

**Food-web Interactions and  
Population Variability of Leaf beetles in  
Managed and Natural Willow Stands**

**Peter Dalin**

*Department of Entomology  
Uppsala*

**Doctoral thesis  
Swedish University of Agricultural Sciences  
Uppsala 2004**

**Acta Universitatis Agriculturae Sueciae**  
Silvestria 303

ISSN 1401-6230  
ISBN 91-576-6537-0  
© 2004 Peter Dalin, Uppsala  
Tryck: SLU Service/Repro, Uppsala 2004

## Abstract

Dalin, P. 2004. Food-web interactions and population variability of leaf beetles in managed and natural willow stands. Doctor's dissertation.  
ISSN 1401-6230, ISBN 91-576-6537-0.

It is generally believed that diversity leads to stability in ecological systems. One consequence would be that insect outbreaks (*i.e.* drastic increases in insect density) should be more frequent in managed systems, such as forest plantations and crop fields, than in natural and more diverse systems. The leaf beetle *Phratora vulgatissima* is a major insect pest in plantations of the willow *Salix viminalis* ('energy forests') and outbreaks are frequently observed. In this thesis, food-web interactions and population fluctuations of leaf beetles are compared between managed (*Salix viminalis*) and natural (*S. cinerea*) willow stands. In a five-year study, we found no difference in temporal variability of leaf beetle populations between managed and natural willow stands. However, drastic increases in leaf beetle density ('outbreaks') tended to be more frequent in managed stands.

The two willow species studied responded differently to leaf beetle attack. The natural willow (*S. cinerea*) responded to grazing by adult beetles by producing new leaves with an increased density of trichomes (leaf hairs). Larvae were shown deterred from feeding on the induced leaves. This type of plant response may reduce the overall damage done by leaf beetles. However, no induced defence in response to adult grazing could be detected for the willow used in plantations, *S. viminalis*.

Among the main predators attacking egg aggregations laid by leaf beetles, one type (mirid bugs) often stay and consume most eggs before moving on to search for other prey, a behaviour characterised as 'find and stay'. Another type (anthocorid bugs) have more of a 'run and eat' behaviour; they visit many aggregations but consume fewer eggs within aggregations than mirids. In a simulation model, populations of leaf beetles were less likely to establish and to increase in abundance when attacked by 'find and stay' predators than when attacked by 'run and eat' predators. In the field, the leaf beetle *P. vulgatissima* occurred at low densities, and the predation on eggs was high, in natural willow stands where 'find and stay' mirids were abundant. The results suggest that a high abundance of heteropteran predators may prevent outbreaks of the leaf beetle *P. vulgatissima*.

Key-words: diversity, stability, Chrysomelidae, *Phratora vulgatissima*, induced plant responses, predation, Heteroptera, *Orthotylus marginalis*, *Closterotomus fulvomaculatus*, *Anthocoris nemorum*.

Author's address: Peter Dalin, Department of Entomology, SLU, P.O. Box 7044, SE-750 07, UPPSALA, Sweden. E-mail: Peter.Dalin@entom.slu.se



# **Contents**

## **Introduction, 7**

Aims of the thesis, 9

Study organisms, 9

*Willows, 9*

*The leaf beetle, 10*

*Natural Enemies, 11*

Study sites and basic approach, 11

## **Results and discussion, 12**

Induced responses in willows (Paper I and II), 12

Predator feeding habits and prey population dynamics (Paper III), 13

Plant quality or natural enemies? (Paper IV), 15

Population variability in managed and natural willow stands (Paper V), 17

## **Conclusions, 19**

## **References, 21**

## **Acknowledgements, 25**

# Appendix

## Papers I – V

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Dalin P. & Björkman C. 2003. Adult beetle grazing induces willow trichome defence against subsequent larval feeding. *Oecologia* 134, 112-118. Erratum: *Oecologia* 134, 554.
- II. Dalin P., Björkman C. & Eklund K. 2004. Leaf beetle grazing does not induce willow trichome defence in the coppicing willow *Salix viminalis*. *Agricultural and forest entomology*, 6, 105-109.
- III. Dalin P., Kindvall O. & Björkman C. Effects of generalist predator feeding habits on prey population dynamics. Manuscript.
- IV. Dalin P. Habitat difference in willow leaf beetle abundance: plant quality or natural enemies? Manuscript.
- V. Dalin P., Björkman C. & Kindvall O. Population variability of leaf beetles in managed and natural willow stands. Manuscript.

Paper I and II are reproduced with the kind permission of the publishers.

## Introduction

Herbivorous insects often show great variation in abundance, both in time and space (*e.g.* Berryman 1988). Some insect populations exhibit extreme changes in numbers and sporadically reach very high densities (Berryman 1987). During high-density periods, the insects may damage the host plants, which can result in reduced plant growth and even plant mortality (Kulman 1971; Björkman *et al.* 2000; Cedervind & Långström 2003). Defoliation by insects may also weaken the plants, which increases the risk of secondary attack by other insects, such as bark beetles (Lekander 1953; Cedervind *et al.* 2003). Herbivory is a common feature of all ecosystems, which influences vegetation structure, plant community development and nutrient cycling (Schowalter *et al.* 1986; Kosola *et al.* 2001). However, when the insects increase in number and become a nuisance, or when their damage exceeds what is economically tolerable, the insects are often called pests and their high abundance is referred to as insect outbreaks (Scriber & Hainze 1987). Therefore, to be able to understand and predict changes in herbivorous insect populations, we need to understand the mechanisms that usually keep their densities at low levels.

Factors that influence herbivorous insects include bottom-up forces mediated through host plants (Rhoades 1983), top-down forces from natural enemies (Price 1987), environmental conditions (Azerefegne *et al.* 2001) and competition (Denno *et al.* 1995) (Fig. 1). There is an extensive number of studies showing that variation in host plant traits, such as morphology, nutrients and secondary chemistry, influence the host plant selection and performance of herbivorous insects (see *e.g.* in Bernays & Chapman 1994; Hartley & Jones 1997; Schoonhoven *et al.* 1998). Variation in plant traits that affect individual insects can then translate into effects at the population level (Larsson *et al.* 2000; Underwood & Rausher 2000). The effect of natural enemies on herbivorous insect populations can be very strong, because insects often outbreak in the absence of natural enemies (Price 1987; Maron *et al.* 2001; Raymond *et al.* 2002). Environmental factors, such as temperature and humidity, may also determine the distribution and abundance of insects on the plants (Sipura *et al.* 2002). Competition among herbivorous insects influences both their populations and the community of insects and is often mediated indirectly through the plants (*e.g.* through depletion of resources), natural enemies and/or environmental factors (Denno *et al.* 1995).

The question about how insect populations can be maintained at low densities has identified two basic types of variables: density-independent and density-dependent factors (see *e.g.* Berryman 1999; Turchin 2003). Density-dependent factors are processes that respond to changes in population density. For example, the quality of a host plant can change in response to insect feeding; a phenomenon called induced plant responses (Karban & Baldwin 1997). The strength of induced plant responses often depends on insect density and may provide a negative density-dependent feedback effect on the herbivore populations if the response increases plant resistance against further herbivory (Edelstein-Keshet & Rausher

1989; Underwood & Rausher 2002). Natural enemies can also be part of feedback processes since they may respond, either functionally or numerically, to increases in herbivore numbers (Murdoch & Oaten 1975; Hassell 1978). Consequently, a low population density of herbivorous insects may be because of a poor abiotic and/or biotic environment for the herbivore, and/or because density-dependent feedback processes restricts population fluctuations at low-density levels (Berryman *et al.* 1987).

It is generally believed that insect outbreaks more frequently occur in managed systems, such as forest plantations and crop fields, than in natural and more diverse systems (Elton 1958; Pimentel 1961; Risch 1987; Altieri 1991). It has therefore been proposed that diverse communities, with many interacting species, may prevent populations of individual species from fluctuating wildly and ultimately reaching outbreak levels (MacArthur 1955; Elton 1958). Although this diversity-stability hypothesis has stimulated a great theoretical interest (see *e.g.* McCann 2000 for a review), we still lack studies comparing insects in managed and natural systems (Risch 1987). Insect outbreaks in managed systems have also been suggested to be because interactions among plants and animals are not persistent enough, in time and space, to provide the stability and equilibrium characteristics of a natural system (Murdoch 1975; Ferro 1987). Managed systems are often influenced by disturbances, such as harvest and pesticide applications, which may, for example, disrupt the control by natural enemies (DeBach & Rosen 1991). Thus, by comparing insects in managed and natural systems, an increased knowledge may be gained for important ecological processes that could prevent insect populations from fluctuating wildly and, thus, avoid insect outbreaks in managed systems.

Leaf beetles (Coleoptera: Chrysomelidae) are among the most important pests in willow (Salicaceae) plantations in north west of Europe and outbreaks have frequently been reported (Sage 1994; Sage & Tucker 1998). Willows used in short rotation forestry are grown on agricultural land, mainly for biomass production. In Sweden, the leaf beetle *Phratora vulgatissima* L. is the most abundant in plantations of the willow *Salix viminalis* L. (Björkman *et al.* 2004). The leaf beetle often shows a wide variation in abundance, both in time and space (Peacock *et al.* 1999; Björkman *et al.* 2004; III; IV; V). During periods of high densities, *P. vulgatissima* may severely defoliate willow plants, which can lead to substantial plant growth reductions (Björkman *et al.* 2000). Using insecticides to control leaf beetles is not an option, not only because it is technically very difficult, but also because it is not environmentally or economically sound. Therefore, an increased knowledge is required about what other factors may prevent leaf beetle outbreaks. The leaf beetle *P. vulgatissima* is also a common herbivore on the willow *S. cinerea* L., which grows naturally in Sweden, along rivers, ditches and on wet pastures. Several studies have considered the population dynamics of *P. vulgatissima* in willow plantations (Kendall *et al.* 1996b; Peacock *et al.* 1999; Björkman *et al.* 2004). However, there is little knowledge about its temporal and spatial dynamics in natural willow stands.



## Aims of the thesis

The overall aim of this thesis is to increase our knowledge about food-web interactions and population fluctuations of herbivorous insects in managed and natural systems. This thesis focuses on the willow leaf beetle *Phratora vulgatissima*, which is studied on both managed (*Salix viminalis*) and natural (*S. cinerea*) willows. Experiments that test specific hypotheses concerning interactions between the leaf beetle *P. vulgatissima* and its biotic environments are presented. In papers I and II, we investigate whether the two willow species *S. cinerea* and *S. viminalis* respond to adult leaf beetle grazing by increasing plant resistance against subsequent larval feeding. In paper III, we examine if behavioural variation within the enemy complex that attacks eggs and young larvae of *P. vulgatissima* could lead to any difference in the population dynamics of the leaf beetle. Possible causes for habitat differences in leaf beetle abundance are investigated in paper IV, where the relative effects of plant quality and natural enemies are evaluated in the field. Finally, in paper V, the temporal variability in leaf beetle population density is compared between managed and natural willow stands. The purpose of paper V is to test the diversity-stability hypothesis, which predicts that populations should be more stable in natural than in managed systems.

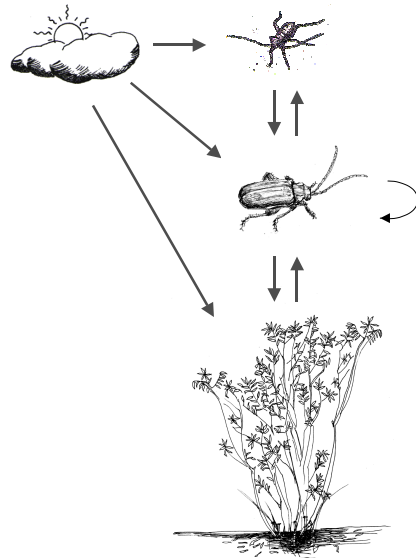


Fig. 1. Schematic illustration of factors influencing the population dynamics of willow leaf beetles.

## Study organisms

### *Willows*

The willow, *Salix viminalis* L. (Salicaceae), is the most common plant species used in short rotation forestry in Sweden (Ledin & Willebrand 1995). It was

originally introduced into Sweden and has been naturalised since the mid 1700s (Hyllander 1971). The willow grows rapidly and has an efficient re-sprouting of new shoots after harvest, which makes it a suitable plant species to use in short rotation forestry (Sirén *et al.* 1987). Willow plantations are established on agricultural land by planting stem cuttings in rows with a density of about two cuttings per square meter. A willow plantation normally consists of one or a few willow genotypes and plants are harvested during wintertime with an interval of 4-5 years. During the period between harvests, plants grow into bushes 3-5 meters high. Today, approximately 15 000 hectares of willows are used for biomass production in Sweden (<http://www.agrobransle.se>; 18-Mar-2004). Recently, short rotation willows have also been studied for their possible usage for cleaning of radiologically and heavy metal polluted soils (Vandenhove *et al.* 2001, Klang-Westin & Eriksson 2003).

The willow *S. cinerea* L. is native to Sweden and grows on relatively wet, moderately nutritious, soils. It forms dense shrubs along rivers, ditches and wet pastures and plants grow into bushes 1-4 meters high, but can sometimes become trees of 15 meters height (Jonsell 2000). The species is characterised by densely hair-covered current year shoots and inversely egg shaped (obovate) leaf blades (Jonsell 2000). The secondary plant chemistry of *S. cinerea* is similar with that for *S. viminalis* (Julkunen-Tiitto 1986). For example, both *S. cinerea* and *S. viminalis* contain relatively low concentrations of phenolic glycosides (Julkunen-Tiitto 1986). Phenolic glycosides have been shown to influence host plant selection and performance of many herbivorous insects feeding on willows (Rowell-Rahier 1984, Denno *et al.* 1990, Kolehmainen *et al.* 1995, Rank *et al.* 1998).

#### *The leaf beetle*

The leaf beetle *Phratora vulgatissima* L. can be found on several species of willows (Maisner 1974). In south central Sweden, it is mainly found on the willows *S. viminalis*, *S. cinerea* and *S. aurita* (P. Dalin, personal observation). Larvae grow equally well on *S. viminalis* and *S. cinerea* ( $T = 0.25$ , d.f. = 29,  $P = 0.805$ ; data from 'control plants' in paper I and II; laboratory study), which indicates no major difference in plant quality. *Phratora vulgatissima* is generally deterred from feeding on willow species containing high concentrations of phenolic glycosides, such as *S. purpurea* and *S. burjatica* (Kelly & Curry 1991a; Kendall *et al.* 1996a). It over winters as an adult; is univoltine in Sweden and adults starts to graze on the host plants early in the season, usually in the beginning of May. When adult beetles emerge from winter hibernation, they often aggregate at the edges of willow plantations (Sage *et al.* 1999). Beetles are attracted to volatiles emitted from damaged plants (Peacock *et al.* 2001a; Peacock *et al.* 2001b), which often leads to a clustered distribution on specific host plant individuals (Peacock *et al.* 1999). The egg laying period extends from late May to the middle of June in Sweden. One female can lay more than 400 eggs during a season (Maisner 1974). The eggs are laid in clusters (*i.e.* egg batches) consisting of 5-50 eggs, which are placed on the underside of leaves at the base of shoots and the eggs hatch after approximately 15 days (Kendall *et al.* 1996b). Larvae feed gregariously on leaves during the first and second instar. They become more mobile during the third instar and continue to feed solitary on the plants. After

passing through three instars, larvae pupate in the soil. The next generation of adult beetles emerges in August. After a short period of feeding, adult beetles leave the plants in late season to find hibernation sites in the bark crevices of trees and in cracks of buildings and wood materials (Kelly & Curry 1991b; Kendall *et al.* 1996b; Kendall & Wiltshire 1998).

### *Natural enemies*

The most common natural enemies of *P. vulgatissima* have been identified to be three species of heteropteran predators: the anthocorid *Anthocoris nemorum* L. and the two mirid species *Orthotylus marginalis* Reut. and *Closterotomus fulvomaculatus* De Geer (Björkman *et al.* 2003). These omnivorous generalist predators attack the eggs and young larvae of *P. vulgatissima*. The mirid *O. marginalis* is the most abundant to be found in the field, whereas *C. fulvomaculatus* and *A. nemorum* generally occur at lower densities but are frequently found attacking eggs and larvae (Björkman *et al.* 2003; Björkman *et al.* 2004; III; IV). The eggs and larvae of *P. vulgatissima* are also attacked by larval syrphids (*Syrphid* spp), which sometimes can be relatively common in some willow stands (Björkman *et al.* 2003). The adult syrphids lay their eggs singly on or near the eggs of *P. vulgatissima* and the larva hatch before the leaf beetle eggs start to hatch. At the present date, we do not know which species of syrphids are attacking the leaf beetle. We have also observed shield bugs (Heteroptera, Pentatomidae) to be feeding on larvae in the field (Björkman *et al.* 2003). However, shield bugs occur at relatively low densities compared with the two more common mirids and the anthocorid (P. Dalin, unpublished data). Large spiders have also been observed capturing adult beetles in the field (P. Dalin, personal observation). Ants and birds may also attack the larvae of willow leaf beetles (Sipura 1999; Sipura 2002).

### **Study sites and basic approach**

The basic approach of this PhD-project was to study populations of leaf beetles (*P. vulgatissima*) in a number of managed and natural willow stands for five years (1999-2003). Willow plantations (short rotation forests) consisting of the willow species *S. viminalis* were used as 'managed willow stands'. The willow plantations were all growing in agricultural landscapes (Fig. 2A). Populations of leaf beetles were also studied in natural willow stands (*S. cinerea*), located in both agricultural landscapes, 'farmland natural stands' (Fig. 2B), and in forests, 'forest natural stands' (Fig. 2C). The natural stands were growing on wet soils; in ditches or on wet meadows in the farmland habitat, or in wet areas (*e.g.* ditches) in the forest habitat. The forest natural stands were surrounded by conifer dominated mixed forests. In total, leaf beetle populations were studied in 20 managed, 12 forest natural and 10 farmland natural willow stands. As knowledge about the system was accumulated, hypothesis concerning interactions between the leaf beetle and its biotic environments were formulated and tested.

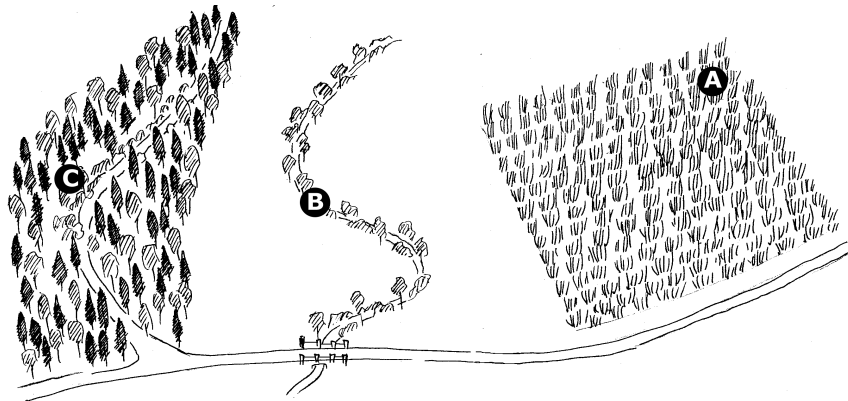


Fig 2. Illustration showing the three types of willow habitats studied in this thesis. **A** = managed stands (short rotation forests, *Salix viminalis*), **B** = farmland natural stands (*Salix cinerea*) and **C** = forest natural stands (*S. cinerea*). (Illustration made by Claes Hellqvist).

## Results and discussion

### Induced responses in willows (Paper I and II)

Willows are fed upon by adults of the leaf beetle *P. vulgatissima* in spring. The plants are generally attacked again later in the season when larvae hatch. Larvae usually cause the most severe damage to the plants, both because they can be very numerous and since they feed on the plants during the whole summer. It was observed that plants of *S. cinerea*, grazed upon by adult beetles in spring, had a higher leaf trichome density (leaf trichomes = leaf hairs) compared with non-grazed plants (P. Dalin; unpublished data). Leaf trichomes are considered to play an important role in many plants defence-system against herbivory and induced trichome responses have previously been reported for the perennial plant species alder *Alnus incana* (L.) (Baur *et al.* 1991) and the willow *S. borealis* (L.) (Zvereva *et al.* 1997).

In paper I we show that *S. cinerea* responds to adult beetle grazing by increasing the density of trichomes within plants, from old mature leaves to young leaves. The response was shown to be relatively rapid since it was expressed in plants within 22 days. Larvae were shown to be deterred from feeding on the induced leaves of *S. cinerea*. This was since larvae consumed a smaller total leaf area and showed a more dispersed feeding on previously adult grazed plants compared with larvae on control plants. However, the willow *S. viminalis*, used in plantations, was shown not to respond to adult leaf beetle grazing by increasing the number of trichomes (II). On *S. viminalis*, we found an overall decrease in trichome density, from mature to young leaves, within all plants. Also, we found no difference in larval feeding between previously adult grazed and control plants of *S. viminalis*. Although trichome density was shown to be higher on leaves of *S. viminalis*

compared with that on *S. cinerea*, larval growth was similar on the two willow species. This suggests that trichomes may not be of importance in *S. viminalis* defence against the leaf beetle *P. vulgatissima*. Larvae on densely trichome-covered leaves of *S. viminalis* appeared to feed at the base of trichomes and thereby removed the trichomes when feeding, a behaviour that was not observed for larvae feeding on *S. cinerea*. The trichomes of *S. viminalis* are generally longer and thinner compared with the rather short and thick trichomes on *S. cinerea*, indicating that the morphology of trichomes may be of importance. The results from paper I suggest that the induced response of *S. cinerea* function as a defence against subsequent larval feeding by deterring leaf beetle larvae from feeding on young leaves. The results from paper II show that *S. viminalis* seem to lack any type of induced response to adult grazing, chemical or morphological

It has been suggested that herbivore-induced plant responses may play an important role in influencing herbivorous insect populations (Haukioja & Neuvonen 1987; Edelman-Keshet & Rausher 1989). However, because the effects of induced plant responses on herbivore growth and survival often have been shown to be rather small (*e.g.* Nykänen & Koricheva 2004), the potential role in affecting insects at the population level has been questioned (Fowler & Lawton 1985). In the present study (I), we did not find any significant effect of the induced response of *S. cinerea* on larval growth. Although larvae consumed a smaller total leaf area, we found no significant difference in larval weight between induced and control plants. Thus, the effect of the response in affecting leaf beetles at the population level, or even at the individual level, is uncertain. Induced plant responses may, however, be most important from the perspective of the plants. For example, changes in quality within plants may redirect insect feeding away from the most valuable parts of plants, *e.g.* young leaves that may be of importance in the plant's competition for light (Edwards *et al.* 1992).

One can only speculate why we did not detect any induced defence in *S. viminalis*. A possible explanation is that the plants simply 'ignore' the attacker and allocate resources into growth; a phenomenon often referred to as tolerance (Strauss & Agrawal 1999). There are indications that *S. viminalis* can compensate at least for moderate levels of defoliation by *P. vulgatissima* (Björkman *et al.* 2000). Thus, it is possible that tolerance and defence are alternative strategies to cope with leaf beetle herbivory in this system.

### **Predator feeding habits and prey population dynamics (Paper III)**

Comparative studies on the life-history traits of herbivorous insect species known to often outbreak ('outbreak species'), and species that rarely outbreak ('non-outbreak species'), have revealed a variety of traits that differ between the two groups (see *e.g.* Price 2003). One of the more evident patterns is that outbreak species often feed or lay their eggs in aggregations (Hanski 1987; Hunter 1991; Larsson *et al.* 1993; Hunter 1995). The leaf beetle, *P. vulgatissima*, lays the eggs in aggregations (*i.e.* egg batches) and larvae feed gregariously as young. Although the reason for why an aggregated living should lead to a greater likelihood to

outbreak is still unknown, it indicates that spatial behaviours may be an important part in that which drives population dynamics (Cappuccino *et al.* 1995). It has been suggested that an aggregated living may lead to a greater protection from natural enemies (Vulinec 1990). Several studies have shown a higher per capita survival of herbivorous insects in dense patches, compared with those in less dense patches, when attacked by generalist predators (Cappuccino 1987; 1988; Stamp & Bowers 1988; Turchin & Kareiva 1989). However, predators may differ in their efficiency of finding prey aggregations and how they respond to dense prey patches (Wiskerke & Vet 1994). For example, when attacking egg batches of *P. vulgatissima*, the two mirids *O. marginalis* and *C. fulvomaculatus* were shown to consume a greater proportion of eggs within egg batches than the anthocorid *A. nemorum* (Björkman *et al.* 2003). However, the anthocorid was shown to visit (*i.e.* eat eggs from) more egg batches than the mirids. The two feeding habits were characterised as ‘find and stay’ for the mirids and ‘run and eat’ for the anthocorid (Björkman *et al.* 2003) (Fig. 3).



Fig. 3. Cartoon illustrating two types of predator feeding habits: ‘run and eat’ and ‘find and stay’. In principal, the ‘find and stay’ predator often stay and consume most eggs before moving on to search for other prey. The ‘run and eat’ predator consumes fewer eggs within egg batches but visits more egg batches than the ‘find and stay’ predator. Among the common predators attacking eggs of the leaf beetle *Phratora vulgatissima*, the ‘run and eat’ behaviour characterises the anthocorid *Anthocoris nemorum*, whereas the ‘find and stay’ behaviour characterises the two mirids *Orthotylus marginalis* and *Closterotomus fulvomaculatus*. (Cartoon made by Göran Johansson)

In paper III we investigate if the two feeding habits ‘find and stay’ and ‘run and eat’ could make any difference in the population dynamics of the leaf beetle *P. vulgatissima*. By using a stochastic exponential growth model we showed that prey can experience different temporal dynamics when exposed to predators that differ in the probabilities of finding egg batches, and in the probabilities to consume eggs within egg batches. Model prey populations colonising a willow stand with ‘find and stay’ predators were less likely to establish and to increase in abundance compared with prey exposed to predators with the ‘run and eat’ type of behaviours. Also, prey populations fluctuating at carrying capacity were more likely to decrease in abundance when exposed to ‘find and stay’ predators than when exposed to ‘run and eat’ predators.

In order to evaluate the results from the simulation model we conducted a field study where the abundance of predators and leaf beetles were studied in the field. The densities of leaf beetles and predators were surveyed in 21 natural willow (*S. cinerea*) stands for three years (2000-2002). Our prediction was that lower densities of leaf beetles would be found in willow stands dominated by ‘find and stay’ mirids. The results showed that ‘find and stay’ mirids (especially the mirid *O. marginalis*), in general, were more abundant than the ‘run and eat’ anthocorid *A. nemorum* in all willow stands studied. We found low densities of leaf beetles in willow stands growing in open agricultural landscapes (farmland natural stands) where the density of ‘find and stay’ mirids was almost three times higher than that in willow stands growing in forest habitats (forest natural stands) (Fig. 4). Also, farmland natural stands were more often unoccupied by leaf beetles than forest natural stands. Although we may not be able to separate the effects of predator behaviour and predator abundance in affecting these patterns of leaf beetle abundance, the results suggested that ‘find and stay’ mirids can have a significant effect on the distribution and abundance of leaf beetles. High population density of leaf beetles was only observed in forest natural stands, less dominated by ‘find and stay’ predators.

### **Plant quality or natural enemies? (Paper IV)**

The results from paper III showed that the leaf beetle *P. vulgatissima* occurred at lower densities on *S. cinerea* growing in farmland habitats than on plants growing in forest habitats (Fig. 4). It was hypothesised that this could be due to predation, because the abundance of heteropteran predators (especially mirids) was higher on *S. cinerea* growing in farmland habitats than on plants growing in forest habitats (Fig. 4). However, because plant quality traits of importance for insects, such as nutrition and secondary chemistry, can be determined not only genetically but also environmentally (Karban & Baldwin 1997; Koricheva *et al.* 1998), it is not unlikely that there also can be habitat differences in the quality of host plants (Sipura *et al.* 2002).

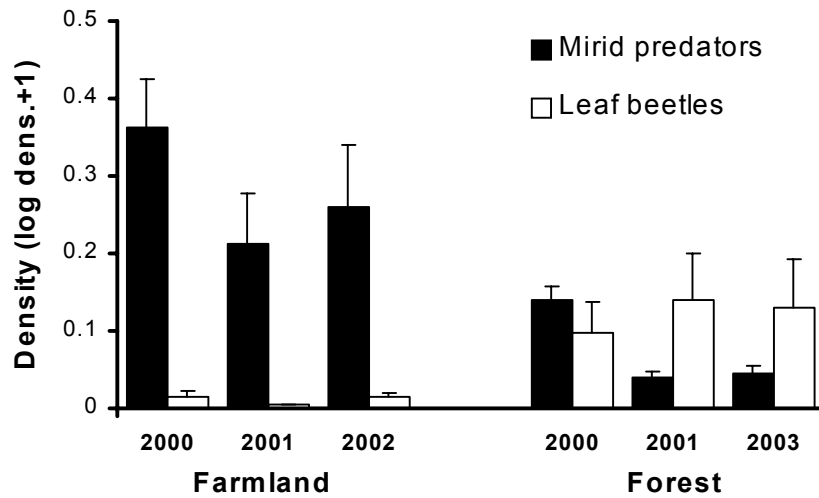


Fig. 4. Densities of mirid predators (*Orthotylus marginalis* and *Closterotomus fulvamaculatus* added together) and the leaf beetle *Phratora vulgatissima* during three years in *Salix cinerea* stands located in farmland (n = 9) and forest (n = 10) habitats.

The purpose of paper IV was to evaluate the relative effects of plant quality and natural enemies on the abundance of *P. vulgatissima* in stands of *S. cinerea* growing in farmland and forest habitats. Two hypotheses were formulated. The plant quality hypothesis states that *S. cinerea* growing in forests is of better quality for the leaf beetle than plants growing in farmlands. To test this hypothesis, female egg laying and larval performance (growth and survival) were studied by keeping caged adults and larvae on plants in the field. The prediction was that female beetles would lay more eggs and larvae would perform better in the forest than in the farmland habitat. The natural enemy hypothesis states that the forest is better for *P. vulgatissima* because the abundance of predators is lower compared with that in the farmland habitat. The survival of eggs exposed to natural enemies was measured in the field. The prediction was that the survival should be higher in the forest habitat than in the farmland habitat. Ten stands of *S. cinerea* growing in farmland habitats and ten stands growing in forest habitats were used to test the two hypotheses in year 2003.

The results indicated no difference in plant quality; female egg laying and larval performance did not differ between the forest and the farmland habitats. Consistent to what was found in paper III, omnivorous heteropterans (mainly the mirid *O. marginalis*) were more than twice as abundant on farmland willows than on forest willows. Consequently, the survival of eggs was lower in the farmland habitat (Fig. 5). Every experimental egg batch ( $n = 60$  egg batches) was preyed upon in the farmland habitat, whereas in the forest habitat, 12 % of the egg batches were left unattacked. The survival of eggs was negatively correlated with the abundance of the most common heteropteran, the mirid *O. marginalis*. The results suggested that the low abundance of *P. vulgatissima* on *S. cinerea* growing in



farmlands most likely is explained by a high predation, and not by a poor plant quality. Overall, the predation was very high, 100 % egg mortality was not uncommon in the farmland habitat. The study seems to corroborate the predictions from paper III, which suggest that mirids, when occurring at high densities, can cause an extensive mortality of prey, which seem to prevent the leaf beetle from increasing in abundance.

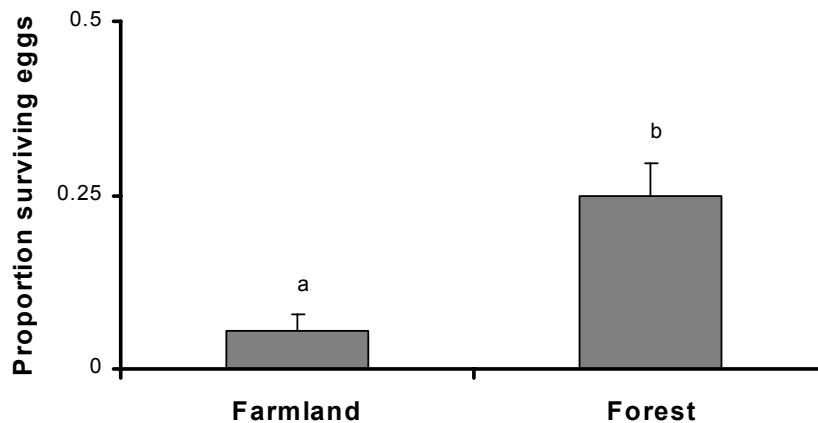


Fig. 5. Proportion of leaf beetle (*Phratora vulgatissima*) eggs that survived 14 days in the field when exposed to natural enemies. Bars represent the mean (+ S.E.) from stands of *Salix cinerea* growing in forest habitats and in farmland habitats. Different superscripts indicate significant difference (at the 5% level) as revealed by a Mann Whitney U-test.

### Population variability in managed and natural willow stands (Paper V)

Outbreaks of leaf beetles frequently occur in willow plantations (Sage 1994; Sage & Tucker 1998). It has been hypothesised that diverse systems, with many interacting species, may prevent populations of individual species from fluctuating wildly in size and to occasionally outbreak (MacArthur 1955; Elton 1958). In paper V, we test this hypothesis by comparing the temporal variability of leaf beetle, *P. vulgatissima*, population density in willow plantations (*Salix viminalis*) with that in natural (*S. cinerea*) willow stands. The density of leaf beetles was measured in 18 willow plantations and in 21 natural willow stands for five years. In accordance with the diversity-stability hypothesis, our prediction was that leaf beetles should fluctuate less in density in natural stands than in willow plantations, assuming that plantations are less diverse than natural stands. The coefficient of variation (CV) in beetle density, calculated over the five years, was used as a measure of temporal variability.

We found no difference in temporal variability between willow plantations and natural willow stands. Leaf beetle densities were, on average, as variable in natural willow stands as in willow plantations. Natural willow stands were more diverse

than willow plantations in terms of plant species diversity and structural complexity of the vegetation. Neither of these diversity indices (plant diversity or stand structural complexity) could explain any significant amount of variation in leaf beetle CV. Thus, we found no relationship between diversity and population stability of leaf beetles in this system (e.g. Fig. 6).

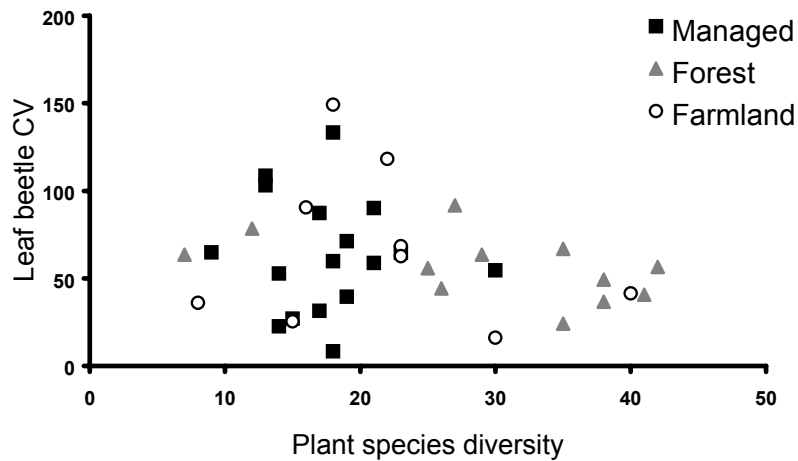


Fig. 6. Relationship between plant species diversity and population variability (i.e. the coefficient of variation, CV, in density) of the leaf beetle *Phratora vulgatissima*. The CV (x 100) calculated from density data over five years from 17 managed *Salix viminalis* plantations, 12 natural *S. cinerea* stands in forest habitats and 9 natural *S. cinerea* stands in farmland habitats.

The density of leaf beetles correlated negatively with the abundance of generalist predators (i.e. ants and heteropteran predators). The density of leaf beetles was low during the whole study period in all natural willow stands growing in farmland habitats. The abundance of heteropteran predators (*O. marginalis*, *C. fulvomaculatus* and *A. nemorum*) was almost three times higher in the farmland natural stands compared with that in both willow plantations and natural stands growing in forest habitats. High ‘outbreak’ densities of leaf beetles were observed in both willow plantations and natural willow stands, but only for natural stands growing in the forest habitats. The outbreak stands were characterised by a low density of predators.

The leaf beetle went from relatively low densities to high outbreak densities within a few years in two out of the 18 willow plantations studied (see example in Fig. 7). Such a pattern was not observed in any of the natural willow stands where the leaf beetle either fluctuated at low (e.g. in the farmland natural stands) or high (e.g. in some of the forest natural stands) densities during the whole study period. There was no direct cause-and-effect relationship between low predator abundance and a high density of leaf beetles in willow plantations. Thus, the leaf beetle occurred at low densities also in willow plantations with a low abundance of predators. A possible explanation for this could be that the populations of leaf beetles have not had the time to build up in numbers in some of the willow

plantations during the study period. On average, we found no significant differences in temporal variability of leaf beetle populations between managed and natural willow habitats. However, it is possible that the conclusions may have been different if the pattern of going from low to high densities had been observed in more than two willow plantations.

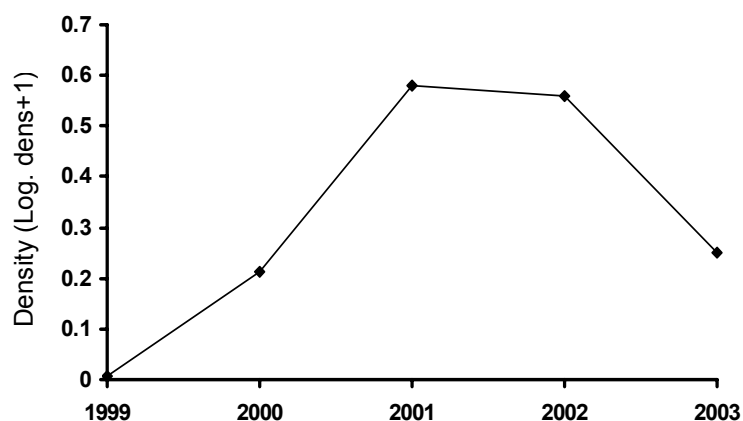


Fig. 7. Example of a drastic increase in leaf beetle (*Phratora vulgatissima*) density observed in a willow plantation (*S. viminalis*). Density represents the average number of leaf beetles per 35-cm parts of plants, presented on a log-scale (Log. [density + 1]).

## Conclusions

High population densities of the leaf beetle *Phratora vulgatissima* can be found in both willow plantations (*Salix viminalis*) and in natural willow (*S. cinerea*) stands. The populations of leaf beetles studied did not, on average, fluctuate more or less in willow plantations compared with that in natural willow stands. Thus, we found no evidence for that population should be more stable in natural willow systems than in managed willow systems. However, drastic increases in leaf beetle density ('outbreaks') tended to be more frequent in managed stands. What seems to have the potential to prevent leaf beetle outbreaks in willow stands is a high abundance of predators, especially omnivorous heteropterans. The leaf beetle occurred at low densities on *S. cinerea* growing in agricultural landscapes (farmland natural willow stands) where the mirid *Orthotylus marginalis* was shown to be abundant. Experimental leaf beetle eggs put out on farmland natural willows had a very low survival. The willow stands with high ('outbreak') densities of leaf beetles were characterised by a low abundance of predators. The results from the studies suggest that heteropteran predators can have a strong influence on the abundance of willow leaf beetles.

Willow plantations are regularly harvested in wintertime (every 4-5 years), which has been shown to influence both leaf beetle and heteropteran predator populations (Björkman *et al.* 2004). However, the greatest negative effect of harvesting was shown to be for mirid predators (Björkman *et al.* 2004). This is probably because mirids over-winter as eggs on the plants (Southwood & Leston 1959; Wheeler 2001). Hence, it seems that mirids are removed by the harvesting regime, which may disrupt the control of leaf beetles (Björkman *et al.* 2004). The leaf beetles, however, usually leave the plantations in autumn to find hibernation sites in the vicinity of the plantations and are thereby less influenced by harvest. One possible way to increase heteropteran predator abundance in willow plantations could be to favour natural willows, such as *S. cinerea*, in the agricultural landscapes. Although this needs further investigations, natural willows in the vicinity may speed up the colonising process of heteropteran predators into plantations. Further studies are also needed on what determines the abundance of heteropterans in the field. For example, why does the mirid *O. marginalis* occur at higher densities on *S. cinerea* growing in farmland habitats than on plants growing in forest habitats? An increased knowledge may, for example, give indications on how to manipulate the abundance of heteropterans in willow plantations.

It may be surprising to find mirids to be major predators in this system, since they are primarily known to be plant-feeders (Wheeler 2001). However, because they can feed and survive on multiple trophic levels, they are unlikely to starve or emigrate when, for example, leaf beetles are scarce. Consequently, they can occur at high densities independently of leaf beetles and may thereby continue to attack the eggs and larvae of leaf beetles also when the leaf beetle occurs at low densities. Also, the results from the simulation model showed that the 'find and stay' behaviour of the mirids was more likely to suppress and prevent increases in leaf beetle numbers than the 'run and eat' behaviour that may characterise many other generalist predators. This highlights the potential role of omnivorous mirids in influencing the abundance and distribution of willow leaf beetles. The usage of mirids in biological control programs has to a large extent been neglected (Coll & Ruberson 1998). However, the results from this thesis strongly recommend that they need more attention.

The two willow species studied in this thesis were shown to respond differently to leaf beetle attack. The natural willow *S. cinerea* responded by producing new leaves with an increased density of trichomes and larvae were deterred from feeding on these induced leaves. This type of induced defence may reduce overall damage done to the plants and could potentially be utilised in plant protection in short rotation forestry. However, the willow species *S. viminalis* most commonly used in short rotation forestry, was shown not to respond to beetle grazing by increasing the density of trichomes. Also, larval leaf beetles did not seem to be affected by the long and thin trichomes of *S. viminalis*. Further studies are therefore needed for willow genotypes with suitable characteristics with respect to both plant growth and hairiness. To optimise the selection, this approach will have to be extended, to also study the effects of trichomes on other insects attacking willows.

## References

- Altieri M.A. 1991. Increasing biodiversity to improve insect pest management in agroecosystems. In: *The biodiversity of microorganisms and invertebrates: its role in sustainable agriculture* (ed. D.L. Hawksworth). CAB International, Wallingford. pp. 165-182.
- Azerfegne F., Solbreck, C. & Ives A.R. 2001. Environmental forcing and high amplitude fluctuations in the population dynamics of the tropical butterfly *Acraea acerata* (Lepidoptera: Nymphalidae). *Journal of animal ecology*, 70, 1032-1045.
- Baur R., Binder S. & Benz G. 1991. Non glandular leaf trichomes as short-term inducible defence of the grey alder, *Alnus incana* (L.), against the chrysomelid beetle, *Agelastica alni* L. *Oecologia*, 87, 219-226.
- Bernays E.A. & Chapman R.F. 1994. *Host-plant selection by phytophagous insects*. Chapman and Hall, New York.
- Berryman A.A. 1987. The theory and classification of outbreaks. In: *Insect Outbreaks* (eds. P. Barbosa & J.C. Schultz). Academic Press, San Diego. pp. 3-30.
- Berryman A.A. 1988. *Dynamics of forest insect populations*. Plenum press, New York.
- Berryman A.A. 1999. *Principles of population dynamics and their application*. Stanley Thorns, Cheltenham.
- Berryman A.A., Stenseth N.C. & Isaev A.S. 1987. Natural regulation of herbivorous forest insect populations. *Oecologia*, 71, 174-184.
- Björkman C., Höglund S., Eklund K. & Larsson S. 2000. Effects of leaf beetle damage on stem wood production in coppicing willow. *Agricultural and forest entomology*, 2, 131-139.
- Björkman C., Dalin P. & Eklund K. 2003. Generalist natural enemies of a willow leaf beetle (*Phratora vulgatissima*): abundance and feeding habits. *Journal of insect behaviour*, 16, 747 – 764.
- Björkman C., Bommarco R., Eklund K. & Höglund S. 2004a. Harvest disrupts biological control in a short-rotation coppice system. *Ecological application*. In press.
- Björkman C., Dalin P. & Eklund K. 2004b. Skinnbaggar som predatorer på skadeinsekter i Salixodlingar. *Entomologisk Tidskrift* 125, In press.
- Cappuccino N. 1987. Comparative population dynamics of two goldenrod aphids: spatial patterns and temporal constancy. *Ecology*, 68, 1634-1646.
- Cappuccino N. 1988. Spatial patterns of goldenrod aphids and the response of enemies to patch density. *Oecologia*, 76, 607-610.
- Cappuccino N., Damman H. & Dubuc J.F. 1995. Spatial behaviour and temporal dynamics of outbreak and nonoutbreak species. In: *Population dynamics, new approaches and synthesis* (eds. N. Cappuccino & P.W. Price). Academic Press, San Diego. pp. 65-82.
- Cedervind J. & Långström B. 2003. Tree mortality, foliage recovery and top-kill in stands of Scots Pine (*Pinus sylvestris*) subsequent to defoliation by the pine looper (*Bupalus piniaria*). *Scandinavian journal of forest research*, 18, 505-513.
- Cedervind J., Pettersson M. & Långström B. 2003. Attack dynamics of the pine shoot beetle, *Tomicus piniperda* (Col.; Scolytinae) in Scots pine stands defoliated by *Bupalus piniaria* (Lep.; Geometridae). *Agricultural and forest entomology*, 5, 253-261.
- Coll M. & Ruberson J.R. 1998. Predatory heteroptera: an important yet neglected group of natural enemies. In: *Predatory heteroptera: their ecology and use in biological control* (eds. M. Coll & J.R. Ruberson). Thomas Say Publications, Lanham MD, Entomological Society of America. pp. 1-6.
- DeBach P. & Rosen D. 1991. *Biological control by natural enemies*. Cambridge University Press, Cambridge.
- Denno R.F. Larsson S. & Olmstead K.L. 1990. The role of enemy-free space and plant quality in host-plant selection by willow beetles. *Ecology*, 71, 124-137.
- Denno R.F., McClure M.S. & Ott J.R. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual review of entomology*, 40, 297-331.

- Edelstein-Keshet L. & Rausher M.D. 1989. The effects of inducible plant defences on herbivore populations. 1. Mobile herbivores in continuous time. *American naturalist*, 133, 787-810.
- Edwards P.J., Wratten S.D. & Parker E.A. 1992. The ecological significance of rapid wound-induced changes in plants: insect grazing and plant competition. *Oecologia*, 91, 266-272.
- Elton C.S. 1958. *The ecology of invasions by animals and plants*. Methuen, London.
- Ferro D.N. 1987. Insect pest outbreaks in agroecosystems. In: *Insect outbreaks* (eds. P. Barbosa & J.C. Schultz). Academic Press, San Diego. pp. 195-215.
- Fowler S.V. & Lawton J.H. 1985. Rapidly induced defences and talking trees: the devil's advocate position. *American naturalist*, 126, 181-195.
- Hanski I. 1987. Pine sawfly population dynamics: patterns, processes, problems. *Oikos*, 50, 327-335.
- Hartley S.E. & Jones C.G. 1997. Plant chemistry, or why the world is green. In: *Plant ecology* (ed. M.J. Crawley). Blackwell Science, Oxford. pp. 284-324.
- Hassell M.P. 1978. *Arthropod predator-prey systems*. Monographs in population biology, 13. Princeton University Press, New Jersey.
- Haukioja E. & Neuvonen S. 1987. Insect population dynamics and induction of plant resistance: the testing of hypotheses. In: *Insect outbreaks* (eds. P. Barbosa & J.C. Schultz). Academic Press, San Diego. pp. 411-432.
- Hunter A.F. 1991. Traits that distinguish outbreaking and nonoutbreaking Macrolepidoptera feeding on northern hardwood trees. *Oikos*, 60, 275-282.
- Hunter A.F. 1995. Ecology, life history, and phylogeny of outbreak and nonoutbreak species. In: *Population dynamics, new approaches and synthesis* (eds. N. Cappuccino & P.W. Price). Academic Press, San Diego. pp. 41-64.
- Hylander N. 1971. Första litteraturuppgift för Sveriges vildväxande kärllväxter jämte uppgifter om första fynd. *Svensk botanisk tidskrift*, 64, 1-322.
- Jonsell B. (ed.) 2000. *Flora Nordica*. Bergius Foundation, Stockholm.
- Julkunen-Tiitto R. 1986. A chemotaxonomic survey of phenolics in leaves of northern salicaceae species. *Phytochemistry*, 25, 663-667.
- Karban R. & Baldwin I. 1997. *Induced responses to herbivory*. The University of Chicago Press, Chicago.
- Kelly M.T. & Curry J.P. 1991a. The influence of phenolic compounds on the suitability of three *Salix* species as hosts for the willow beetle *Phratora vulgatissima*. *Entomologia experimentalis et applicata*, 61, 25-32.
- Kelly M.T. & Curry J.P. 1991b. The biology and population density of the willow leaf beetle (*Phratora vulgatissima* [L.]) on *Salix viminalis* in reclaimed cutaway peat. *Journal of applied entomology*, 111, 44-56.
- Kendall D.A., Hunter T., Arnold G.M., Liggitt J., Morris T. & Wiltshire C.W. 1996a. Susceptibility of willow clones (*Salix* spp.) to herbivory by *Phyllodecta vulgatissima* (L.) and *Galerucella lineola* (Fab.) (Coleoptera, Chrysomelidae). *Annals of applied biology*, 129, 379-390.
- Kendall D.A., Wiltshire C.W. & Butcher M. 1996b. *Phenology and population dynamics of willow leaf beetles (Coleoptera; Chrysomelidae) in short-rotation coppiced willows at Long-Ashton*. ETSU (DTI) Biofuels Study B/M4/00487/14/REP. IACR Long Ashton Research Station, Long Ashton, Bristol.
- Kendall D.A. & Wiltshire C.W. 1998. Life-cycles and ecology of willow leaf beetles on *Salix viminalis* in England. *European journal of forest pathology*, 28, 281-288.
- Klang-Westin E. & Eriksson J. 2003. Potential of *Salix* as phytoextractor for Cd on moderately contaminated soils. *Plant and soil*, 249, 127-137.
- Kolehmainen J., Julkunen-Tiitto R., Roininen H. & Tahvavainen J. 1995. Phenolic glycosides as feeding cues for willow leaf beetles. *Entomologia experimentalis et applicata*, 74, 235-243.
- Koricheva J., Larsson S., Haukioja E. & Keinänen M. 1998. Regulation of woody plant secondary metabolism by resource availability: hypothesis testing by means of meta-analysis. *Oikos*, 83, 212-226.

- Kosola K.R., Dickmann, D.I., Paul, E.A. & Parry, D. 2001. Repeated insect defoliation effects on growth, nitrogen acquisition, carbohydrates, and root demography of poplars. *Oecologia*, 129, 65-74.
- Kulman H.M. 1971. Effects of insect defoliation on growth and mortality of trees. *Annual review of entomology*, 16, 289-324.
- Larsson S., Björkman C. & Kidd N.A.C. 1993. Outbreaks of diprionid sawflies: why some species and not others. In: *Sawfly life history adaptations to woody plants* (eds. M.R. Wagner & K.F. Raffa). Academic Press, San Diego. pp. 453-484.
- Larsson S., Ekbohm B. & Björkman C. 2000. Influence of plant quality on pine sawfly population dynamics. *Oikos*, 89, 440-450.
- Ledin S. & Willebrand E. 1995. *Handbook on how to grow short rotation forests*. IEA Bioenergy, Swedish University of Agricultural Sciences, Uppsala.
- Lekander B. 1953. Über das Auftreten von Blastophagus piniperda und Pissodes pini im Wald vorher befallen von Panolis- und Bupalus- Raupen. *Meddelande från statens skogsforskningsinstitut*, 44, 31.
- MacArthur R. 1955. Fluctuations of animal populations, and a measure of community stability. *Ecology*, 36, 533-536.
- Maisner N. 1974. Chrysomelidae, Blattkäfer. In: *Die forstschädlinge Europas, vol. 2* (ed. W. Schwenke). Parey, Hamburg. pp. 202-236.
- Maron J.L., Harrison S. & Greaves M. 2001. Origin of an insect outbreak: escape in space or time from natural enemies? *Oecologia*, 126, 595-602.
- McCann K.S. 2000. The diversity-stability debate. *Nature*, 405, 228-233.
- Murdoch W.W. 1975. Diversity, complexity, stability and pest control. *Journal of applied ecology*, 12, 795-807.
- Murdoch, W.W. & Oaten A. 1975. Predation and population stability. *Advances in ecological research*, 9, 1-131.
- Nykänen H. & Koricheva J. 2004. Damage-induced changes in woody plants and their effects on insect herbivore performance: a meta-analysis. *Oikos*, 104, 247-268.
- Peacock L., Herrick S. & Brain P. 1999. Spatio-temporal dynamics of willow beetle (*Phratora vulgatissima*) in short-rotation coppice willows grown as monocultures or a genetically diverse mixture. *Agricultural and forest entomology*, 1, 287-296.
- Peacock L., Lewis M. & Herrick S. 2001a. Factors influencing the aggregative response of the blue willow beetle, *Phratora vulgatissima*. *Entomologia experimentalis et applicata*, 98, 195-201.
- Peacock L., Lewis M. & Powers S. 2001b. Volatile compounds from *Salix* spp. varieties differing in susceptibility to three willow beetle species. *Journal of chemical ecology*, 27, 1943-1951.
- Pimentel D. 1961. Species diversity and insect population outbreaks. *Annals of the entomological society of America*, 54, 76-86.
- Price P.W. 1987. The role of natural enemies in insect populations. In: *Insect outbreaks* (eds. P. Barbosa & J.C. Schultz). Academic Press, San Diego. pp. 287-312.
- Price P.W. 2003. *Macroevolutionary theory on macroecological patterns*. Cambridge University Press, Cambridge.
- Rank N.E., Köpf A., Julkunen-Tiitto R. & Tahvanainen J. 1998. Host preference and larval performance of the salicylate-using leaf beetle *Phratora vitellinae*. *Ecology*, 79, 618-631.
- Raymond B., Vanbergen A., Hartley S.E., Cory J.S. & Hails R.S. 2002. Escape from pupal predation as a potential cause of outbreaks of the winter moth, *Operophtera brumata*. *Oikos*, 98, 219-228.
- Rhoades D.F. 1983. Herbivore population dynamics and plant chemistry. In: *Variable plants and herbivores in natural and managed systems* (eds. R.F. Denno & M.S. McClure). Academic Press, New York. pp. 155-220.
- Risch S.J. 1987. Agricultural ecology and insect outbreaks. In: *Insect outbreaks* (eds. P. Barbosa & J.C. Schultz). Academic Press, San Diego. pp. 217-238.
- Rowell-Rahier M. 1984. The food plant preference of *Phratora vitellinae*. *Oecologia*, 64, 369-374.

- Sage R.B. 1994. *A review of the status and control strategies of known and perceived insect pests on Salix and Populus in North West Europe*. ETSU B/M3/00388/10/REP. The Game Conservancy Trust, Fordingbridge.
- Sage R.B. & Tucker K. 1998. The distribution of *Phratora vulgatissima* (Coleoptera: Chrysomelidae) on cultivated willows in Britain and Ireland. *European journal of forest pathology*, 28, 289-296.
- Sage R.B., Fell D., Tucker K. & Sotherton N.W. 1999. Post hibernation dispersal of three leaf-eating beetles (Coleoptera: Chrysomelidae) colonising cultivated willows and poplars. *Agricultural and forest entomology*, 1, 61-70.
- Schowalter T.D., Hargrove W.W. & Crossley D.A. 1986. Herbivory in forested ecosystems. *Annual review of entomology*, 31, 177-196.
- Schoonhoven L. M., Jermy T. & van Loon J.J.A. 1998. *Insect-plant biology*. Chapman and Hall, London.
- Scriber J.M. & Hainze J.H. 1987. Geographic invasion and abundance as facilitated by differential host plant utilization abilities. In: *Insect outbreaks* (eds. P. Barbosa & J.C. Schultz). Academic Press, San Diego. pp. 433-468.
- Sipura M. 1999. Tritrophic interactions: willows, herbivorous insects and insectivorous birds. *Oecologia*, 121, 537-545.
- Sipura M. 2002. Contrasting effects of ants on the herbivory and growth of two willow species. *Ecology*, 83, 2680-2690.
- Sipura M., Ikonen A., Tahvanainen J. & Roininen H. 2002. Why does the leaf beetle *Galerucella lineola* F. attack wetland willows? *Ecology*, 83, 3393-3407.
- Sirén G., Sennerby-Forsse L. & Ledin S. 1987. Energy plantations – short rotation forestry in Sweden. In: *Biomass* (eds. D.O. Hall & R.P. Overend). John Wiley, London. pp. 119-143.
- Southwood T.R.E. & Leston D. 1958. *Land and water bugs of the British Isles*. Frederick Warne, London.
- Stamp N.E. & Bowers M.D. 1988. Direct and indirect effects of predatory wasps (*Polistes* sp.: Vespidae) on gregarious caterpillars (*Hemileuca lucina*: Saturniidae). *Oecologia*, 75, 619-624.
- Strauss S.Y. & Agrawal A.A. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in ecology and evolution*, 14, 179-185.
- Turchin P. 2003. *Complex population dynamics*. Monographs in population biology, 35. Princeton University Press, New Jersey.
- Turchin P. & Kareiva P. 1989. Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. *Ecology*, 70, 1008-1016.
- Underwood N. 2000. Density dependence in induced plant resistance to herbivore damage: threshold, strength and genetic variation. *Oikos*, 89, 295-300.
- Underwood N. & Rausher M.D. 2000. The effects of host-plant genotype on herbivore population dynamics. *Ecology*, 81, 1565-1576.
- Underwood N. & Rausher M. 2002. Comparing the consequences of induced and constitutive plant resistance for herbivore population dynamics. *American naturalist*, 160, 20-30.
- Vandenhove H., Thiry Y., Gommers A., Goor F., Jossart J.M., Holm E., Gaufert T., Roed J., Grebenkov A. & Timofeyev S. 2001. Short rotation coppice for revaluation of contaminated land. *Journal of environmental radioactivity*, 56, 157-184.
- Wiskerke J.S.C. & Vet L.E.M. 1994. Foraging for solitary and gregariously feeding caterpillars: a comparison of two related parasitoid species (Hymenoptera: Braconidae). *Journal of insect behaviour*, 7, 585-603.
- Wheeler A.G. 2001. *Biology of the plant bugs*. Cornell University Press, New York.
- Vulinec K. 1990. Collective security: aggregation by insects as a defence. In: *Insect defences* (eds. D.L. Evans & J.O. Schmidt) State University of New York Press, Albany.
- Zvereva E.L., Kozlov M.V., Niemelä P. & Haukioja E. 1997. Delayed induced resistance and increase in leaf fluctuating asymmetry as responses of *Salix borealis* to insect herbivory. *Oecologia*, 109, 368-373.



## Acknowledgements

First of all I would like to thank my supervisor Christer Björkman. I really appreciate the way you have supervised me throughout these years. Importantly, you have always provided me with great support and encouragement, which has given me the inspiration and force to finish this thesis. I am also obliged to you for all the time you have taken to discuss, comment on manuscripts and to help me with different parts of the daily work. I want you to know that I have learned a lot and really enjoyed my time as a PhD-student!

My gratitude goes also to Oskar Kindvall, my assistant supervisor, and to Karin Eklund, not formally a supervisor, but anyway a great supervisor in the world of leaf beetles and willows. Oskar, I have learned a lot from our collaboration and your big knowledge has been a great inspiration. Karin, your knowledge about the system has been invaluable and I am grateful for all the help and support you have provided me.

Ever since my days as an undergraduate student, I have found the Department of Entomology a stimulating and friendly place to be. This thank you is therefore directed to every person at our department. Also, I am still very proud about my victory in the Lucia-election!

I am also very happy about my stay at the Ecology and Entomology Group in Christchurch, New Zealand. It was a very important part of my PhD-education and I am grateful to Steve Wratten, who took great care of me. Many thanks also to Stefan Thomsen for letting me live in his house and for visiting me in Uppsala last summer. Blas Lavandero was also one of those persons how made my stay in New Zealand a great period of my life.

I would also like to thank all the assistants and students that has been involved in the project: Karin Ahrné, Jorge Calvo Carrillo, Adriana Jerlström-Maj, Erica Johannesson, Niklas Jönsson and Anna-Sara Liman. Many thanks also to Claes Hellqvist and Göran Johansson for making the illustrations to this thesis and to Richard Hopkins for the comments on the summary.

Finally, I would like to thank my mother, father and friends (you know who you are!) for always supporting me. I would also like to take the opportunity to thank my former schoolteachers Berndt Larsson and Åke Persson, who once upon a time introduced me into the exciting world of nature (especially bird-watching!).