I did not clean traps, or reapply conditioning materials, during the experiment.

All traps were baited with racemic 3-hydroxyhexan-2-one, synthesized from 1-hexyn-3-ol as described in Millar et al. (2009). The (*R*)-enantiomer of 3-hydroxyhexan-2-one is an important component, or the sole component, of aggregation pheromones for many cerambycid species in the subfamily Cerambycinae, and its attractiveness to beetles is generally unaffected by the presence of the (*S*)-enantiomer when the racemate is used as a trap lure (e.g., Hanks et al. 2007; Lacey et al. 2007, 2009). Pheromone lures consisted of clear polyethylene sachets (press-seal bags, Bagette model 14770, 5.1 × 7.6 cm, 0.05 mm wall thickness, Cousin Corp., Largo, FL) that were loaded with 50 mg of the racemic pheromone in 1 ml of 95% ethanol. Ethanol is an efficient carrier of the synthetic pheromone and has negligible if any activity alone at these volumes (e.g., Hanks et al. 2007). Lures lasted ~5 d in the field. Control ("blank") lures consisted of sachets loaded with 1 ml of ethanol. The experiment included the following trap/lure treatments: Fluon/pheromone, Rain-X/pheromone, and control/pheromone traps (to test the conditioning effect), Fluon/blank traps (to compare with the Fluon/pheromone treatment to test the influence of the pheromone), and control/blank traps (to compare with the Fluon/blank treatment to test the influence of Fluon alone, and with the control/pheromone treatment to test the influence of pheromone lures in traps that are untreated). I did not include a Rain-X/blank treatment because our previous research already had confirmed that very few cerambycid beetles respond to such traps (e.g., Hanks et al. 2007).

Traps were set up in a linear transect through the woods, in three blocks that each contained one trap for each treatment (20 m apart, position assigned randomly), with blocks separated by at least 20 m. Traps were checked for beetles every 1-2 d, and captured beetles were returned to the laboratory for identification. I sexed beetles of the two best-represented species (see Results), *Neoclytus m. mucronatus* (F.) and *Xylotrechus colonus* (F.). A few beetles could not be sexed because they had been damaged in trap jars or escaped during handling. Trap treatments were rotated within blocks and lures were replaced every 5 d.

Differences between trap treatments in the number of beetles captured per trap were tested with the nonparametric Friedman's test (PROC FREQ with CMH option; SAS Institute 2001) because assumptions of analysis of variance were violated by heteroscedasticity (Sokal and Rohlf 1995). I include in that analysis only *N. m. mucronatus* and *X. colonus* because the numbers of beetles of the remaining species were insufficient to allow meaningful statistical comparison. I did not include a beetle species effect in the analysis because the two species responded to trap treatments in a similar manner (Table 1; species term in ANOVA $P > 0.05$). I therefore combined the data for the two species, which improved the statistical power of the test of trap treatment on capture rate of cerambycine species in general. Date and block combinations that contained fewer than ten beetles were eliminated from the analysis (N = 13 replicates remaining). Low numbers of captured beetles on some dates were attributable to unfavorable weather (rain, wind, cool temperatures). I tested differences between the preplanned pairs of treatment means (as defined above) with orthogonal contrasts (Sokal and Rohlf 1995; PROC GLM contrast statement, SAS Institute 2001). I also used the Shannon-Wiener index (*H′*; Peet 1974, Hayek and Buzas 1997) to quantify the species diversity of cerambycines that were captured in the different treatments, and tested differences in diversity between treatments with the Student *t*-test (Magurran 1988).

I used the data from Experiment 1 to test whether the effect of Fluon conditioning on trap capture rate would change over the ~1-month period that traps were exposed to the elements. As mentioned above, heavy rain fell on many days during the experiment, but traps were never retreated. For this analysis, I again combined data for *N. m. mucronatus* and *X. colonus*. I include only data for treatments with pheromone lures because few beetles were captured by traps with blank lures (see Results). I also averaged the data for the Rain-X/pheromone and control/pheromone treatments, by date and block, into a single “nonFluon” treatment because Rain-X conditioning had no significant effect on trap capture rate (see Results). I tested the hypothesis that the percentage of the total number of beetles captured per day would decline over time for the Fluon/pheromone treatment as that conditioning treatment degraded. The linear relationship between this percentage and date was tested with regression analysis (PROC REG, SAS Institute 2001), and the hypothesis would be supported by a significant and negative relationship. Sample dates on which fewer than five beetles were captured were eliminated from the data set (12 dates remaining).

Experiment 2 was an independent field bioassay, at a different site, to compare more directly the efficiency of Fluon/pheromone and Rain-X/pheromone treatments (conditioned and baited as described above). The study site was the municipal Landscape Recycling Center in Urbana, IL (Champaign Co.), an 11-ha area where plant waste, including woody material, is recycled into mulch and compost. The Center is surrounded by a 54-ha natural area with tallgrass prairie and mixed hardwood forest habitats. On 22 June 2009, I set up a linear transect of five blocks of traps, each of which contained one Fluon/pheromone and one Rain-X/pheromone trap (20 m apart). Blocks were separated by at least 20 m, with trap treatments alternating down the transect. The bioassay was run until 23 July 2009 (weather conditions as described above), with beetles collected every 1 to 3 d, traps rotated within blocks and lures replaced every five days. I tested differences between treatments in species diversity of cerambycine beetles, and numbers of beetles captured (*N. m. mucronatus* and *X. colonus*, combined) as described above. The analysis included only date and block combinations that contained at least three beetles (N = 10 replicates; this threshold number of beetles was lower than in Experiment 1 due to the lower population density at the study site).

I combined data from Experiments 1 and 2 to maximize the statistical power for testing the hypothesis that adult female and male beetles (*N. m. mucronatus* and *X. colonus*) are influenced differently by trap treatments. I used data only for traps that were baited with pheromone lures, and tested differences between treatments in sex ratios of beetles with the *G* goodness-of-fit test (Sokal and Rohlf 1995; sex ratio of beetles in Fluon treatments used to calculate the “expected” number of each sex for Rain-X and control treatments). The hypothesis would be supported if trap treatments differed significantly in beetle sex ratio. Statistical power of the test was limited by the relatively small number of beetles captured by Rain-X and control traps (see Results).

The large number of beetles that were captured by Fluon/pheromone traps (see Results) raised a new hypothesis: Traps with Fluon act as sinks during bioassays, removing beetles from the habitat that otherwise eventually would have been captured by Rain-X/pheromone or control/pheromone traps. Experiment 3 tested this hypothesis with an independent bioassay at Allerton Park during 31 July – 7 August 2009 (average maximum air temperatures: 25.5 ± 1.2^{o}C; wind speed at dusk: 7.9 ± 3.1 kph; rain on three days, total precipitation 2.0 cm). More specifically, the experiment was designed to test the secondary hypothesis that Rain-X/pheromone traps would capture fewer beetles when they were in proximity to Fluon/pheromone traps. Our experimental treatments were sets of two traps that were 3 m apart: 1) a Rain-X/pheromone trap neighboring a Fluon/pheromone trap, and 2) two neighboring Rain-X/pheromone traps. For the latter sets, I randomly designated one of the Rain-X traps as the "study" trap (i.e., the trap that would be influenced by its neighbor). The Rain-X traps that neighbored Fluon traps were the study traps within those sets. Sets of traps were positioned in a linear transect, with two sets (one of each combination of treatments) constituting a block (sets separated by 20 m), and with five such blocks that were separated by at least 20 m. Beetles were collected every 1 to 2 d. Differences between treatments in the number of adult *N. m. mucronatus* and *X. colonus* that were captured by Rain-X study traps were tested by ANOVA (data were homoscedastic) blocked by day and trap block. All data were included in the analysis because at least 10 beetles were captured on every sample date. Our secondary hypothesis would be supported if Rain-X study traps that neighbored another Rain-X trap captured more beetles than Rain-X traps that neighbored a Fluon trap.

Experiment 4 was a preliminary laboratory study of the influence of Rain-X and Fluon conditioning on the mobility of beetles on traps. Test animals were adult *Megacyllene robiniae* (Förster), a diurnal species, that I had collected from inflorescences of goldenrod (*Solidago* species) four days earlier. Beetles were housed in the laboratory in an aluminum screen cage and provided 10% sucrose solution and fresh inflorescences of goldenrod as food. I used the funnel-shaped bases of the panel traps for this study, conditioning one with Fluon (as described above), another with Rain-X, and leaving a third untreated (control). I included a fourth trap base, from a trap that was conditioned with Fluon and left in the field from June through mid September, so that I could determine whether exposure to the elements would alter the effect of Fluon on beetle mobility. Trap bases were positioned, tapered end down, on a laboratory bench with the opening flush against the bench. Thus, beetles could be released individually at the bottom and attempt to escape by walking up the side. I allowed each beetle 2 min to reach the rim by walking (all beetles walked rather than attempting to fly), and videotaped each trial. I tested ten beetles (both sexes, but chosen arbitrarily for each trial) per treatment, using each beetle only once. Differences between treatments in the percentage of beetles that escaped were tested with the *G* goodness-of-fit test. The experiment was conducted during 1300 – 1500 h on 15 September 2009 under laboratory conditions (~12:12 h L:D, ~20ºC, ~50% RH).

Experiment 5 further evaluated the influence of trap conditioning on mobility of beetles, but more specifically on their ability to escape from trap jars (often a significant problem with intercept traps that lack a killing agent; Morewood et al. 2002, de Groot and Nott 2003, Sweeney et al. 2006). I conditioned the interior surfaces of trap jars and their funnel attachments (see trap design, above) with Fluon or Rain-X, or left them untreated (controls; three jars per treatment). Jars were positioned arbitrarily on the floor of a polyethylene camping tent (~2 m square × 1.5 m tall) in the backyard of a private residence in Urbana, IL (Champaign Co.) during 13 to 16 September 2009 (maximum air temperatures: 27-29^{o}C; partly cloudy). I again used adult *M. robiniae* for this experiment, but different individuals than were used in Experiment 4. I placed six beetles (three of each sex) into each jar and allowed them 2 d to escape (the maximum time that beetles are held in traps jars during field bioassays), and the experiment was repeated once. I recorded the number of beetles remaining in jars after 48 h. Differences between treatments in the percentage of beetles that escaped were tested with the G goodness-of-fit test.

Results and Discussion

During Experiment 1, I captured 263 beetles of 12 cerambycine species over the 32 d period (Table 5.1). The most numerous species were *N. m. mucronatus* (58% of total) and *X. colonus* (31%), males of which produce pheromones that include (*R*)-3-hydroxyhexan-2-one as a component (Lacey et al. 2007, 2009). These two species are endemic to North America, the larvae are polyphagous on species of hardwood trees, and the adults are active between April and October in the area of our studies (Lingafelter 2007; pers. obs.).

Trap treatments differed dramatically in the number of *N. m. mucronatus* and *X. colonus* that were captured (Fig. 5.1; Friedman's $Q_{4,49} = 27.8$, $P < 0.0001$), with the mean for Fluon/pheromone traps at least 14 times greater than the means for the other treatments. Several beetles that I observed arriving at Fluon/pheromone traps immediately fell into the trap jar after striking the panels, apparently unable to alight on and cling to the conditioned surfaces. The mean for the Fluon/pheromone treatment was significantly larger than that for the Rain-

X/pheromone and control/pheromone, and from the mean for the Fluon/blank treatments (orthogonal contrasts for all comparisons: $F_{1,52} > 460$, $P < 0.0001$), confirming that conditioning pheromone-baited panel traps with Fluon greatly increased the number of beetles that they captured. There was no significant difference between the means for Rain-X/pheromone and control/pheromone treatments ($F_{1,52} = 0.1$, $P = 0.76$), indicating that Rain-X had no effect on trap efficiency, as reported in an earlier publication (Sweeney et al. 2004; but see Czokaljo et al. 2002; de Groot and Nott 2003). The mean for the Fluon/blank treatment was not significantly different than that for the control/blank treatment ($F_{1,52} = 2.5$, $P = 0.13$), confirming that beetles were not attracted to unbaited traps conditioned with Fluon. Finally, control/pheromone traps did not capture significantly more beetles than control/blank traps ($F_{1,52} = 2.38$, $P = 0.13$), suggesting that a very large percentage of beetles that were attracted to control traps by pheromones had managed to escape. This last finding was disappointing, because for many years I have relied on panel traps that were untreated, or conditioned with Rain-X, in our bioassays for identifying pheromones of cerambycine species (Hanks et al. 2007; Lacey et al. 2004, 2008, 2009; Ray et al. 2009). Consequently, I achieved statistical significance between pheromone treatments in some of those studies only by using large numbers of replicates.

The ten remaining species of cerambycines that were captured during Experiment 1 were all caught in Fluon/pheromone traps (Table 1), including four species that have male-produced pheromones that contain (*R*)-3-hydroxyhexan-2-one, or structurally-related compounds: *Neoclytus a. acuminatus* (F.), *Sarosesthes fulminans* (F.), *Anelaphus pumilus* (Newman), and *Cyrtophorus verrucosus* (Olivier) (Lacey et al. 2004, 2009; unpub. data). Too few specimens of these species were captured to allow a robust statistical test of treatments (Table 5.1). Nevertheless, it is highly improbable that all 29 beetles of those species would have been captured by Fluon/pheromone traps by mere chance. In fact, a goodness-of-fit test that combined the data for just those ten species was highly significant (G-test $P < 0.0001$), confirming that the Fluon/pheromone traps captured a greater number of cerambycine beetles, in general, than traps in the other treatments. Therefore, it is not surprising that species diversity of cerambycines was significantly greater for Fluon/pheromone traps (Shannon-Weiner $H' = 1.14$) than for Rain-X/pheromone and control/pheromone traps ($H' = 0.69$, 0.64, respectively; t-tests $P < 0.05$). Beetles that were captured by traps conditioned with Fluon ranged in size (elytron length) by ~350%, from 4.0 mm for a *Euderces picipes* (F.) to 14.5 mm for a *Parelaphidion aspersum* (Haldeman) (standard deviation: 1.5). Attraction of all twelve species to the racemic synthetic pheromone provides further evidence of widespread response of cerambycine species to (R)-3-hydroxyhexan-2-one and related compounds (Hanks et al. 2007, Lacey et al. 2009, Millar et al. 2009).

The hypothesis that the efficacy of Fluon-conditioned traps would degrade over time was not supported: the percentage of all beetles that were captured by Fluon traps was not significantly correlated with sample date (regression analysis $F_{1,11} = 0.5$, $P = 0.50$). The percentage of beetles that were in Fluon traps, averaged across sample dates, was 92.5 ± 6.7 (SD). In fact, traps with Fluon consistently captured more than 90% of beetles during 8-27 July, approximately the last half of the experiment. The durability of Fluon conditioning was further indicated by the great numbers of beetles captured by Fluon traps in field bioassays that were conducted later in 2009, and that used the same traps as in the present studies, but without retreatment (unpub. data). I conclude from these data that a single treatment of panel traps with Fluon is sufficient to render them highly effective in capturing beetles throughout an entire season, at least under the climatic conditions of central Illinois.

In Experiment 2, which compared only the Fluon/pheromone and Rain-X/pheromone treatments at a different study site, I captured 79 cerambycid beetles of seven species over the 26-d period (Table 5.1). *Neoclytus m. mucronatus* represented 75% of the total and *X. colonus* represented 15%. Fluon traps captured ~6 times as many beetles as did traps in the Rain-X treatment (means 3.7 ± 0.62 and 0.60 ± 0.22, respectively; significantly different: Friedman's $Q_{1,19} = 10.1$, $P = 0.0015$). There also were smaller numbers of four other cerambycine species (10% of the total), and all but one of those beetles were in the Fluon/pheromone traps (Table 5.1).

There was no support for the hypothesis that trap treatments would influence adult female and male beetles differently: trap treatments did not differ significantly in the sex ratios of adults that were captured in Experiments 1 and 2 (all *G*-tests $P > 0.05$). Pheromone-baited Fluon, Rain-X, and control traps captured female *N. m. mucronatus* in ratios of 55, 33, and 42% respectively, and female *X. colonus* in ratios of 59, 60, and 60%, respectively. I cannot extend these sex ratio data to speculate on differences between the sexes in the probability of their being captured by panel traps because I do not know the operational sex ratio of the wild population from which they had been sampled.

Experiment 3 did not support the hypothesis that Fluon traps act as sinks during bioassays, removing beetles from the habitat that otherwise eventually would have been captured by traps in the other treatments. I captured 54 cerambycid beetles, of which *N. m. mucronatus* and *X. colonus* accounted for all but two. Traps conditioned with Rain-X captured very small numbers of beetles whether they neighbored a trap with Fluon trap or another Rain-X trap: means 0.15 ± 0.1 and 0.1 ± 0.1 beetles per trap, respectively (not significantly different, ANOVA $F_{8,39} = 0.4$, $P = 0.91$). Fluon traps, on the other hand, captured 3.6 ± 0.31 beetles per trap during the study (not compared statistically with other treatments). I therefore conclude that traps conditioned with Fluon did not interfere with traps with Rain-X, and low numbers of beetles in the Rain-X treatments of Experiments 1 and 2 were entirely due to the inherent inefficiency of those traps.

In Experiment 4, none of the adult *M. robiniae* escaped from trap bases treated with Fluon, including the trap base that had been in the field during summer and fall. On the other hand, 100% of beetles escaped from trap bases that were treated with Rain-X, or untreated trap bases (treatments significantly different, *G*-test $P < 0.0001$), and did so within 5.8 ± 0.8 and 6.0 ± 0.5 s (mean ± SD), respectively. The probability of escape in all control treatments was obviously independent of the sex and body size of beetles.

In Experiment 5, only 17 ± 8.4% of the adult *M. robiniae* escaped from trap jars (and attached funnels) that were treated with Fluon within 48 h, whereas more than four times as many escaped from jars conditioned with Rain-X and control jars (69 ± 2.7% and 81 ± 8.9%, respectively; treatments significantly different, *G*-test $P < 0.0001$). Percentages for the Rain-X and control jars were not significantly different from one another (*G*-test $P > 0.05$). Beetles escaped from the Rain-X and control jars by crawling, but the few that escaped from the Fluon jars apparently did so by flying. Across treatments, 57% of males and 54% of females escaped, and the treatments did not differ in the proportion of females versus males that escaped (ratios not significantly different, *G*-test $P < 0.0001$).

In summary, our experiments clearly demonstrate that conditioning panel traps with Fluon greatly enhances their efficiency in capturing cerambycid beetles, both by preventing them from clinging to trap surfaces when they land (such that they immediately drop into the collection jar) and by minimizing escape from collecting jars. Moreover, the Fluon treatment is quite durable, even in inclement weather, and conditioned traps capture beetles of a fairly broad range of body sizes. Nevertheless, it is unlikely that conditioning surfaces of traps with Fluon would influence capture rates of very large species (e.g., *Prionus* species; Rodstein et al. 2009). I conclude that conditioning with Fluon will significantly enhance the efficacy, and thus the sensitivity of sentinel traps deployed to detect incursions of a diversity of exotic cerambycid species, or for monitoring threatened species, at very low population densities. Fluon also is likely to improve trap efficiency for other types of saproxylic beetles, but is less likely to affect trapping efficacy of insects that are more agile in flight, such as moths. Further research will be necessary to determine how the efficiency of traps is affected when they are conditioned with different formulations of Fluon, and traps are exposed to different climatic conditions.

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Tables

Table 5.1. Identity and number of cerambycine beetles captured with panel traps during Experiments 1 and 2 according to trap and lure treatment. Traps were conditioned with Fluon, Rain-X, or were untreated (control traps), and lures were loaded with synthetic pheromone in ethanol ("pheromone") or ethanol alone ("blank"). Sexes of beetles were determined only for the species *N. m. mucronatus* and *X. colonus* (F = female, M = male, U = unknown).

		Trap/lure treatment						
		Experiment 1					Experiment 2	
Tribe	Species	Fluon/ pheromone	Rain-X/ pheromone	Control/ pheromone	Fluon/ blank	Control/ blank	Fluon/ pheromone	Rain-X/ pheromone
Elaphidiini	*Anelaphus parallelus* (Newman)	1	-	-	-	-	-	-
Elaphidiini	*Anelaphus pumilus* (Newman)	4	-	-	-	-	-	-
Elaphidiini	*Anelaphus villosus* (F.)	1	-	-	-	-	1	-
Elaphidiini	*Elaphidion mucronatum* (Say)	4	-	-	-	-	1	-
Elaphidiini	*Parelaphidion aspersum* (Haldeman)	4	-	-	-	-	2	-

Table 5.1 (cont.)

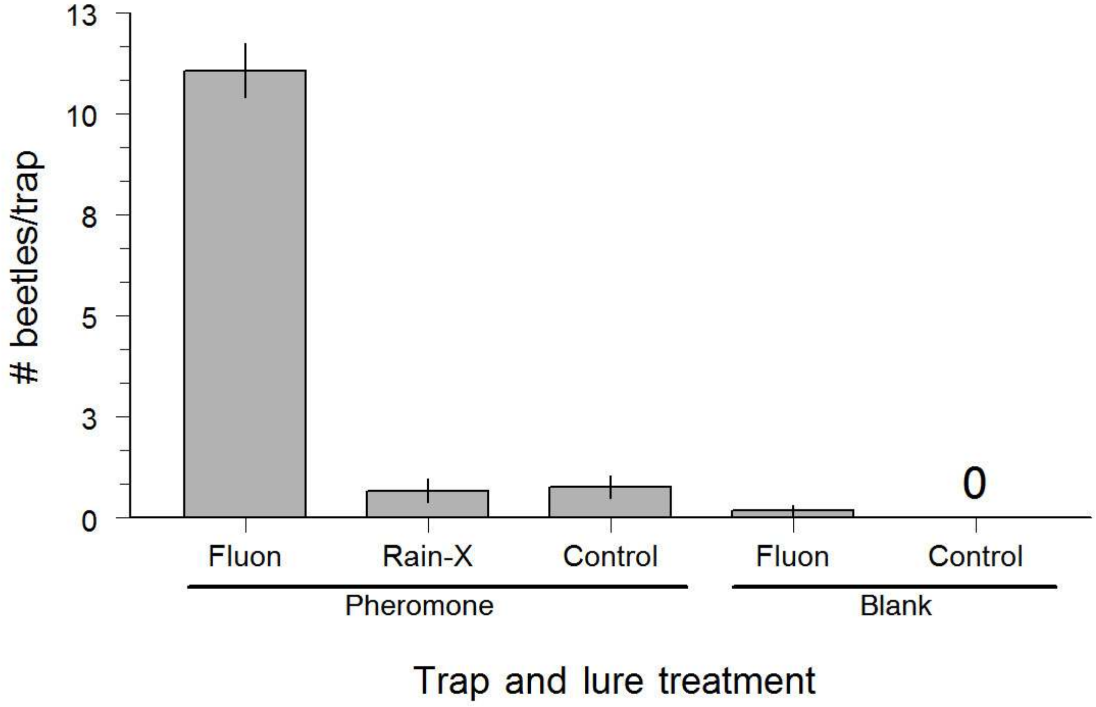
		Trap/lure treatment						
		Experiment 1					Experiment 2	
Tribe	Species	Fluon/ pheromone	Rain-X/ pheromone	Control/ pheromone	Fluon/ blank	Control/ blank	Fluon/ pheromone	Rain-X/ pheromone
Elaphidiini	*Parelaphidion incertum* (Newman)	1	-	-	-	-	-	-
Anaglyptini	*Cyrtophorus verrucosus* (Olivier)	2	-	-	-	-	-	-
Clytini	*Neoclytus a. acuminatus* (F.)	6	-	-	-	-	3	1
Clytini	*Neoclytus m. mucronatus* (F.)	61M, 68F, 4U	5M, 2F	7M, 5F	1F	-	25M, 29F	5M
Clytini	*Sarosesthes fulminans* (F.)	1	-	-	-	-	-	-
Clytini	*Xylotrechus colonus* (F.)	33M, 35F, 1U	1M, 5F	3M, 2F, 1U	1U	-	2M, 9F	1M
Tillomorphini	*Euderces picipes* (F.)	4	-	-	-	-	-	-

Table 5.1 (cont.)

		Trap/lure treatment						
		Experiment 1					Experiment 2	
Tribe	Species	Fluon/ pheromone	Rain-X/ pheromone	Control/ pheromone	Fluon/ blank	Control/ blank	Fluon/ pheromone	Rain-X/ pheromone
Total # of species (tribes)		12 (4)	2 (1)	2 (1)	2 (1)	0	6 (2)	3 (1)

Figure legends

Fig. 5.1 Mean (± SEM) number of beetles of the species *N. m. mucronatus* and *X. colonus* (combined) that were captured in Experiment 1 by traps that were conditioned with Fluon, Rain-X, or that were untreated (Control), and baited either with lures that were loaded with synthetic pheromone diluted in ethanol ("Pheromone") or lures containing only ethanol ("Blank"). Statistically significant differences between treatments (orthogonal contrasts: $F_{1,52} > 460$, $P < 0.0001$): Fluon/Pheromone versus Rain-X/Pheromone, Control/Pheromone, and Fluon/Blank. Treatment means not significantly different (orthogonal contrasts $P > 0.1$): Rain-X/Pheromone versus Control/Pheromone, Control/Pheromone versus Control/Blank, Fluon/Blank versus Control/Blank.



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Biography

I am a native of Illinois, born and raised on the southside of Chicago. I attended the University of Illinois between 1996 and 2000 majoring in Natural Resources and Environmental Science. After graduation I went on to be a volunteer for the Peace Corps, serving in Bulgaria. There I met my cat, Ray Tanzarian, learned a language 8 million people speak, and taught everyone in my office how to play freecell on the computer. After returning from Bulgaria I became a substitute teacher for a high school freshman biology course. This showed me that I do not want to EVER teach high school. I then worked in the education department of the Field Museum, where I drove the Soil Adventure Mobile out to school and taught elementary students about the wonders of soil. I then decided I should learn some more myself and went back to school to receive my M.S. in Forest Ecology and Management from Michigan Technological University in 2005, working with Dr. Andrew Storer. My research focused on chemical communication among two different species of bark beetles, *Dendroctonus simplex* and *Ips pini*. I also established an emerald ash borer detection survey for the state of Michigan while I was there. I returned to Urbana in January of 2005 and immediately felt at home wearing my orange t-shirts again. I made incredible friends, had great teaching experiences, and was taught by amazing faculty. I also managed to see Bruce Springsteen (solo and with E Street) 15 times during my five years here! He's the real Boss, and I always report to him. Now I am headed to Lansing, Michigan for a post doctoral position at Michigan State University. I will be working with Therese Poland researching the best trap and lure for monitoring cerambycid beetles. I am excited about this next chapter of my life but am sad to leave Urbana behind!