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The Effects of Clearcutting and Glyphosate Herbicide Use on Parasitic Wasps in Maine Forests

Kristopher J. Abell

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**THE EFFECTS OF CLEARCUTTING AND GLYPHOSATE
HERBICIDE USE ON PARASITIC WASPS IN MAINE FORESTS**

By

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B.S. University of North Carolina at Charlotte, 2000

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Ecology and Environmental Sciences)

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University of Maine

May, 2007

Advisory Committee:

Dr. Stephen A. Woods, Associate Professor of Entomology, Advisor

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An Abstract of the Thesis Presented
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Parasitic wasps (parasitoids) play an important role as natural enemies of insects and contribute substantially to world biodiversity (May, 1988), yet they have received relatively little attention outside of agricultural settings. Clear-cut harvesting and herbicide (glyphosate) application are frequent and widespread disturbances in Maine forests that drastically alter the local environment. Parasitoids are particularly susceptible to disturbance for several reasons: 1) they are vulnerable to small changes in environmental conditions, 2) they occupy a high trophic level, and 3) many are host specific. However, there may be potential benefits of disturbance such as increased food resources (floral nectaries) and increased abundance and diversity of hosts. This thesis discusses a study of several wasp taxonomic families within managed forest in western Maine.

To investigate the effects of clear-cut timber harvesting and glyphosate application on parasitoids this study compared five forest treatment types to mature forest in western Maine (Somerset county). The forest types consisted of young (3-5 years

since harvest) glyphosate treated clear-cuts, young untreated clear-cuts, old (14-21 years since harvest) glyphosate treated clear-cuts, old untreated clear-cuts, plantations (14-17 years since harvest, glyphosate treated, and planted with black spruce seedlings), and mature forest (more than 50 years old). Wasp communities were sampled using two malaise traps in each replicated forest treatment type throughout the summers of 2000 and 2001. To investigate the relationship between floral resources and parasitoid abundance in forest ecosystems, floral communities were sampled in each site along four 40m linear transects.

Although not always significant, parasitoid abundance at the family level tended to be greater in plantations and lower in young clear-cuts compared to mature forest. Braconidae abundance tended to be greater in old clear-cuts compared to mature forest, but equivalent for other families. At the family level, parasitoid abundance was not affected by glyphosate. The effect of forest type on parasitoid morphospecies was inconsistent in 2000 and 2001. The effect of floral communities on wasp family abundance was inconsistent between years, but overall appeared to have no effect. However, the abundance of the native perennial plant, bunchberry (*Cornus canadensis*), was correlated with the abundance of Ichneumonidae, Braconidae, and Pompilidae, as well as several morphospecies. Chalcidoidea abundance was correlated with the abundance of wild strawberry (*Fragaria* spp.). Taken together, the results of this study suggest that clear-cutting has an overall negative short-term effect on parasitoid abundance, but a positive (particularly when replanted with spruce) or neutral long-term effect. These effects appear to be unrelated to floral community, but specific floral

species may provide direct benefit or be indicators. Host availability, microclimate and habitat complexity are likely to be important factors to consider for future studies of this nature.

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Chapter 1

THE EFFECTS OF CLEAR-CUT TIMBER HARVESTING AND GLYPHOSATE APPLICATION ON HYMENOPTERAN PARASITIDS

Abstract

The short-term and long-term effects of clear-cutting, post-harvest glyphosate application and post-harvest replanting on parasitic and predatory Hymenoptera were studied. Six forest types were chosen for this study: 1) young glyphosate treated clear-cuts (4-5 years post harvest), 2) young untreated clear-cuts, 3) old glyphosate treated clear-cuts (14-15 years post harvest), 4) old untreated clear-cuts, 5) old glyphosate treated clear-cuts replanted with black spruce (plantations), and 6) mature forest (> 50 years) not treated with glyphosate. Parasitoids were identified to family and the four most common morphospecies (B, D, PA1, and PP15) in the superfamily Ichneumonoidea were tallied. In the first year of the study, glyphosate had no effect on parasitoid abundance at the family level. Ichneumonidae, Braconidae and Chalcidoidea abundance in plantations and young and old clear-cuts was not different compared to mature forest. However, Ichneumonidae and Braconidae abundance in young clear-cuts was lower than in plantations and old clear-cuts. Pompilidae abundance was the same in all forest types except plantations, where it was greater. Abundance of three morphospecies (PA1, PP15, and D) was not affected by glyphosate. Abundance of the same three morphs in plantations and old clear-cuts was not different compared to mature, but was lower in young clear-cuts compared to all other forest types. Abundance of the fourth morphospecies (B) in all forest types was no different from mature forest, except in old glyphosate treated clear-cuts, where it was greater. In the second year of the study,

Ichneumonidae, Chalcidoidea and Pompilidae abundance in young glyphosate treated clear-cuts, and old clear-cuts was not different compared to mature forest. Abundance of these three families was greater in plantations and lower in young untreated clear-cuts compared to mature forests. There was no effect of glyphosate on Braconidae abundance. Braconidae abundance was greater in old clear-cuts and plantations compared to mature forest and young clear-cuts. There was no effect of glyphosate on morphospecies in the second year of the study. The abundance of morphospecies B was greater in old clear-cuts compared to mature forest, as well as plantations. Morphospecies D abundance was greater in old clear-cuts and plantations compared to mature forest and young clear-cuts. There was no difference in abundance of two morphospecies (PA1 and PP15) among all forest types. Overall, the results of this study suggest that clear-cutting has an overall negative short-term effect on parasitoid abundance, but a positive (particularly in plantations) or neutral long-term effect.

Introduction

Forests cover approximately 90% of Maine, of which over 97% are managed for timber harvesting (Maine Forest Service, 2002). Understanding the effects that management has on such a large portion of the state is of critical importance for assessing ecosystem stability and addressing biodiversity concerns. In managed forests, a variety of techniques are employed to harvest timber. Of these techniques, clear-cutting has perhaps the greatest potential for disturbance and long-term effects on forest ecosystems. Clear-cutting causes abrupt changes in microclimatic conditions, existing food webs are disrupted, and new food webs are formed (Didham et al., 1996 and Barnes et al., 1998). Significant landscape level effects associated with clear-cutting include habitat loss, habitat fragmentation, and edge effects. In Maine, herbicide use and plantation establishment are often used in conjunction with clear-cutting to create stands of commercially desirable tree species (Maine Forest Service, 2002). These practices have the potential to further influence the effects of clear-cutting.

Herbicides are used post-harvest to facilitate the establishment of crop trees. In Maine, crop trees are typically coniferous species (e.g. spruce and fir) to be used as pulp in paper production. The most common silvicultural herbicide used in Maine today is glyphosate (McCormack, 1994 and Lough-Guisepepe et al., 2006). Typically applied aerially, glyphosate is most effective at killing herbaceous vegetation and deciduous trees. This releases coniferous trees from competition and allows them to grow quickly, thus minimizing the time required before the next harvest. However, such changes in the vegetation necessarily affect ecosystem structure and function and therefore can have a

cascading effect on forest fauna. These effects have been documented in numerous studies and several are reviewed below.

The effects of glyphosate on wildlife, both short-term and long-term, have been the focus of numerous studies. Fewer moose were found to use 1-2 year old clear-cuts treated with glyphosate compared to those not treated with glyphosate (Escholz et al., 1996). The same was not true for older clear-cuts. More moose were found to use 7-10 year old clear-cuts treated with glyphosate compared to those not treated with glyphosate. This was probably due to greater availability of winter browse and cover provided by the higher densities of conifers in the treated sites. Additionally, bird diversity and abundance were both found to be lower for up to three years in glyphosate treated clear-cuts compared to untreated clear-cuts (Santillo et al., 1989a). Within treated sites, skip areas (areas missed by herbicide) had greater abundance and diversity of birds as well as invertebrates. These skip areas may be important refugia for both vegetation and wildlife. Insectivorous small mammal abundance was found to be lower for three years in clear-cuts treated with glyphosate than in untreated clear-cuts (Santillo et al., 1989b). Herbivorous small mammal abundance was found to be lower for two years in clear-cuts treated with glyphosate than in untreated clear-cuts. No difference in omnivorous small mammal abundance was found in glyphosate treated versus untreated clear-cuts.

Very little research has been conducted to determine if the observed effects of glyphosate on vertebrates are similar for invertebrates. To date, only the Santillo et al. (1989b) study has investigated insect abundance in herbicide treated clear-cuts compared to untreated clear-cuts. Sweep net and pitfall sampling found 89% fewer herbivorous insects 1 year after herbicide application vs. untreated sites and 25% fewer 3 years after

herbicide application vs. untreated sites. No difference in predatory insect abundance was found. There are no other published studies to corroborate these findings. There have, however, been several studies on the effects of clear-cutting on insects, although they have largely focused on beetles. Carabid beetle diversity and abundance was found to be greater in clear-cuts compared to mature forest (Niemela et al., 1993; Beaudry et al., 1997). However, most were generalist species, many of the specialist species found in mature forest were not found in clear-cuts, even those in the latest stages of succession. In addition, there was indication of long-term detrimental effects of large-scale even-aged stands created by clear-cutting on even the more abundant generalist species.

The lack of studies on the effects of clear-cut harvesting and herbicide application on insects represents a large and important gap in our knowledge regarding the effects of forest management on this fauna. Insects play many keystone roles as herbivores, predators, prey, parasitoids, pollinators, and recyclers. Additionally, insects comprise the majority of the world's biodiversity, they account for more than half of all described taxa (May, 1988). Of all insects, parasitic wasps are one of the most understudied groups, yet are largely responsible for maintaining biodiversity and ecological balance (Lasalle and Gauld, 1993). Many parasitoids function as keystone species by regulating other insect populations. Numerous examples of this phenomenon have been documented in biological control programs. One of the most dramatic was the accidental introduction of the cassava mealybug to Africa. A single parasitic wasp species, *Epidinocarsis lopezi*, was released and effectively controlled the cassava mealybug (Norrgard, 1988). Purple scale, alfalfa blotch leafminer, and the walnut aphid are just a few other examples of pest insects successfully controlled by parasitoids in agricultural biological control programs

(Debach and Rosen, 1990). Such regulation is beneficial both economically and ecologically by decreasing crop loss and pesticide use respectively.

As keystone species, parasitoids also play an important role in promoting and maintaining biodiversity. By regulating dominant competitors, parasitoids may prevent the competitive exclusion of other insect species. In addition to promoting diversity, parasitoids themselves are a diverse group. May (1988) found that a typical herbivorous insect is host to 5 to 10 parasitoid species. Add to that their respective hyperparasitoids, and parasitoids may constitute a large portion of the world's biodiversity. Since there is no way to predict what insects will become pests in the future, this vast diversity of parasitoids represents an important resource to conserve for future biological control needs.

Unfortunately, parasitoids are particularly vulnerable to local extinction. Many parasitoid species regulate host populations so well that they occur in very low numbers themselves. There is evidence that this is the rule rather than the exception. A canopy fogging study in Borneo found that out of 1455 Chalcidoidea, 739 were separate species and 437 of those were represented by only one individual (Stork, 1988). Such rarity may greatly increase extinction risk for parasitoids. A paper by Shaw and Hochberg (2001) suggested that parasitoids are especially susceptible to local extinction for three reasons: 1) at low population densities male-dominated sex ratios are likely to occur, due to their haplo-diploid reproductive system, 2) most parasitoids are extremely host specific, and 3) parasitoids are dependant on specific climatic conditions. Dyer and Landis (1996) found that adult longevity of an Ichneumonid parasitoid decreased by almost two thirds when

temperature increased 8 °C (from 20 °C to 28 °C). Mendel (1988) found that longevity of all three bark beetle parasitoids in his study decreased as temperature increased.

To date, only one disturbance related ecological field study of parasitoids in forest ecosystems has been published (Lewis and Whitfield, 1999). The study investigated the effects of varying levels of forest disturbance on the parasitoid wasp family Braconidae. The study found that one year after a disturbance both diversity and abundance of Braconidae were greater in highly disturbed sites compared to moderately disturbed and undisturbed sites. The study attributed this to greater parasitoid host range availability resulting from the great diversity of colonizing early succession plants. However, many of the Braconidae species present before the disturbance were absent after the disturbance. This is important, because although diversity increased at the local level, it decreased at the landscape level. Several species of parasitoids were eliminated because of unfavorable microclimate or loss of hosts resulting from the disturbance. The forest disturbance in this study consisted of partial cutting and selection harvests, which may not be comparable to clear-cut harvesting. In addition, the long-term effects of these disturbances were not investigated. Therefore, it is unknown if wasp species present before the disturbance are able to reestablish over time. Furthermore, none of the sites in the study were treated with herbicide. Whether the observed increase of Braconidae abundance and diversity in disturbed sites would hold if treated with herbicide is unknown.

Given the importance of parasitic wasps to ecosystem stability, their potential as biological control agents, their substantial diversity, their sensitivity to microclimate, their rarity, and the fact that the vast majority of Maine is managed forest, it is essential

to document the effects of clear-cutting and herbicide application on parasitic wasps. The objectives of this study were 1) to determine the short-term and long-term effects of clear-cut harvesting on parasitic wasp abundance and community composition, 2) to determine the effects of plantations on parasitic wasp abundance and community composition, 3) to determine baseline parasitic wasp abundance and community composition in mature forests, and 4) to determine the short-term and long-term effects of glyphosate application on parasitic wasp abundance and community composition.

Materials and Methods

Study Area

The study area consisted of sites chosen within four adjacent townships (Mayfield, Moscow, Bald Mountain, and Caratunk) in Somerset County, Maine in order to minimize geographic and environmental variation. Eighteen sites representing six different standard silvicultural treatment types were initially chosen for the study based on land use history records kept by the landowner, Plum Creek Timber Company. The six forest types were as follows: 1) young glyphosate treated clear-cuts (4-5 years post harvest) (YH), 2) young untreated clear-cuts (Y), 3) old glyphosate treated clear-cuts (14-15 years post harvest) (OH), 4) old untreated clear-cuts (O), 5) old treated clear-cuts replanted with black spruce, plantations (P), and 6) mature forest (> 50 years) not treated with herbicide (M). The size of the study sites ranged from 0.2-2.0 ha. Elevation of study sites was 368 to 485 meters above sea level. Young clear-cuts, both treated and untreated, were almost completely dominated by forbs and grasses. Old untreated clear-cuts were composed primarily of randomly distributed trees, both coniferous and

deciduous of varying age, with areas of open and closed canopy. Old treated clear-cuts were composed primarily of randomly distributed coniferous trees of varying age with areas of open and closed canopy. Plantations were composed of evenly distributed spruce of the same age with an open canopy. Mature forests were composed of trees (most > 50 years old) both deciduous and coniferous with a closed canopy, except for some tree fall gaps. Refer to Table 1.1 for a complete list of sites with their associated treatments, harvest dates, and herbicide dates.

After a visual inspection of the sites, it was determined that OH treatment sites displayed two distinct types of vegetation communities. One type had a high density of conifers with a closed canopy, the other type had a lower density of conifers in a patchy distribution resulting in large areas of open canopy. One additional OH site was added to the study resulting in two of each of the low conifer density and high conifer density within the OH treatment. An additional O site was added for balance. Therefore, a total of 20 sites were used for the initiation of the study in 2000 (Table 1). Following vegetation data analysis from 2000 (Georgitis, 2001) it was confirmed that there were in fact two distinctly different vegetation communities within the O and OH treatment sites. Based on visual inspection of additional old clear-cuts in the area, it was determined that low conifer density in a patchy distribution was the most common old clear-cut vegetation community. In order to increase the statistical power of the experiment the less common high conifer density sites were dropped (sites 8, 11, 19, and 20) and two new low conifer density sites (21 and 22) were added for the 2001 field season. Additionally, site 9 displayed evidence of a recent fire event, subsequently it was dropped

from the study and replaced with a new site (site 23). As a result of these changes, in 2001 there were three sites for each treatment group for a total of 18 sites.

Wasp Sampling

Several trap types were used to estimate wasp abundance and diversity. In each site malaise traps, flight intercept traps, and pitfalls were used. Malaise traps consisted of four 96cm tall x 46cm wide panels of clear plastic sewn together lengthwise at 90° to one another creating four perpendicular panels. The panels were supported by a frame of EMT conduit. The frame consisted of a vertical 1m length of conduit topped with an electrical junction box from which four 50cm sections of conduit were attached horizontally and perpendicular to one another creating a “+” shape when viewed from above. These horizontal sections of conduit supported the plastic panels laterally. An additional 0.6m section of conduit attached vertically to the top of the junction box. This section of conduit supported a tent of white mesh over the plastic panels that acted as a funnel into a clear plastic collecting jar attached at the top. The collection jar was partially filled with propylene glycol to preserve captured insects until they were collected. Two malaise traps were placed in each site roughly equidistant from each other and the boundary of each site to avoid edge effects.

In order to sample wasps that may be present above 1.3m, two 15m rigid conduit towers were erected in each site. Five flight intercept traps were suspended from the towers at 1, 4.5, 8, 11.5, and 15m above the ground. In mature sites where the canopy exceeded 15m, 25m towers were erected with additional flight intercept traps located at 18.5, 22, and 25m above the ground. Flight intercept traps consisted of two 23cm x 30cm panes of clear Plexiglas® bisecting each other lengthwise at 90°. A 20cm diameter

Table 1.1. Study sites located in Somerset Co., ME and their associated forest management types. *Harvest year for site 19 was unknown, but was chosen based on its similarity to sites 8 and 9.

Site Number	Year Included in Study	Treatment	Clear-cut Year	Herbicide Year
1	Both	Young Herbicide	1995	1997
2	Both	Young	1995	--
3	Both	Young	1997	--
4	Both	Young Herbicide	1996	1998
5	Both	Young	1996	--
6	Both	Young Herbicide	1996	1997
7	Both	Old Herbicide	1986	1989
8	2000	Old	1985	--
9	2000	Old	1986	--
10	Both	Old Herbicide	1986	1993
11	2000	Old Herbicide	1985	1987
12	Both	Old	1985	
13	Both	Plantation	1983	1986
14	Both	Plantation	1986	1989
15	Both	Plantation	1986	1990
16	Both	Mature	--	--
17	Both	Mature	--	--
18	Both	Mature	--	--
19	2000	Old	*	--
20	2000	Old Herbicide	1979	1984
21	2001	Old Herbicide	1986	1989
22	2001	Old	1983	--
23	2001	Old	1980	--

opaque plastic funnel terminating in an opaque plastic collecting cup was attached to either end of the Plexiglas® panes. A piece of Hot Shot No-Pest Strip® (2,2 – Dichlorovinyl dimethyl phosphate) was placed in each collection cup as a killing agent to minimize escape (some undoubtedly escaped). Two holes were drilled into the bottom cup to allow water to escape and lined with hosiery to prevent insect escape. The towers were located approximately equidistant from one another and the boundary of each site to avoid edge effects.

In order to sample wasps foraging on the substrate (particularly wingless Hymenoptera), pitfall traps were employed. Four pitfall traps were placed 20 m apart roughly 14 m from center of each site. Pitfall traps were constructed from 20oz. plastic soda bottles. The top third of the bottle was removed and inverted to act as a funnel and fit into the bottom two thirds of the bottle where a collection cup was located. Approximately 30 ml of propylene glycol was added to the collection cup as a preservative. The entire assembly was buried flush with the ground and care was taken to minimize disturbance. Squares of tin (13 cm) were suspended 5cm above each pitfall by metal spikes to act as a rain shield to prevent trap flooding. In addition, holes were drilled into the bottom of each trap for drainage.

All traps were set and left in place for 14 days, after which the samples were collected and the traps reset. A 14 day interval was considered the optimal compromise to balance sample decomposition and the costs associated with collecting the samples. This was done continuously beginning 1 June through 24 August in 2000 and from 21 May through 30 August in 2001. Samples were rinsed and preserved in 70% ethanol. Wasps were sorted from samples and identified to family using keys by Borror,

Triplehorn, and Johnson (1989). Genus and species identifications of select Braconidae and Ichneumonidae specimens were conducted by John Luhman at the Minnesota Department of Agriculture. Reference specimens were stored in the Insectary at the University of Maine.

Data Analysis

The superfamily Chalcidoidea and the families Ichneumonidae, Braconidae, and Pompilidae were the most common taxa sampled in both 2000 and 2001. The abundance of individuals in each family was pooled for each site by year for analysis of treatment effects. Winged wasps were depauperate in samples collected from pitfalls and flight intercept traps and were excluded from analyses. All wasp abundance data were transformed by adding a constant value and taking the logarithm (base 10) and weighted by the inverse of the variance within treatments in order to meet the assumptions of normality and correct for potential differences in variance. The unit of replication was site.

In order to simplify the interpretation of statistical analyses, wasp families that were determined to respond similarly to treatments were grouped. Groupings were determined by performing a three-way ANOVA (forest type, herbicide treatment, and wasp family) (PROC GLM, SAS Institute 1996) to detect significant wasp family interactions (family x forest type, family x herbicide treatment, or family x forest type x herbicide treatment). If any interaction involving taxa was significant ($P < 0.05$), then a backward stepwise approach was used in which the family with the highest contribution to the overall sum of squares was removed one at a time until the interactions were no

longer significant. The abundance estimates of the resulting family groups were subsequently averaged by site and each group or individual family analyzed separately.

After appropriate groupings were determined, an ANOVA was performed on each group (with removal of non-significant interactions) and, if significant, linear contrasts were then used to determine differences in treatment effects on wasp abundance (Toothaker, 1991).

The family level analyses described above were also used to analyze treatment effects on the four most common morphospecies in the superfamily Ichneumonoidea.

Results

In both 2000 and 2001, the superfamily Chalcidoidea and the families Ichneumonidae and Braconidae were well represented in traps. In addition, a substantial number of predatory spider wasps (family Pompilidae) were collected, and so were included in analyses.

Effects of Clear-cutting and Glyphosate Application on Abundance of Parasitic and Predatory Wasp Families

In 2000, there was a wasp family abundance x forest type interaction ($F_{9,45} = 3.42$, $P = 0.0028$). No significant family groupings were found, therefore families were analyzed separately. Abundance of families was not affected by glyphosate in either young or old clear-cuts, therefore, glyphosate treated sites were pooled with untreated sites within each age class (young and old). Ichneumonidae and Braconidae abundance in young clear-cuts, old clear-cuts and plantations was equivalent to mature forest, but abundance in old clear-cuts and plantations was greater than in young clear-cuts.

Pompilidae abundance in young and old clear-cuts was equivalent to mature forest, and was higher in plantations compared to all other forest types. There was no difference in Chalcidoidea abundance between forest types (Fig. 1.1).

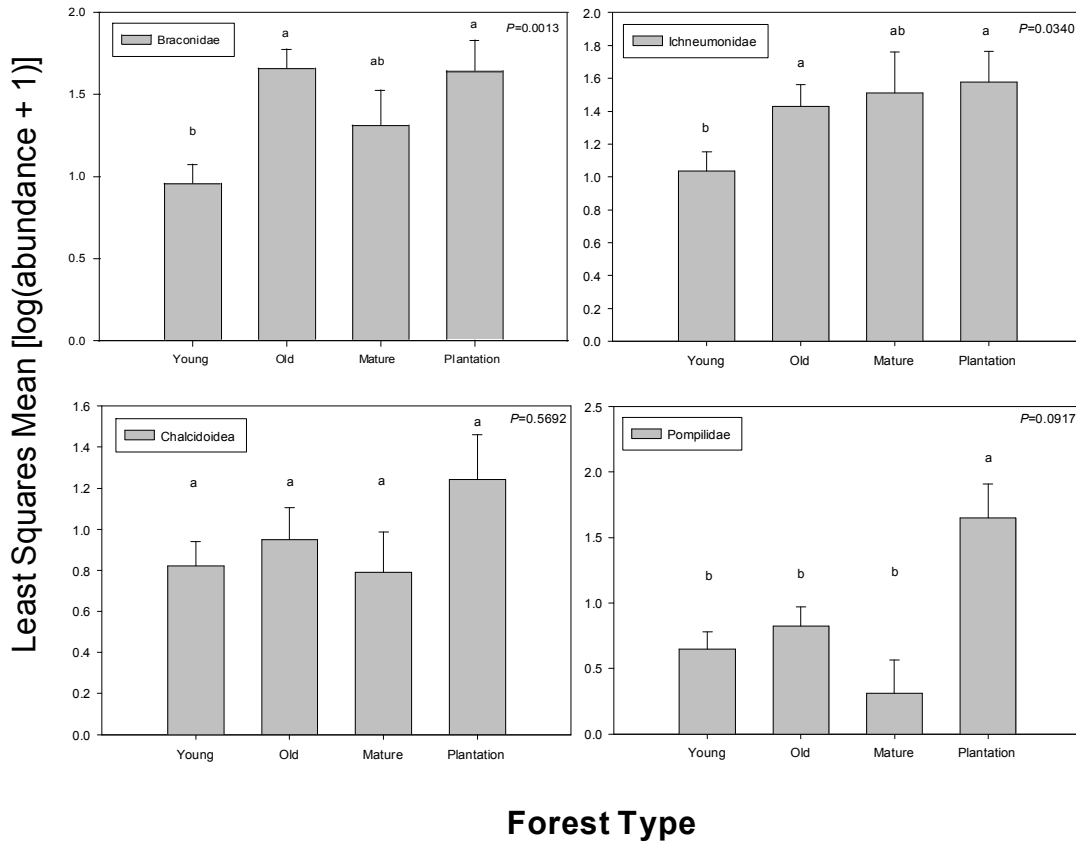


Figure 1.1. Least squares mean (\pm SE) abundance of Ichneumonidae, Braconidae, Chalcidoidea and Pompilidae in four forest types [young clear-cuts (4-5 years post harvest), old clear-cuts (14-15 years post harvest), mature forest (> 50 years old), and glyphosate treated clear-cuts replanted with black spruce (plantations)] in 2000. There was no effect of glyphosate application in young and old clear-cuts, therefore glyphosate treated sites were pooled with untreated sites. Letters above bars (a, b) indicate significant differences ($P < 0.05$) between forest types.

In 2001, there was a wasp family abundance x forest type interaction ($F_{9,39} = 2.90$, $P = 0.0100$). The abundance of Chalcidoidea, Ichneumonidae and Pompilidae was similar, so these families were grouped. There was a significant effect of glyphosate on this group ($F_{1,12} = 5.27$, $P = 0.0405$), so these treatments were analyzed and presented separately. Although not always significant, the general pattern was similar to that seen in 2000. Abundance for this group was highest in plantations and equivalent in all other forest types except young untreated sites, which was significantly lower than mature forests and old clear-cuts (Fig. 1.2). Glyphosate did not have a significant effect on Braconidae abundance in either young or old clear-cuts, and so was pooled within age class. Braconidae abundance was greatest in old clear-cuts and plantations, and lowest in mature forests and young clear-cuts (Fig. 1.2).

Effects of Clear-cutting and Glyphosate on Ichneumonidae and Braconidae

Morphospecies Abundance

Ichneumonidae morphospecies PP15 and PA1 were identified as *Ichneumon clasma* Carlson and *Lissonota sp.* by Dr. John Luhman at the Minnesota Department of Agriculture. Species identifications for Braconidae morphospecies B and D were not obtained.

In 2000, there was a morphospecies abundance by forest type interaction ($F_{9,45} = 3.43$, $P = 0.0027$). PP15, PA1, and D abundance were similar across forest types and were therefore grouped (group 1), while morphospecies B was analyzed separately. There was no effect of glyphosate on group 1, therefore glyphosate treated and untreated sites were pooled within each age class. There was an effect of glyphosate on morphospecies B ($F_{1,14} = 4.72$, $P = 0.0475$). Group 1 wasp abundance was greatest in old

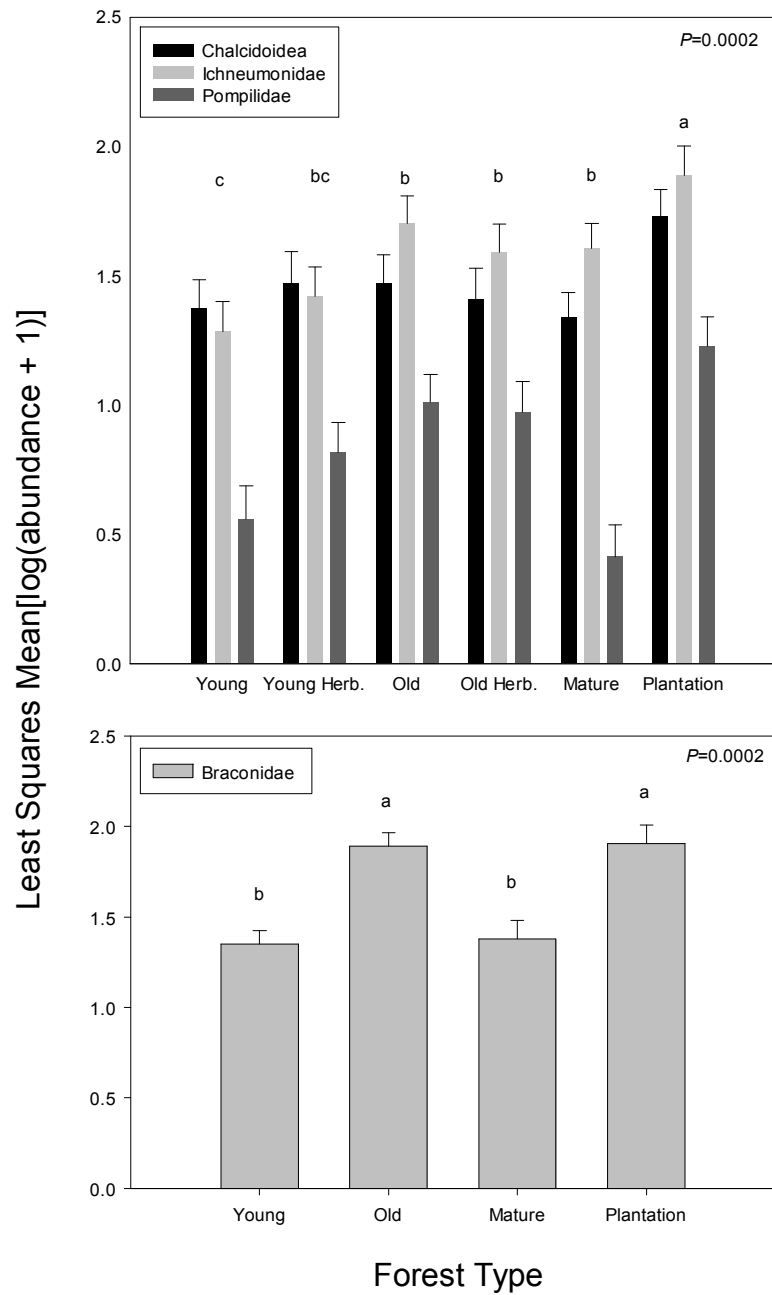


Figure 1.2. Least squares mean (\pm SE) abundance of Ichneumonidae, Braconidae, Chalcidoidea and Pompilidae in forest types [young untreated clear-cuts (4-5 years post harvest), young glyphosate treated clear-cuts, old untreated clear-cuts (14-15 years post harvest), old glyphosate treated clear-cuts, mature forest ($>$ 50 years), and old treated clear-cuts replanted with black spruce (plantations)] in 2001. Chalcidoidea, Ichneumonidae and Pompilidae abundance was similar among forest types and so these families were pooled to increase the statistical power in determining significant differences between forest types. Families are shown separately to be more informative. Braconidae abundance was not affected by glyphosate application in young and old clear-cuts, therefore herbicide treated sites were pooled with untreated sites. Letters above bars (a-c) indicate significant differences ($P < 0.05$) between forest types.

clear-cuts, mature forests, and plantations, and low in young clear-cuts (Fig. 1.3).

Morphospecies B abundance was greatest in old glyphosate treated clear-cuts, low in old untreated treated clear-cuts and young clear-cuts, and absent in plantations and mature forests (Fig. 1.3).

In 2001, there was a morphospecies abundance x forest type interaction ($F_{9,39} = 9.86, P < 0.0001$). Morphospecies PA1 and PP15 relative abundance was consistent across forest types and were therefore grouped (group 1). None of the four morphospecies were affected by glyphosate in either young or old clear-cuts, therefore, glyphosate treated sites were pooled with untreated sites within each age class. There was no effect of forest type on group 1 morphospecies abundance (Fig. 1.4). Morph B abundance was greatest in old clear-cuts, intermediate in young clear-cuts, and low in mature forests and plantations (Fig. 1.4). Morph D abundance was higher in old clear-cuts and plantations, compared to mature forests and young clear-cuts (Fig. 1.4).

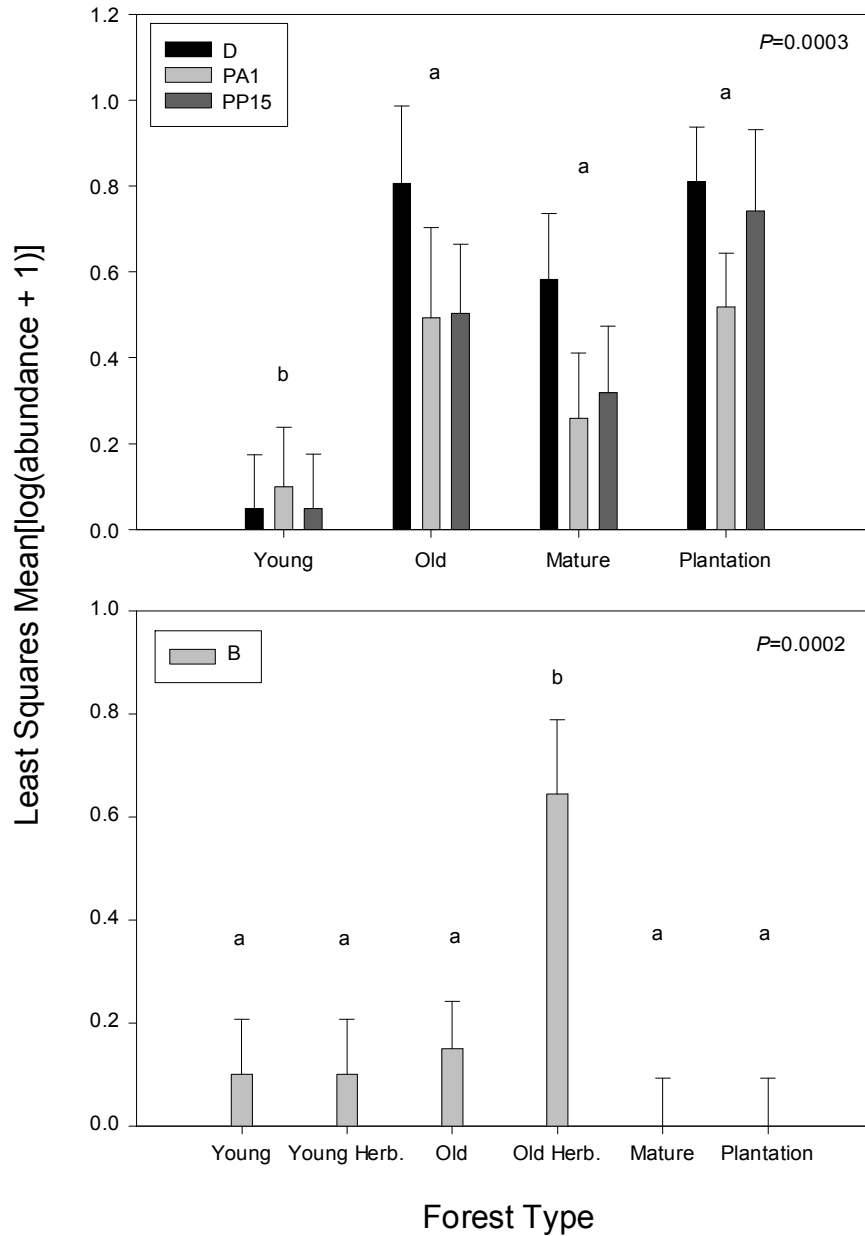


Figure 1.3. Least squares mean (\pm SE) abundance of morphospecies D (Braconidae), PA1 (*Lissonota* sp.), PP15 (*Ichneumon clasma* Carlson), and B (Braconidae) in forest types [young untreated clear-cuts (4-5 years post harvest), young glyphosate treated clear-cuts, old untreated clear-cuts (14-15 years post harvest), old glyphosate treated clear-cuts, mature forest (> 50 years), and old glyphosate treated clear-cuts replanted with black spruce (plantations)] in 2000. Abundance of all morphospecies, except B, was similar among forest types. These morphospecies were subsequently pooled to increase the statistical power in determining significant differences between forest types. Morphospecies are shown separately to be more informative. Letters above bars (a, b) indicate significant differences ($P < 0.05$) between forest types.

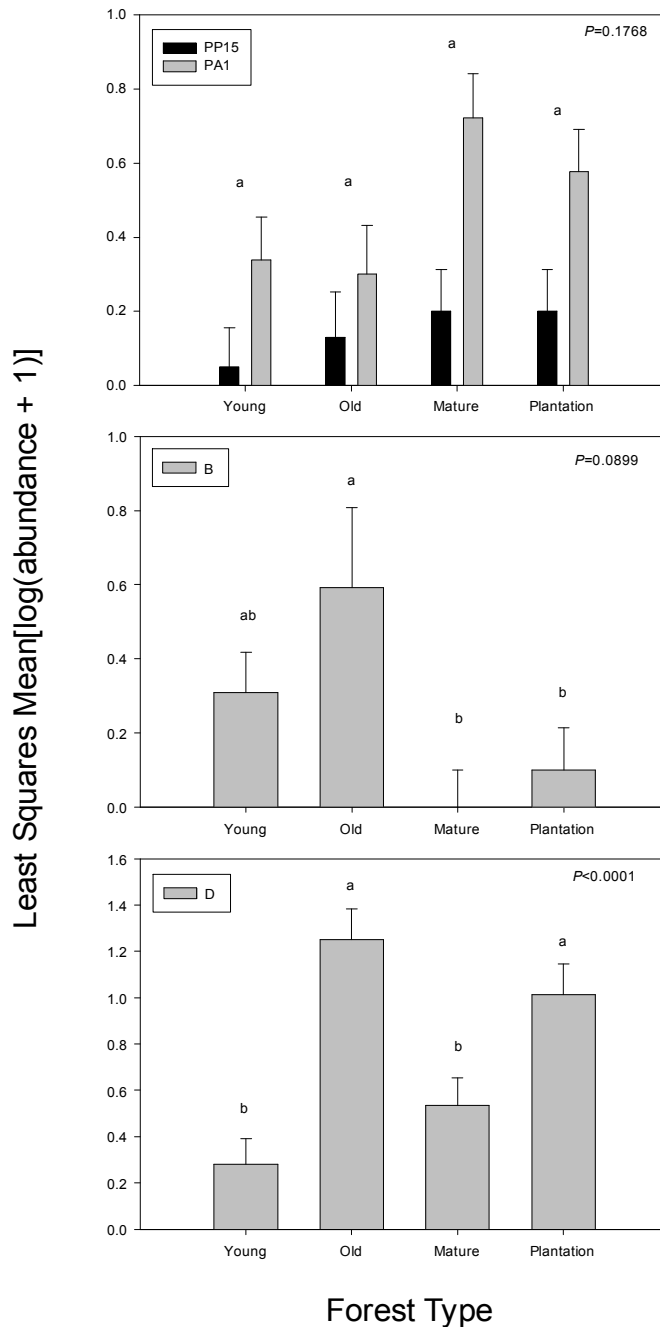


Figure 1.4. Least squares mean (\pm SE) abundance of morphospecies B (Braconidae), D (Braconidae), PA1 (*Lissonota* sp.), and PP15 (*Ichneumon clasma* Carlson) in forest types [young clear-cuts (4-5 years post harvest), old clear-cuts (14-15 years post harvest), mature forest (> 50 years), and old glyphosate treated clear-cuts replanted with black spruce (plantations)] in 2001. Morphospecies PP15 and PA1 abundance was similar among forest types and so they were pooled to increase the statistical power in determining significant differences between forest types. Morphospecies are shown separately to be more informative. Letters above bars (a, b) indicate significant differences ($P < 0.05$) between forest types.

Discussion

Effects of clear-cut timber harvesting on Parasitic Hymenoptera Abundance

For a number of reasons, it was difficult to determine the root causal effects of the observed differences in parasitoid abundance among forest types seen in this study. Probably the single greatest reason for this is the lack of data on parasitoid host abundance, without which it cannot be definitively determined if a change in parasitoid abundance is due to a change in host abundance or to some other factor(s) (floral resources, microclimate, habitat structure) mediated by clear-cutting. Even if such data were collected, however, the host range for many parasitoids is unknown, therefore any correlation (or lack of) between parasitoid abundance and host abundance may be spurious. Further, parasitoid species identification requires taxonomic specialists and even then is difficult and time consuming. Many other reasons common to most field studies, such as natural population fluctuation, trap placement, patchiness, site to site variation, and the small number of replicates both in space and time likely also contributed to the difficulty in drawing conclusions in this study. Nevertheless, a few general patterns emerged from this study and reasonable explanations for these patterns can be inferred based on general knowledge of parasitoid biology.

The primary objective of this study was to determine the effects that clear-cut harvesting and glyphosate application have on parasitoid abundance in comparison with mature forests, which represent relatively undisturbed natural habitat. It was hypothesized that young clear-cuts may in fact have greater relative parasitoid abundance given that clear-cuts are quickly colonized by a diverse number of flowering plants at high densities (Messier and Kimmins, 1991; De Grandpre and Bergeron, 1997; Roberts

and Zhu, 2002; Schumann et al, 2003) and agricultural studies have shown a strong relationship between parasitoid abundance and floral abundance and diversity (Leius, 1961b and 1967a; Foster and Ruesink, 1984; Bugg, 1989; Stephens et al, 1998; Baggen et al, 1999; English-Loeb, 2003; Bostanian et al, 2004). Given the results of this study, this hypothesis appears to be false, because parasitoid abundance tended to be equivalent or sometimes lower in young clear-cuts compared to mature forests. This in spite of the fact that mature forests had virtually no floral resources (see Appendix). In mature forests, parasitoids may utilize floral resources outside of the forest, along forest margins, extra-floral nectaries, or as Hougardy and Gregoire (2000) suggested, aphid honeydew within the forest.

In contrast to young clear-cuts, old clear-cuts and particularly plantations often had greater parasitoid abundance compared to mature forests. Further, plantations and old clear-cuts almost always had greater parasitoid abundance compared to young clear-cuts, despite having similar floral densities (see Appendix). Taken together, the results of this study seem to support the conclusion that, in general, clear-cutting has a negative short-term effect, but a positive long-term effect (particularly when combined with replanting) on parasitoid abundance. In addition, floral density does not appear to be a limiting factor for parasitoid abundance in forest ecosystems. It is possible that floral community composition or individual floral species impact parasitoid abundance, but this also appears to be false (see chapter 2). There are several possible explanations to support these conclusions.

First, a number of studies have shown that parasitoid longevity and fecundity are strongly affected by temperature and humidity (Gross, 1988; Mendel, 1988; and Dyer and

Landis, 1996). Conditions in young clear-cuts are likely to be harsher than in old clear-cuts and therefore may exclude many parasitoids species, particularly forest species that were present prior to clear-cutting. Second, because of their small size, most parasitoids are poor dispersers. This means that it may take a number of years for appropriate parasitoid species to disperse into clear-cuts if they were not present beforehand, particularly if a clear-cut is surrounded by uncut forest. These two factors are mediated in old clear-cuts and plantations, which may help to explain why these forest types had greater parasitoid abundance. Trees may have grown large enough to moderate microclimate in favor of parasitoids, yet the canopy has not yet closed, so there is an abundant flowering understory. This intermediate type of forest likely provides the broadest spectrum of microclimatic and structural complexity, therefore supporting the greatest number of parasitoids. Indeed, several studies have demonstrated that parasitoids respond to landscape structure, with some taxa showing preference for open habitat and other taxa for sheltered habitat (Roland et al, 1997; Roland and Taylor, 1997). The combination of open area and shelter area (14 year old trees) may provide for a greater number and diversity of parasitoids both in terms of microclimate and host availability. Additionally, non-forest parasitoid species have had more than 14 years to disperse into plantations and old clear-cuts. However, these hypotheses are particularly difficult to address because (as seen in this study) the increase in parasitoid abundance may not be great enough to result in a statistically significant difference, particularly when compared to mature forests. While this explanation can only be speculative in this study, it is clear nevertheless that at the family level, there are more parasitoids in old clear-cuts and plantations compared to young clear-cuts.

Parasitoid morphospecies analysis yielded inconsistent results, most likely due to the rarity of individual species. More intensive sampling, focused sampling, or sampling of known host(s) should be done in order to draw any conclusions about individual parasitoid species in this type of study.

Finally, it should be noted that nothing definitive can be inferred about the parasitoid species level community assemblage present in each forest type. It is possible that the high abundances in plantations and old clear-cuts represent different species assemblages from each other or compared to mature forests or young clear-cuts. This is an important caveat, because greater abundance may not mean greater diversity, which can have important implications for forest stand and landscape level management.

Effects of Glyphosate Application on Parasitic Hymenoptera Abundance

An effect of glyphosate application on the abundance of parasitic Hymenoptera families and morphospecies was not found in this study. As noted above, this result does not imply that glyphosate has no effect on the parasitoid community. It is entirely possible that parasitoid diversity was quite different in herbicide treated versus untreated sites.

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Chapter 2

THE EFFECTS OF FLORAL COMMUNITIES ASSOCIATED WITH CLEAR-CUTTING AND GLYPHOSATE APPLICATION ON HYMENOPTERAN PARASITOIDS

Abstract

The first objective of this study was to characterize the short and long-term effects of clear-cutting, tree replanting and glyphosate application on flowering plant species composition. The second objective was to determine if parasitoid and predatory Hymenoptera abundance respond to differences in flowering plant species composition brought about by clear-cutting, tree replanting and glyphosate application. The final objective was to determine if there was a relationship between individual flowering plant species and parasitoid and predatory wasp abundance. Six forest types were chosen for this study as follows: 1) young glyphosate treated clear-cuts (4-5 years post harvest), 2) young untreated clear-cuts, 3) old glyphosate treated clear-cuts (14-15 years post harvest), 4) old untreated clear-cuts, 5) old glyphosate treated clear-cuts replanted with black spruce (plantations), and 6) mature forest (> 50 years) not treated with glyphosate. In the first year of the study, NMS (non-metric multidimensional scaling) ordination indicated that irrespective of herbicide application, 1) all of the plantations and all but one young clear-cut had similar forb species compositions, 2) mature forest stands had similar forb species compositions to one another, and 3) old clear-cuts displayed high variation in forb community composition. There was no correlation between the three primary ordination axes and any of the parasitoid families or morphospecies. Step-wise regression indicated a potential positive relationship between bunchberry (*C. canadensis*)

density and Braconidae, *Ichneumon clasma* Carlson, morphospecies B, and morphospecies D abundance, as well as between wild strawberry (*Fragaria* spp.) density and Chalcidoidea abundance. In the second year of the study, NMS ordination indicated that irrespective of herbicide application, 1) plantations and all but one young clear-cut had similar forb species composition, 2) old clear-cuts had variable forb species composition, and 3) two mature forests had similar forb species composition, but a third was very different. There was a strong correlation between Chalcidoidea abundance and axis one (accounted for 63.4% of variation) of the NMS ordination ($r = -0.506$). The first axis was most strongly correlated with the following forb species: pearly everlasting (*Anaphalis margaritacea*) ($r = -0.726$), wild strawberry ($r = -0.614$), field hawkweed (*Hieracium caespitosum*) ($r = -0.716$), common wood sorrel (*Oxalis acetosella*) ($r = 0.647$), and goldenrod (*Solidago* spp.) ($r = -0.793$). There was no correlation between the second NMS axis (accounted for 28.2%) and any of the parasitoid families or morphospecies. Step-wise regression indicated a potential positive relationship between Ichneumonidae, Braconidae and morphospecies D abundance and bunchberry ($P = 0.0286$, $P = 0.0017$, and $P = 0.0130$), as well as between Chalcidoidea abundance and wild strawberry ($P = 0.0018$).

Introduction

A carbohydrate source is essential for most adult parasitoid survival (Bugg et al, 1989). The principal component of most parasitoids' energy budget comes from floral nectar and pollen, although some species may survive on extrafloral nectar (Bugg et al, 1989) or aphid honeydew (Idris and Grafius, 1995 and Hougaard and Gregoire, 2000;). Numerous controlled studies have demonstrated that the lack of a carbohydrate source significantly decreases both parasitoid survival and fecundity (Leius 1961a and b, Mendel 1988).

The importance of floral resources for parasitoids has also been demonstrated in field studies. Leius (1967a) found that parasitism of tent caterpillar pupae was 18 times greater and egg parasitism 4 times greater in orchards with rich wildflower undergrowth. The black cut-worm parasitoid *Meteorus rubens* attacked significantly more hosts and had significantly higher parasitism rates in corn fields with flowering weeds compared to those without flowering weeds (Foster and Ruesink, 1984). Bostanian et al. (2004) found significantly more parasitoids and significantly less pest damage in apple orchards seeded with flowering plants. In an extensive review, Bugg and Waddington (1994) concluded that flowering plants attract beneficial arthropods, including parasitoids. However, not all flowers are equally beneficial for parasitoids. Leius (1962) found that pollen from two flower species significantly increased both longevity and fecundity of the female parasitoid *Scambus buolianae*, while other flower species only increased longevity or fecundity individually, and some had no effect at all. Unlike many other nectar feeding insects, parasitoids do not have mouthparts specialized for nectar feeding. Therefore, parasitoids are restricted to feeding on flowers that possess nectaries that are compatible

with the size and shape of their head and mouth parts (Patt et al., 1996). Among the floral species that are morphologically compatible, umbelliferous flowers are preferred by most parasitoid species studied over other flower types (Leius, 1960; Leius, 1967b; Jervis et al, 1992 and 1993; and Patt et al, 1996).

Clear-cuts are quickly colonized by early successional herbaceous vegetation. This vegetation provides an abundance of new floral resources resulting in a substantial increase in floral nectaries at the local level. This increase may potentially positively impact the diversity and carrying capacity of parasitic wasps. However, any benefits resulting from increased floral resources may be lost with the application of glyphosate. In the short-term, glyphosate may simply kill newly established vegetation thereby eliminating or reducing floral resources for one or more years. In the long-term, glyphosate may alter the floral community in a manner that reduces the abundance of compatible floral species.

The short-term effects of glyphosate applications on plant communities in clear-cuts have been fairly well documented. In Maine, large numbers of herbaceous plants were killed and vegetation cover was greatly reduced in clear-cuts after spraying with glyphosate (Freedman et al, 1993). However, there was little change in species diversity or richness. Herbaceous vegetation quickly recovered in the first and second post-spray seasons from seed banks and wind blown seed, but several species never recovered to pre-spray levels. This lack of recovery occurred for relatively few species and it was unclear if this resulted in significant ecosystem effects. A different study in Maine found no difference in flowering plant abundance between treated and untreated clear-cuts in the first post-spray season (Vreeland, 1998). In contrast to abundance, total cover,

density, and height of flowering plants and grasses in clear-cuts were found to be lower for up to three years after glyphosate application compared to untreated clear-cuts (Santillo et al, 1989a and 1989b). Similarly, flowering plant species composition in three to five year old clear-cuts was different in sites treated with glyphosate compared to untreated sites (Georgitis 2001). In general, short-term studies indicate that vegetation abundance quickly recovers following glyphosate application, but density, cover, and species composition are affected for up to five years after application.

Glyphosate application has the long-term effect of increasing conifer density, but the long-term effect on the rest of the vegetation community is less well known. Significantly greater abundance of flowering plants was found in treated vs. untreated 7-10 year-old clear-cuts (Vreeland, 1998). Alternately, Georgitis (2001) did not detect differences in treated and untreated clearcuts that were 10-15 years old. These are the only two studies that I am aware of that followed treatment differences beyond seven years.

Because of the many reasons discussed about, both the short- and long-term effects of glyphosate applications on floral communities in forest ecosystems are likely to impact parasitic wasp communities. Any potential benefit realized from the increase in floral resources in clear-cuts may be eliminated by the use of glyphosate, especially in the first several years after application. The objectives of this experiment were to 1) characterize the differences in forb community composition between young clear-cuts, old clear-cuts, plantations and mature forest, 2) characterize the differences in forb

community composition between glyphosate treated and untreated clear-cuts, both young and old, and 3) to determine how 1) and 2) influence parasitic wasp abundance and community composition.

Materials and Methods

Study Area

The study area consisted of sites chosen within four adjacent townships (Mayfield, Moscow, Bald Mountain, and Caratunk) in Somerset County, Maine in order to minimize geographic and environmental variation. Eighteen sites representing six different standard silvicultural treatment types were initially chosen for the study based on land use history records kept by the landowner, Plum Creek Timber Company. The six treatment types were as follows: 1) young glyphosate treated clear-cuts (4-5 years post harvest), 2) young untreated clear-cuts, 3) old glyphosate treated clear-cuts (14-15 years post harvest), 4) old untreated clear-cuts, 5) old glyphosate treated clear-cuts replanted with black spruce (plantations), and 6) mature forest (> 50 years) not treated with glyphosate. The size of the study sites ranged from 0.2-2.0 ha. Elevation of study sites was 368 to 485 meters above sea level. Young clear-cuts, both treated and untreated, were almost completely dominated by forbs and grasses. Old untreated clear-cuts were composed primarily of randomly distributed trees, both coniferous and deciduous of varying age, with areas of open and closed canopy. Old treated clear-cuts were composed primarily of randomly distributed coniferous trees of varying age with areas of open and closed canopy. Plantations were composed of evenly distributed spruce of the same age with an open canopy. Mature forests were composed of trees

(most > 50 years old) both deciduous and coniferous with a closed canopy, except for some tree fall gaps. Refer to Table 1.1 for a complete list of sites with their associated treatments, harvest dates, and herbicide dates.

After a visual inspection of the sites, it was determined that both OH treatment sites displayed two distinct types of vegetation communities. One type had a high density of conifers with a closed canopy, the other type had a lower density of conifers with a patchy distribution resulting in large areas of open canopy. One additional OH site was added to the study resulting in two of each of the low conifer density and high conifer density within the OH treatment. An additional O site was added for balance. Therefore, a total of 20 sites were used for the initiation of the study in 2000 (Table 1.1). These sites were the same sites reported in Georgitis (2001) but include changes described below for 2001. Following vegetation data analysis from 2000 (Georgitis 2001) it was confirmed that there were in fact two distinctly different vegetation communities within the O and OH treatment sites. Based on visual inspection of additional old clear-cuts in the area, it was determined that low conifer density in a patchy distribution was the most common old clear-cut vegetation community. In order to increase the statistical power of the experiment the less common high conifer density sites were dropped (sites 8, 11, 19, and 20) and two new low conifer density sites (21 and 22) were added for the 2001 field season. Additionally, site 9 displayed evidence of a recent fire event and was subsequently dropped from the study and replaced with a new site (site 23). As a result of these changes, in 2001 there were three replicates for each of six treatments for a total of 18 sites.

Wasp Sampling

Several trap types were used to estimate wasp abundance and diversity. In each site malaise traps, flight intercept traps, and pitfalls were used. Malaise traps consisted of four 96cm tall x 46cm wide panels of clear plastic sewn together lengthwise at 90° to one another which created four perpendicular panels. The panels were supported by a frame of EMT electrical conduit. The frame consisted of a vertical 1m length of conduit topped with an electrical junction box from which four 50cm sections of conduit were attached horizontally and perpendicular to one another creating a “+” shape when viewed from above. These horizontal sections of conduit supported the plastic panels laterally. An additional 0.6m section of conduit attached vertically to the top of the junction box. This section of conduit supported a tent of white mesh over the plastic panels that acted as a funnel into a clear plastic collecting jar attached at the top. The collection jar was partially filled with propylene glycol to preserve captured insects until they were collected. Two malaise traps were placed in each site roughly equidistant from each other and the boundary of each site to avoid edge effects.

In order to sample wasps that may be present above 1.3m, two 15m rigid conduit towers were erected in each site. Five flight intercept traps were suspended from the towers at 1, 4.5, 8, 11.5, and 15m above the ground. In mature sites where the canopy exceeded 15m, 25m towers were erected with additional flight intercept traps located at 18.5, 22, and 25m above the ground. Flight intercept traps consisted of two 23cm x 30cm panes of clear Plexiglas ® bisecting each other lengthwise at 90°. A 20cm diameter opaque plastic funnel terminating in an opaque plastic collecting cup was attached to either end of the Plexiglas ® panes. A piece of Hot Shot No-Pest Strip ® (2,2 –

Dichlorovinyl dimethyl phosphate) was placed in each collection cup to prevent insects as a killing agent. Two holes were drilled into the bottom cup to allow water to escape and lined with hosiery to prevent insect escape. The towers were located approximately equidistant from one another and the boundary of each site to avoid edge effects.

In order to sample wingless wasps foraging on the substrate, pitfall traps were employed. Four pitfall traps were placed 20m apart within approximately a 14m radius of the center of each site. Pitfall traps were constructed from 20oz. plastic soda bottles. The top third of the bottle was removed and inverted to act as a funnel and fit into the bottom two thirds of the bottle where a collection cup was located. Approximately 30 ml of propylene glycol was added to the collection cup as a preservative. The entire assembly was buried flush with the ground and care was taken to minimize disturbance. Squares of tin (13cm) were suspended 5cm above each pitfall by metal spikes to act as a rain shield to prevent trap flooding. In addition, holes were drilled into the bottom of each trap for drainage.

All traps were set and left in place for 14 days, after which the samples were collected and the traps reset. This was done continuously beginning 1 June through 23 August in 2000 and from 21 May through 30 August in 2001. Samples were rinsed and preserved in 70% ethanol. Wasps were sorted from samples and identified to family using keys by Borror, Triplehorn, and Johnson (1989). All genus and species identifications were conducted by John Luhman at the Minnesota Department of Agriculture.

Vegetation Sampling

A survey of flowering vegetation was conducted to investigate possible correlations between floral resources and parasitoid wasp abundance. Flowering vegetation sampling was conducted using line transect sampling (Eberhardt, 1978) and coincided temporally with insect trap collections. Four 40m line transects were established in each site using a meter tape. Transects were kept straight and parallel by following a compass bearing. Date, site, species, number of stems, number of flowers, and flower cluster shape and size (diameter) were recorded for each flowering plant that intersected the vertical plane of the transect. These data were then used to calculate a floral density measure for each species. This floral density measure was calculated for each species using the following formula: $y = \sum(a/(b*c))$, where a = total number of flowers per plant, b = estimated diameter of the plant (in meters), c = total length of sampling transect (160m). Transects were located in an arbitrary location during each sampling period to minimize vegetation trampling caused by sampling.

Data Analysis

Nonmetric multidimensional scaling (PCORD, McCune ad Medford, 1999) was used to determine which floral species were responsible for the greatest variation in floral density between sites. The unit of measure used in this analysis was floral density (total number of flowers per square meter calculated as described above) for each sample year. In a separate analysis, the correlation between floral species scores for the first three principal axes and total parasitoid abundance, Ichneumonidae abundance, Braconidae abundance, Chalcidoidea abundance, Pompilidae abundance, Ichneumonidae morphospecies, and Braconidae morphospecies were computed to investigate the

relationship between major floral density differences among sites and respective wasp group abundance. Forward stepwise linear regression (Proc Reg, SAS Institute 1996) was performed to evaluate relationships between floral species density (independent variables) and the abundance values for each of the wasp groups (groups defined in Chapter 1). Floral density and wasp abundance were both log transformed to meet the assumptions of normality and homogeneity of variance. Separate analyses were performed for each sample year.

Results

2000 Field Season

The NMS ordination (Fig. 2.1) of floral density in 2000 accounted for 96.1% of total variation in the data set with three axes. Axis 1 comprised 63.7%, axis 2 comprised 11.8%, and axis 3 comprised 20.6%. Sites 5 and 20 did not group with their respective treatments and old clear-cuts did not group together well. The remaining sites within treatments grouped together relatively well. In site 5 this was primarily due to low floral density and in site 20 to overall high floral density (see Appendix). The first ordination axis appeared to separate sites based on the floral density of shade intolerant species versus shade tolerant species (goldenrod, field hawkweed, pearly everlasting, and wild strawberry versus wild sarsaparilla (*Aralia nudicauli*), Canada mayflower, and common wood sorrel (Table 2.1)). Axis three was related to the floral density of low pH tolerant floral species in each site, with sheep sorrel and blueberry being most highly correlated. Axis two was not easily interpretable, but appears to be primarily driven by Canada mayflower and red raspberry (*Rubus idaeus*) floral density (Table 2.1).

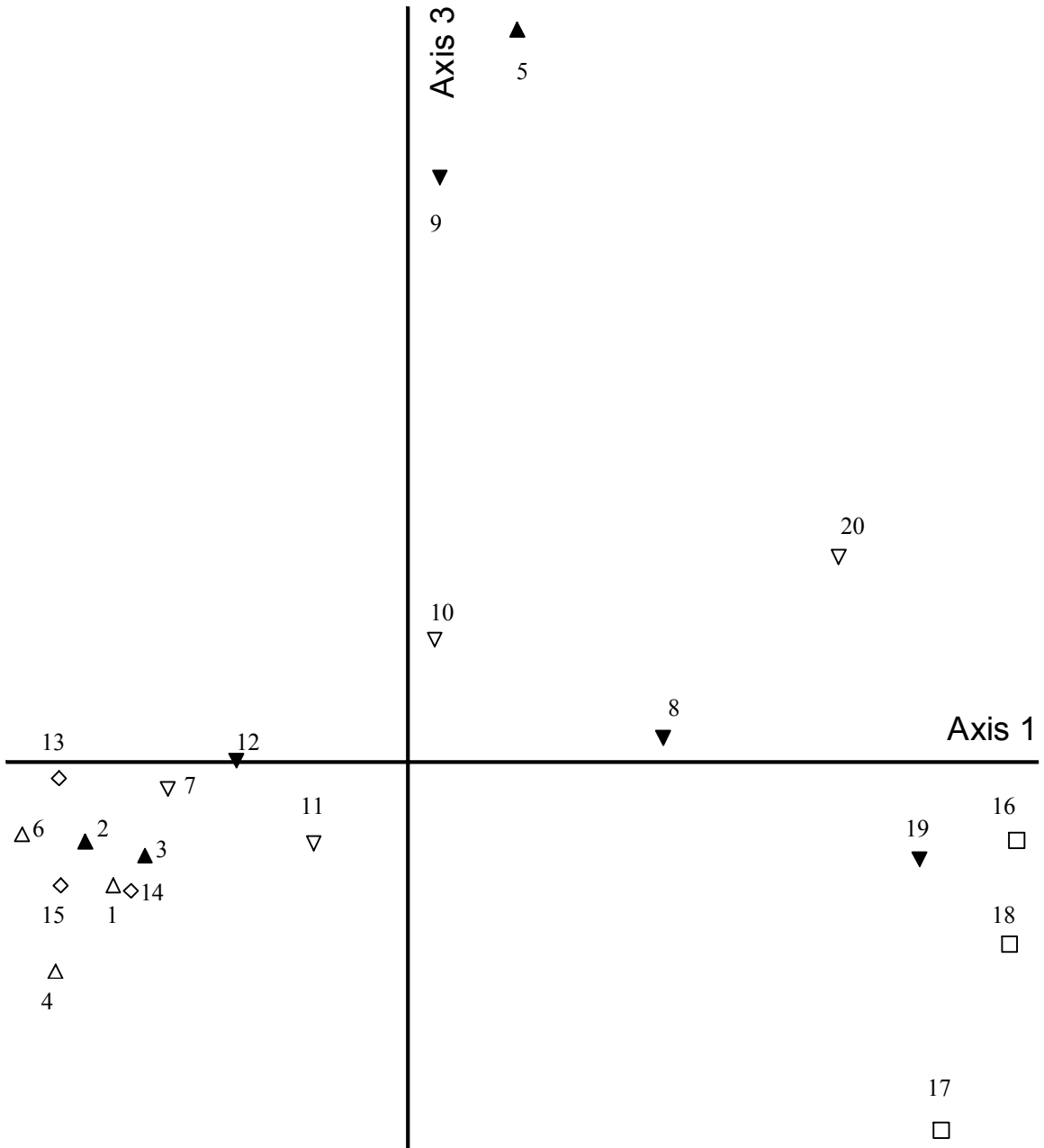


Figure 2.1. NMS ordination of flowering plant communities in species space in six forest types in 2000. Symbols indicate treatments: ▲ young clear-cuts not treated with glyphosate, △ young clear-cuts treated with glyphosate, ▼ old clear-cuts not treated with glyphosate, ▽ old clear-cuts treated with glyphosate, ◇ plantations, and □ mature forest. Site number is located above each symbol.

Table 2.1. Correlations (r) of floral density by species with ordination axes in 2000. Values in bold indicate a significant correlation ($P < 0.05$, $df = 18$). P values for significant correlations are in parentheses.

Common Name	Flower Species	Axis 1	Axis 2	Axis 3
Pearly Everlasting	<i>Anaphalis margaritacea</i>	-0.752 (0.0001)	0.023	-0.322
Bristly Sarsaparilla	<i>Aralia hispida</i>	-0.191	0.107	0.415
Wild Sarsaparilla	<i>Aralia nudicauli</i>	0.548 (0.0124)	0.530 (0.0162)	-0.112
Aster	<i>Aster spp.</i>	-0.505 (0.0231)	0.014	-0.323
Small White Aster	<i>Aster vimineus</i>	-0.318	-0.037	-0.155
Goldthread	<i>Coptis trifolia</i>	-0.174	-0.058	0.252
Bunchberry	<i>Cornus canadensis</i>	-0.263	-0.840 (<0.0001)	0.202
Dewdrop	<i>Dalibarda repens</i>	0.073	-0.187	0.013
Flat-topped White Aster	<i>Doellingeria umbellata</i>	-0.382	0.032	-0.196
Fireweed	<i>Epilobium angustifolium</i>	-0.421	0.051	-0.034
Narrow Leaved Willow Herb	<i>Epilobium leptophyllum</i>	-0.174	0.020	0.176
Spotted Joe-pye	<i>Eupatorium maculatum</i>	-0.334	0.000	-0.178
Wild Strawberry	<i>Fragaria spp.</i>	-0.652 (0.0018)	0.096	-0.220
Sweet Scented Bedstraw	<i>Galium triflorum</i>	-0.123	0.047	-0.257
Orange Hawkweed	<i>Hieracium aurantiacum</i>	-0.613 (0.0041)	0.076	-0.211
Field Hawkweed	<i>Hieracium caespitosum</i>	-0.778 (<0.0001)	0.034	-0.258
Tall Blue Lettuce	<i>Lactuca biennis</i>	-0.453 (0.0449)	0.10	-0.276
Twinflower	<i>Linnaea borealis</i>	0.202	-0.020	-0.200
Indian Tobacco	<i>Lobelia inflata</i>	-0.294	-0.006	-0.212
Northern Bugleweed	<i>Lycopus uniflorus</i>	-0.383	-0.033	-0.176
Canada Mayflower	<i>Maianthemum canadense</i>	0.477 (0.0335)	-0.675 (0.0011)	0.067
Common Wood Sorrel	<i>Oxalis acetosella</i>	0.540 (0.0140)	0.138	-0.114
Fringed Bindweed	<i>Polygonum cilinode</i>	-0.231	-0.034	0.026
Rough Cinquefoil	<i>Potentilla norvegica</i>	-0.234	-0.200	-0.151
Cinquefoil	<i>Potentilla simplex</i>	-0.444 (0.0500)	0.082	-0.158
Healall	<i>Prunella vulgari</i>	-0.116	0.140	-0.208
Blackberry	<i>Rubus allegheniensis</i>	-0.520 (0.0188)	0.435	0.148
Red Raspberry	<i>Rubus idaeus</i>	-0.560 (0.0102)	0.970 (<0.0001)	-0.012
Dwarf Raspberry	<i>Rubus pubescens</i>	-0.254	0.019	-0.181
Sheep Sorrel	<i>Rumex acetosella</i>	-0.004	0.314	0.794 (<0.0001)
Goldenrod	<i>Solidago spp.</i>	-0.906 (<0.0001)	0.110	-0.353
Foamflower	<i>Tiarella cordifolia</i>	0.094	0.194	-0.290
Starflower	<i>Trientalis borealis</i>	0.360	-0.171	-0.107
Blueberry	<i>Vaccinium angustifolium</i>	0.013	0.241	0.654 (0.0018)
Common Speedwell	<i>Veronica officinalis</i>	-0.085	-0.167	-0.061
Northern White Violet	<i>Viola pallens</i>	-0.343	-0.084	-0.166

Correlation analyses of parasitoids and axis scores (Table 2.2) indicated a relationship between axis 3 and Ichneumonidae and Chalcidoidea abundance. This may suggest that low soil pH does not foster floral species that are beneficial to Ichneumonidae or Chalcidoidea. Visual inspection of scatter-plots for all correlations did not reveal curvilinear relationships.

Table 2.2. Correlations (r) of NMS axis scores with parasitoid abundance in 2000. There were no significant correlations ($P < 0.05$, $df = 18$).

Taxa	Axis 1	Axis 2	Axis 3
Total Parasitoids	0.132	-0.213	-0.253
Ichneumonidae	0.150	-0.215	-0.348
Braconidae	0.126	-0.128	-0.052
Chalcidoidea	-0.039	-0.244	-0.430
<i>Lissonota sp.</i>	0.240	-0.178	-0.076
<i>I. clasma</i>	-0.044	-0.205	0.083
Morph B	-0.127	-0.106	0.172
Morph D	0.071	0.008	0.080

Forward step-wise regression selected common speedwell (*Veronica officinalis*) and bunchberry, (in that order) to model total parasitoid, Braconidae, and morph D abundance (Table 2.3). Common speedwell had a negative coefficient, which is counter to traditional theory of floral-parasitoid relationships (i.e. floral species should have either a positive or neutral effect on parasitoid abundance). Common speedwell may be an indicator of poor quality sites for parasitoids (young clear-cuts in this study). A second analysis with common speedwell removed did not result in the selection of another floral species. Conversely, while bunchberry had a lower r^2 , its coefficient was positive, perhaps indicating a positive association between bunchberry and parasitoid abundance. Visual inspection of scatter plots confirmed a positive trend in parasitoid

Table 2.3. Results of forward step-wise regression to model parasitoid abundance with floral species density in 2000.

Taxa	Floral Species	r ²	Coefficient	P
Total Parasitoids	<i>V. officinalis</i>	0.3263	-0.4302	0.0095
	<i>C. canadensis</i>	0.0905	0.2369	0.1228
Ichneumonidae	<i>V. officinalis</i>	0.2470	-0.4212	0.0280
Braconidae	<i>V. officinalis</i>	0.3534	-0.4965	0.0041
	<i>C. canadensis</i>	0.1732	0.3698	0.0232
Chalcidoidea	<i>Fragaria spp</i>	0.1651	0.8570	0.0007
	<i>V. angustifolium</i>	0.1304	-0.4920	0.0012
	<i>V. officinalis</i>	0.1358	-0.5154	0.0043
	<i>H. caespitosum</i>	0.1152	-0.4851	0.0007
	<i>T. cordifolia</i>	0.1338	-0.3724	0.0297
<i>I. clasma</i>	<i>C. canadensis</i>	0.4359	0.6222	0.0015
<i>Lissonota sp.</i>	N/A			
Morph B	<i>V. angustifolium</i>	0.2849	0.2390	0.0396
	<i>C. canadensis</i>	0.1611	0.2961	0.0400
Morph D	<i>V. officinalis</i>	0.3285	-0.5359	0.0043
	<i>C. canadensis</i>	0.2367	0.4192	0.0074

abundance with bunchberry floral density. Common speedwell was the only floral species selected to model Ichneumonidae abundance. As with previous parasitoid groups, the coefficient was negative. Wild strawberry, blueberry, common speedwell, field hawkweed, and foamflower (*Tiarella cordifolia*), (in that order) were selected to model Chalcidoidea abundance. All coefficients were negative except for wild strawberry, perhaps indicating that it has some positive association with Chalcidoidea abundance. Blueberry and bunchberry were selected to model morph B abundance, coefficients for both were positive, potentially indicating a positive association with these floral species. Bunchberry was selected to model *Ichneumon clasma* abundance, the r^2 was high, and the coefficient was positive. This provides some evidence that *I. clasma* abundance is positively associated with bunchberry density. Visual inspection of scatter plots support this conclusion. There were no floral species selected to model *Lissonota sp.* abundance, most likely due to the multitude of zero values recorded for this species.

2001 Field Season

The NMS ordination (Fig. 2.2) of floral density in 2001 accounted for 91.6% of total variation in the data set with two axes, additional axes accounted for very little of the remaining variation. Axis 1 comprised 63.4% and axis 2 comprised 28.2%. Forest types grouped much the same as in 2000, with the exception of site 17. The outlying nature of site 17 was due to the lack of floral resources in site 17 in 2001 (see Appendix). As in 2000, the first ordination axis appeared to separate sites based on the floral density of shade intolerant species versus shade tolerant species (goldenrod, field hawkweed, pearly everlasting, and strawberry versus wild sarsaparilla and common wood sorrel) (Table 2.4). Interpretation of axis 2 was somewhat different than in 2000. Sheep sorrel

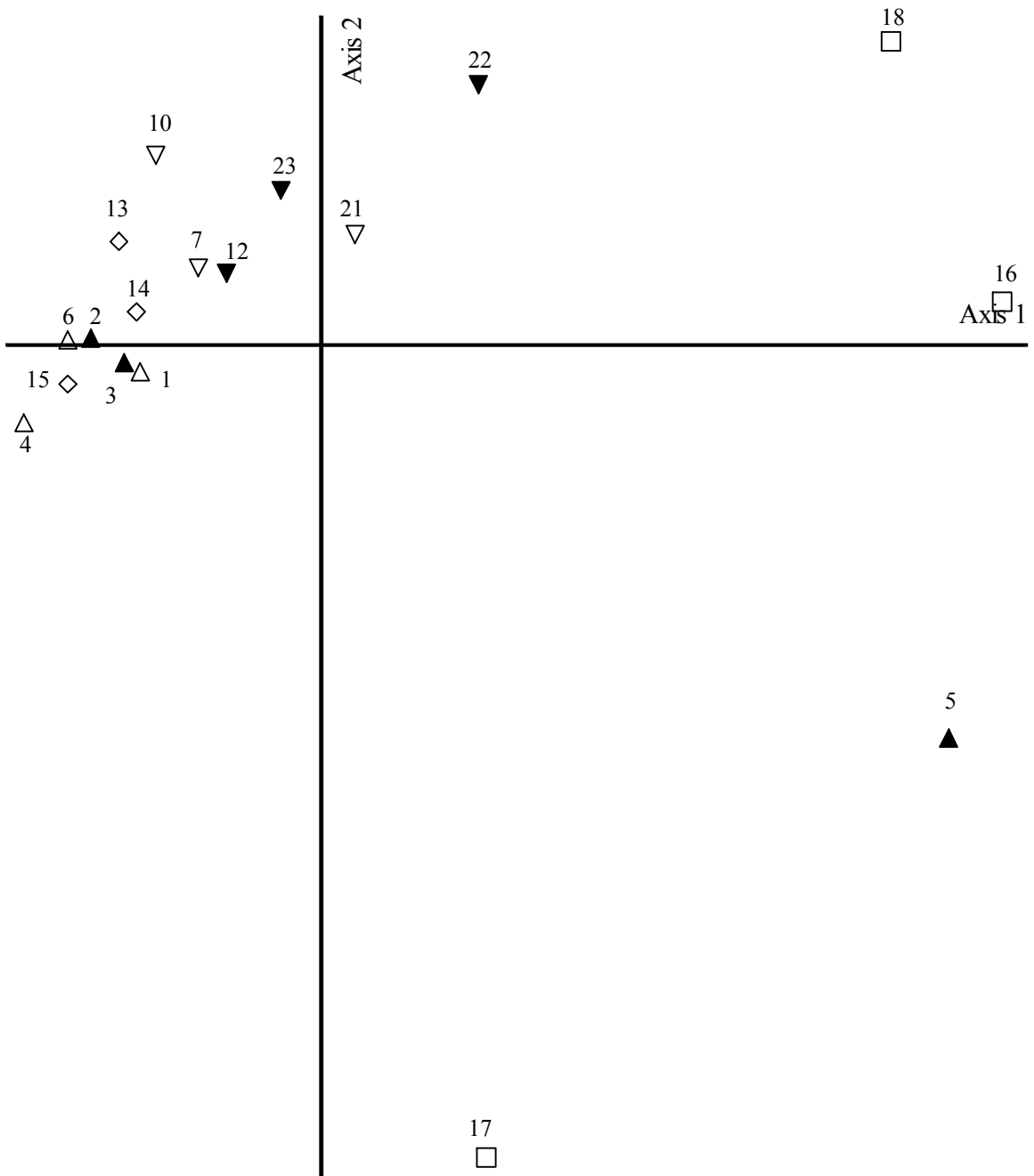


Figure 2.2. NMS ordination of flowering plant communities in species space in six forest types in 2001. Symbols indicate treatments: ▲ young clear-cuts not treated with glyphosate, △ young clear-cuts treated with glyphosate, ▼ old clear-cuts not treated with glyphosate, ▽ old clear-cuts treated with glyphosate, ◇ plantations, and □ mature forest. Site number is located above each symbol.

Table 2.4. Correlations (r) of floral density by species with ordination axes in 2001. Values in bold indicate a significant correlation ($P < 0.05$, $df = 16$).

Common Name	Flower Species	Axis 1	Axis 2
Pearly Everlasting	<i>Anaphalis margaritacea</i>	-0.726 (0.0003)	0.042
Bristly Sarsaparilla	<i>Aralia hispida</i>	0.411	-0.320
Aster	<i>Aster spp.</i>	-0.391	-0.024
Bluebead Lily	<i>Clintonia borealis</i>	-0.219	0.097
Bunchberry	<i>Cornus canadensis</i>	-0.277	0.395
Dewdrop	<i>Dalibarda repens</i>	0.022	0.346
Flat-topped White Aster	<i>Doellingeria umbellata</i>	-0.462	0.046
Fireweed	<i>Epilobium angustifolium</i>	-0.348	0.090
Wild Strawberry	<i>Fragaria spp.</i>	-0.614 (0.0040)	0.146
Orange Hawkweed	<i>Hieracium aurantiacum</i>	-0.281	0.180
Field Hawkweed	<i>Hieracium caespitosum</i>	-0.716 (0.0004)	0.235
Twinflower	<i>Linnaea borealis</i>	0.032	0.240
Canada Mayflower	<i>Maianthemum canadense</i>	-0.135	0.279
Common Wood Sorrel	<i>Oxalis acetosella</i>	0.647 (0.0021)	0.271
Healall	<i>Prunella vulgaris</i>	-0.335	-0.076
Blackberry	<i>Rubus allegheniensis</i>	-0.080	0.085
Red Raspberry	<i>Rubus idaeus</i>	-0.483 (0.0310)	0.164
Dwarf Raspberry	<i>Rubus pubescens</i>	-0.286	0.015
Goldenrod	<i>Solidago spp.</i>	-0.793 (<0.0001)	0.085
Steeplebush	<i>Spirea tomentosa</i>	-0.215	0.027
Crookedstem Aster	<i>Symphyotrichum prenanthoides</i>	0.253	0.206
Purplestem Aster	<i>Symphyotrichum puniceum</i>	-0.254	0.047
Starflower	<i>Trientalis borealis</i>	0.309	0.310
Purple Trillium	<i>Trillium erectum</i>	-0.248	0.030
Painted Trillium	<i>Trillium undulatum</i>	-0.193	0.146
Wild Oat	<i>Uvularia sessilifolia</i>	-0.075	0.150
Barren Strawberry	<i>Waldsteinia fragarioides</i>	-0.110	-0.050

and blueberry did not meet the abundance and density criteria for inclusion in NMS ordination, because the sites in which they happened to be most abundant were dropped and replaced by new sites as explained in the methods section. As a result, the second axis was not related to plant pH requirements as it was in 2000. Instead, axis 2 was most highly correlated to the floral density of a few species adapted to moist, low light conditions like bunchberry, dewdrop, and starflower. Correlation analysis of parasitoids and axis scores indicated several possible relationships (Table 2.5). The strongest relationship was between axis 1 and Chalcidoidea abundance, and may indicate a positive relationship between Chalcidoidea abundance and flowering plant species with high light requirements. There were weaker correlations between axis 2 and total parasitoid, total Braconidae, and total morph D abundance, as well as between axis 1 and total parasitoid and *I. clasma* abundance, but none were significant (Table 2.5).

Table 2.5. Correlations (r) of NMS axis scores with parasitoid abundance in 2001. Values in bold indicate a significant correlation ($P < 0.05$, $df = 16$).

Taxa	Axis 1	Axis 2
Total Parasitoids	-0.327	-0.360
Ichneumonidae	-0.166	-0.236
Braconidae	-0.222	-0.367
Chalcidoidea	-0.506	-0.211
<i>Lissonota sp.</i>	0.279	0.160
<i>I. clasma</i>	0.327	0.096
Morph B	-0.262	-0.196
Morph D	0.027	-0.413

Forward step-wise regression selected bunchberry to model total parasitoid, total Ichneumonidae, total Braconidae, and morph D abundance (Table 2.6). The r^2 for each was moderately high and the coefficients were positive, potentially indicating a positive

association between these parasitoid groups and bunchberry. These results were fairly consistent with 2000 and would seem to indicate that bunchberry itself, or some characteristic of sites with high bunchberry density, has a positive effect on the abundance of total parasitoid, Ichneumonidae, Braconidae, and morph D abundance. Unlike the results of 2000, Canada mayflower was selected to model *I. clasma* abundance, the r^2 was low, and the coefficient negative. Wild strawberry was selected again in 2001 to model Chalcidoidea abundance, the r^2 was moderately high, and the coefficient was positive, supporting the potential positive association between the two. Abundance of *Lissonota sp.* and morph B were too low in 2001 to generate a significant model.

Table 2.6. Results of forward step-wise regression to model parasitoid abundance with floral species density in 2001.

Taxa	Floral Species	r^2	Coefficient	P
Total Parasitoids	<i>C. canadensis</i>	0.4923	0.3387	0.0012
Ichneumonidae	<i>C. canadensis</i>	0.2898	0.2587	0.0286
Braconidae	<i>C. canadensis</i>	0.4697	0.4539	0.0017
Chalcidoidea	<i>Fragaria spp</i>	0.4674	0.3299	0.0018
<i>I. clasma</i>	<i>M. canadense</i>	0.3434	-0.1684	0.0106
<i>Lissonota sp.</i>	N/A			
Morph B	N/A			
Morph D	<i>C. canadensis</i>	0.3280	0.6480	0.0130

Discussion

The characterization of floral communities within and between forest types yielded consistent results for each year of this study. With the exception of one site, all young clear-cuts (both glyphosate treated and untreated) and plantations had similar forb communities in both years of this study. This result suggests that glyphosate application has little effect on forb communities three to four years after application and that despite being more than 10 years older, plantations have floral communities nearly identical to young clear-cuts. The floral communities in old clear-cuts (both glyphosate treated and untreated) were highly variable with some being similar to young clear-cuts/plantations, some to mature forests, and some intermediate. Because of this variability, there is no conclusive evidence that glyphosate application has a long-term effect on floral communities in clear-cuts. However, this result does suggest that after 14-15 years, clear-cuts can have widely variable floral communities when left to regenerate naturally.

Floral community differences across the six forest types in this study appeared to have no effect on the abundance of the dominant parasitoid families and species present in these forest types. Parasitoid abundance was much lower in young clear-cuts compared to plantations (see chapter 1), but, as mentioned above, floral communities in these two forest types were similar. In addition, although floral communities were much different in plantations compared to mature forests (namely, floral density was high in plantations and was extremely low in mature forests, see Appendix), they had similar parasitoid abundance. Therefore, it seems something other than the overall floral community was responsible for the differences in parasitoid abundance among forest types.

Perhaps, rather than the entire floral community, only one or a few floral species affected parasitoid abundance. Such an effect could be obscured by a few floral species whose density dominated the community. For example, several studies (Leius, 1960; Leius, 1963; Leius, 1967b; Jervis et al, 1992 and 1993; and Patt et al, 1996) have demonstrated that many floral species are undesirable, unattractive, or have nectaries that are inaccessible due to morphological restrictions imposed by the parasitoids' mouthparts. A recent study found that some floral species may actually be repellent (Wackers, 2004) and an observational study of floral visitation (Maingay, 1991) found that Ichneumonidae were "virtually absent" from goldenrod. A major component of the primary ordination axis for floral community in this study was goldenrod, so it stands to reason that less dense, yet beneficial floral species may have an effect on parasitoid abundance. Therefore, stepwise regression was used to identify individual floral species that may have affected parasitoid abundance. The only result consistent in both years of this study was the selection of bunchberry for total parasitoid, Braconidae, and morph D abundance and wild strawberry for Chalcidoidea abundance. The coefficient in both cases was positive. In general, the results of this study seem to support the conclusion that bunchberry and wild strawberry, or some characteristic of sites with high bunchberry and wild strawberry density, have a positive effect on their respective parasitoid groups. Laboratory studies or field observations are needed to determine if these floral species are actually utilized or merely indicators. If these floral species were not solely responsible for the observed differences in parasitoid abundance, then microclimate and/or host

availability are the only other factors likely to impact parasitoid abundance among the forest types in this study. These factors and their bearing on this study were discussed in detail in chapter one.

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APPENDIX

Study sites, their associated forest type and total floral density (#flowers/m²) in 2000 and 2001. Total floral density is the sum of all floral species pooled for all sample dates in each year.

<u>Site</u>	<u>Treatment</u>	<u>Year</u>	<u>Total Floral Density</u>
1	Young Herbicide	2000	699
		2001	1276
2	Young	2000	878
		2001	823
3	Young	2000	710
		2001	1330
4	Young Herbicide	2000	874
		2001	2562
5	Young	2000	51
		2001	16
6	Young Herbicide	2000	844
		2001	883
7	Old Herbicide	2000	367
		2001	360
8	Old	2000	34
		2001	n/a
9	Old	2000	346
		2001	n/a
10	Old Herbicide	2000	182
		2001	138
11	Old Herbicide	2000	208
		2001	n/a
12	Old	2000	322
		2001	338
13	Plantation	2000	930
		2001	389

APPENIX (cont.)

14	Plantation	2000 2001	958 718
15	Plantation	2000 2001	671 1393
16	Mature	2000 2001	41 5
17	Mature	2000 2001	17 0
18	Mature	2000 2001	84 10
19	Old	2000 2001	34 n/a
20	Old Herbicide	2000 2001	541 n/a
21	Old Herbicide	2000 2001	n/a 269
22	Old	2000 2001	n/a 33
23	Old	2000 2001	n/a 175

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