Pine weevil feeding in Scots pine and Norway spruce regenerations

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Abstract

Damage caused by the pine weevil, *Hylobius abietis* (L) feeding on conifer seedlings is a major problem in reforested areas in many parts of Europe. The adult weevil feeds on the stem-bark of young seedlings, frequently killing a large proportion of newly planted seedlings.

The aims of the studies underlying this thesis were to investigate whether additional food supplies could decrease the damage caused by pine weevil to seedlings, and to determine whether access to extra food might explain why seedlings beneath shelter trees receive less damage from pine weevils compared to seedlings planted in a clear-cutting. A survey was conducted to study what effect removing shelter trees has on the level of damage pine weevils cause to seedlings. Finally, the influence of factors including fertilization, establishment and soil scarification on the growth and tolerance of Norway spruce seedlings to pine weevil feeding was studied.

Pine weevil damage to seedlings was significantly reduced when extra food (fresh branches of Scots pine) was regularly provided nearby. Feeding by pine weevils in the crowns of large trees occurred during a limited period following their migratory flight but did not seem to be sufficient enough to explain the lower feeding pressure observed on seedlings in shelterwoods over the entire season. During the first year after cutting, roots in the humus layer seemed to be an important food source but were utilized to similar extent in both clear-cuts and shelterwoods. Thus, findings reported provided valuable knowledge about pine weevil feeding on seedlings and other food sources but could not fully explain why seedlings planted beneath shelter trees receive less pine weevil damage compared to seedlings planted on an open clear-cutting.

Before the removal of shelter trees, Norway spruce and Scots pine seedlings need to have reached diameters of 10-12 mm in order to avoid lethal levels of damage from pine weevil attack.

Loading Norway spruce seedlings with nutrients in the autumn before plantation did not lead to more feeding from pine weevils. Treatments that postpone the start of pine weevil feeding enhanced the ability of seedlings to sustain pine weevil damage later on, probably as a result of reduced stress allowing a more rapid establishment of seedlings.

*Keywords: C*onifer seedling, feeding, fertilization, damage, *Hylobius abietis*, large pine weevil, reforestation, shelter trees, shelterwood, tolerance.

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List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Örlander, G., Nordlander, G., Wallertz, K. & Nordenhem, H: 2000. Feeding in the crowns of Scots pine trees by the pine weevil, *Hylobius abietis*. *Scandinavian Journal of Forest research* 15, 194-201.

II Örlander, G., Nordlander, G., Wallertz, K. 2001. Extra food supply decreases damage by the pine weevil *Hylobius abietis*. *Scandinavian Journal of Forest research* 16, 450-454.

III Wallertz, K. Örlander, G. & Luoranen. 2005. Damage by pine weevil *Hylobius abietis* to conifer seedlings after shelterwood removal. *Scandinavian Journal of Forest research* 20, 412-420.

IV Wallertz, K., Nordlander, G. & Örlander, G. 2006. Feeding on roots in the humus layer by adult pine weevil *Hylobius abietis*. *Agricultural and Forest Entomology*. 8: 273-279.

V Wallertz, K. & Petersson, M. Pine weevil feeding on Norway spruce seedlings: effect of nutrient-loading; scarification and physical protection. *Manuscript*.

Papers I-IV are reproduced with the permission of the publishers.

The contribution of Kristina Wallertz to the papers included in this thesis was as follows:

I Örlander and Nordlander were mainly responsible for writing Paper I and for the inspiration behind it, while Wallertz was responsible for the field work, some writing, and part of the data processing

II Örlander and Nordlander were responsible for the experimental design, and most of the writing, while Wallertz was responsible for the field work, some writing and data processing

III Wallertz and Örlander designed the study and were responsible for the literature search and writing of the paper, Luoranen and Wallertz were both responsible for the data processing and data were collected by Wallertz.

IV Örlander and Nordlander were responsible for the design of the experiment and Wallertz undertook the field work and data processing. Wallertz and Nordlander were responsible for writing the paper and for literature research, assisted by Örlander.

V Wallertz and Petersson were responsible for designing the experiment. Wallertz conducted all the field work, data processing and writing of the paper, assisted by Petersson.

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1 Introduction

In 1758 Linnaeus described the large pine weevil in his "Systema Naturae", but the insect was not then considered to be a pest as forests were not really managed at that time (Långström & Day 2004). During the 19th century when forests began to be intensively managed, the pine weevil, *Hylobius abietis*, became the major pest of regenerating forests in several European countries (Ratzeburg 1839). Current silvicultural methods, where coniferous forests are predominantly managed by clearfelling, create an environment highly favourable for pine weevil reproduction (Långström & Day 2004). Pine weevils are attracted to clear-cuttings where roots of the stumps are used as a breeding substrate (Eidmann 1974, Nordlander et al. 1997). The major forestry problem is that the adult weevils feed on the stem-bark of young conifer seedlings, causing severe damage and often high mortality rates (Christianssen 1971, Eidmann 1974, Örlander & Nilsson 1999, Wainhouse et al. 2004, Petersson et al. 2004). *H. abietis* is common in most parts of Europe and Asia where conifer trees occur, and some other *Hylobius* species of economic importance occur in both Asia and North America.

1.1 Biology

Pine weevils migrate by flight in the spring or early summer and invade fresh clearcuts, to which they are attracted by odours emanating from newly dead conifer roots: a material in which they can breed (Escherich 1923, Solbreck & Gyldberg 1979, Schlyter 2004). Although adult weevils can fly long distances (Solbreck 1980), the average distance between fresh clearcuts in southern Sweden is short, implying that most sites are within easy reach of swarming pine weevils. Pine weevils build up their flight muscles before leaving their site of emergence (Nordenhem 1989). Some time after migration to their breeding sites, their flight muscles regress and the weevils remain on the ground for the rest of the season.

In August, when days get shorter, the weevils become less active and they hibernate in the soil, emerging in the following spring (Örlander et al. 1997). The generation time (the time it takes to progress from one stage in their development to the same stage in the subsequent generation) is normally two years in southern Sweden (Bejer-Petersen et al. 1962, Nordenhem 1989, Day et al. 2004). However, adult weevils of the new generation often emerge in late summer about 14 months after oviposition (Leather et al. 1999). These weevils often cause severe damage to seedlings in the autumn before they hibernate in the soil (von Sydow 1997, Örlander & Nilsson 1999). Development time depends on the climate and therefore varies between regions and years (Långström 1982). In the UK, when circumstances are favourable, the new generation can emerge in May the year after the egg has been laid, although cold temperatures often delay the completion of development until between July and September (Day et al. 2004).

Pine weevils feed on the woody stems of several tree species, but prefer conifers (Manlove et al. 1997, Leather et al. 1999, Löf et al. 2004, Månsson & Schlyter, 2004, Löf et al. 2005). The weevils eat the bark of young seedlings, branches on trees, roots in the humus layer and the bark of shrubs. Several factors affect feeding by pine weevils, including temperature, soil type, surrounding vegetation, and the species on which they feed (Christianssen & Bakke 1971, Pohris 1983, Leather et al. 1994, Örlander & Nordlander 2003, Wainhouse et al. 2004, Petersson et al. 2005, 2006). The optimal temperature for pine weevil activity is about 20°C; their activity is reduced at higher and lower temperatures (Christiansen & Bakke, 1968. Wainhouse et al. (2004) showed weevil size to be an important factor affecting feeding rate, suggesting that variation in size within natural populations may contribute to local variations in feeding on seedlings in the field. Moreover, reproductive females eat about 50% more than males or non-reproductive females (Bylund et al. 2004).

1.2 *Hylobius* in Europe

In addition to the large pine weevil *H. abietis*, three other *Hylobius* species occur in Europe. The lesser pine weevil, *Hylobius pinastri*, is considered to be of less importance, and the few published observations suggest that while its life history is similar to that of *Hylobius abietis* (Eidmann 1974, Långström

1982, Nordlander 1990, Långström & Day 2004), its habitat preferences are slightly different. *H. pinastri* has been shown to be more abundant on moist sites dominated by Norway spruce (Långström 1982, Nordlander 1990 and is moderately abundant in Sweden. In a study in southern Sweden the highest catches accounted for 2.4% of the total *Hylobius* population (Örlander et al. 1997). However, *H. pinastri* occurs in many other countries including Poland, Finland, Estonia and Latvia (Karczewski 1961, Långström 1982, Pitkänen et al. 2008, Ozols et al. 1989). Even less common is *H. piceus*, which is mostly found in moist forests breeding in the root collar of living trees and seldom observed to feed on seedlings, although it is sometimes caught in traps (personal observation). A fourth species, *H. transversovittatus*, differs from the others as far as its host, *Lythrium salicaria*, is a perennial plant not related to conifer trees. Interestingly, this plant is an invasive weed of Eurasian origin that has replaced native wetland vegetation in the United States where *H. transversovittatus* is used as a biological control agent (McAvoy et al. 2002).

1.3 Other related *Hylobius* species

In North America there are several species in the genus *Hylobius* (Cerezke 1994, Day et al. 2004). *H. radicis* and *H. warreni* breeds in the root collar region of healthy hosts (Cerezke 1994, Day et al. 2004) while *H. pales* and *H. congener* are known to breed in roots of dying or recently dead trees, as does *H.abietis* (Welty & Houseweart 1985, Day et al. 2004). Moreover, *H. pales* and *H. congener* are similar to *H.abietis* in that they also feed on conifer seedlings and are therefore described here further.

The pales weevil, *H. pales* is a serious pest in new pine plantations and Christmas-tree plantations throughout eastern North America (Peirson 1921, Lynch 1984). The adult weevils are attracted by the odour of freshly cut pine stumps, logs, and slash, and the weevils feed on the tender bark of mature trees, saplings and seedlings. Pest management tactics vary in different areas but the most common are stump treatments, insecticide treatments and delayed planting (Salom 1998).

H. congener is reported to range from North Carolina to the Canadian Maritimes and west to Alaska (Martin 1964, Welty & Houseweart 1985). Several surveys conducted in Nova Scotia have revealed high mortality among seedlings attacked by the weevil (Lyver 2001). Its biology is not well documented but it seems to be similar to *H. abietis*. The larvae feed on the roots and phloem tissue of the residual stumps and logs, and adults feed on young seedlings. However, in several red pine cuttings where logs and slash remained, stumps were hardly used for oviposition, and when weevils were placed in cages and given a choice of logs and stumps, they ignored the stumps and laid their eggs in the logs (Martin 1964). Generation time is reported to be two years (Welty & Houseweart 1985, Pendrel 1990, Lyver 2001). This species caused less debarking in the interior of plantations, on burned or scarified sites, and where litter had been scraped back from the seedling bases (Welty & Houseweart 1985). Lyver (2001) found that when shelter trees were left, the damage caused by *H. congener* to seedlings decreased in correlation with the percentage of over-storey left standing.

Hylobius xiaoi (Zang) is native to south-eastern China where it has become a major pest, mainly attacking two exotic pines: slash pine, *Pinus elliotti,* and loblolly pine, *P. taeda;* and the native masson pine *P. massoniana* (YongSong et al. 2004). The larvae feed on the inner bark of the lower stem and root collar causing severe damage and mortality. Methods to control the insect are spraying with insecticides or removing branches, litter, vegetation and soil from around the tree base (Wen et al. 2006).

1.4 Methods to reduce damage

Several measures can be used to protect seedlings from pine weevil damage, but the most common approach in Europe since the 1950s has been to use insecticides (Leather et al. 1999, Långström & Day 2004). However, because of the environmental and health risks associated with insecticides, their use has been questioned in many countries (Mian & Mulla 1992, Swedish Chemicals Inspectorate 2005). Moreover, the process of forest certification might further reduce the utilization of insecticides (Hansen 1998). Feeding barriers that physically prevent the pine weevil from reaching the seedlings have been developed and tested in Sweden for a long time (Lindström et al. 1986, Eidmann et al. 1996, Petersson et al. 2004, Nordlander et al. 2009). There are two main types: shields - with or without a collar (made of paper, plastic or other materials); or various types of coating applied to the lower part of the stem (Petersson et al. 2004).

Silvicultural measures that can reduce pine weevil damage include scarification and planting under shelterwoods (Söderström et al. 1978, von Sydow 1997, Örlander & Nilsson 1999). Scarification is widely used in Scandinavia and is beneficial both for promoting the establishment of newly planted seedlings (Örlander et al. 1990, Nordborg & Nilsson 2003) and for reducing pine weevil damage to conifer seedlings (Söderström 1978, Björklund et al. 2003, Petersson & Örlander 2003, Petersson et al. 2005). It has been proved that planting under shelter trees reduces damage to conifer seedlings compared to planting in clear-cuttings (von Sydow & Örlander 1994, Nordlander et al. 2003a, 2003b). An additive effect can be achieved if different methods are used (Petersson & Örlander 2003), and combinations of silvicultural measures and seedling protection are commonly applied in practical forestry in Sweden today.

1.5 Other methods

Antifeedant compounds might be a potential alternative to insecticides. Bark extracts from *P. contorta* deter feeding more than extracts from *P. sylvestris* (Bratt et al. 2001). Månsson & Schlyter (2004) found that linden (*T. cordata*) was rejected as a food source by the pine weevil. The bark contains nonanoic acid, a chemical constituent which has a strong antifeedant activity against the pine weevil (Månsson et al. 2005). During oviposition, female weevils defecate on their eggs which causes other females to avoid ovipositing in the same place. Weevil excrement has thus been found to act as a deterrent (Borg-Karlson et al. 2006). The active substance has been identified but finding a suitable carrier has proved to be more difficult than expected. Carvone (Schlyter et al. 2004, Kleipzig & Schlyter 1999) and neem (*Azadirachta indica*) oil (Bryan 2003, Thacker et al. 2003) are other substances that have been shown to have a deterrent effect on pine weevil feeding,

Another approach to reduce pine weevil damage to seedlings is to suppress the pine weevil population. In the UK and Ireland there is great interest in the use of entomopathogenic nematodes and the method has been shown to increase mortality to larvae and pupae of *H. abietis* (Dillon et al. 2007). In Sweden, there are at least two indigenous parasitoid species which attack *H. abietis: Perilitus areolaris* (Gerdin & Hedqvist) (Gerdin & Hedqvist 1985) and *Bracon hylobii* (Ratzeburg) (Henry & Day 2000); the former attacks the adult weevil while the latter attacks the larvae. *P. areolais* may cause high mortality rates, sometimes up to 40% (Bylund et al. unpublished) and the mortality caused by *B. hylobii* has been estimated to be almost 50% (Henry 1995), indicating that these two parasitoids might be potential bio-control agents if the approach of suppressing the populations is considered to be a realistic alternative to other methods.

Removal of stumps is a method that has been reintroduced in Sweden and in Finland during the last few years. Theoretically this method might reduce the breeding potential of the pine weevil and thus in the long run suppress the population. Research in the matter has recently started. However, earlier results indicated that there might be enough amount of roots left in the ground to support a substantial weevil population (Långström and Day 2004).

In regions like southern Sweden, most conifer forests are managed by clear-cutting followed by replanting with conifer seedlings. The short distances between the clear-cuts, and their even geographic distribution, make it possible for weevils to invade most fresh clear-cuts in an area. Therefore, to prevent pine weevil damage to seedlings, methods other than suppressing the weevil population have generally been more favoured in Sweden.

1.6 Soil scarification

Directly after planting, the development of seedlings depends to a great extent on their ability to take up water (Örlander 1986, Grossnickle 1988, Örlander et al. 1998). However, field vegetation competes with the seedlings for water, and other resources such as light and nutrients (Imo & Timmer 1999, Nordborg & Nilsson 2003). Soil scarification is a method whereby the organic layer is removed and the mineral soil surface becomes exposed, although the technique might also result in a mixing of humus and mineral soil. The aims are to improve seedling establishment and growth and reduce the risk of frost injuries, and damage from voles and insects (Örlander et al. 1990). Soil scarification is well known to reduce pine weevil damage to conifer seedlings (Söderström et al. 1978, Lindström et al. 1986, Örlander & Nilsson 1999, Örlander & Nordlander 2003). The reduction is usually most evident in the first year after planting (Örlander & Nilsson 1999) and the best effects are achieved if the seedling is surrounded by pure mineral soil (Björklund et al. 2003, Petersson et al. 2005). According to Långström and Day (2004) scarification as a counter-measure against pine weevil is mainly used in the Scandinavian countries.

Pine weevils move faster and straighter on mineral soil compared to humus and consequently spend less time there (Kindvall et al. 2000). However, Björklund et al. (2003) found that the same number of weevils were caught in traps placed on mineral soil and humus, suggesting that, for some reason, pine weevils do not feed on seedlings planted in mineral soil, even if they pass very closely to them. Some suggested explanations of this behaviour include a lack of hiding places, risk of overheating due to solar radiation, and greater risks of predation while exposed on a mineral soil substrate (Björklund et al. 2003, Örlander & Nordlander 2003).

The dominant soil preparation methods in Sweden are disc trenching and patch scarification/mounding (Strömberg et al. 2001). Soil inversion, where inverted humus is covered with the underlying mineral soil, is a method still under development. Experiments have shown that soil inversion creates a favourable environment for seedling growth and has at least the same effect on pine weevil damage as patch scarification or disc trenching (Örlander et al. 1998). Soil inversion was used as the scarification method in paper V.

1.7 Shelterwoods

When harvesting an old forest, the area can either be completely cleared of trees, or some trees can be left as seed trees or shelter trees. The purpose of a seed tree stand is to produce and distribute seeds, while a shelterwood also provides a sheltering purpose (Hagner 1962, Karlsson 2000). Shelter-woods are used in Scandinavia but also in other parts of Europe and North America (Smith 1986, Matthew 1991, Lyver 2001). Shelter trees not only reduce the risks of damage from frost, they also promote a greater diversity of field vegetation than is normally found in clearcuts (Langvall & Örlander 1991, Hannerz & Hånell 1997). Moreover, in Sweden shelterwood is sometimes used to promote mixed conifer forests, i.e. naturally regenerated pine seedlings derived from the shelter trees are allowed to grow together with planted seedlings of spruce (Nilsson et al. 2006). Several studies in Scandinavia have demonstrated that planting beneath shelter trees reduces damage caused by *H. abietis* to conifer seedlings (von Sydow & Örlander 1994, Nordlander et al. 2003a, Pitkänen et al. 2005) but the reason why is not yet fully understood.

Pine weevils are attracted to new clear-cuts by odours emanating from fresh stumps and fresh slash (Escherich 1923, Nordenhem & Eidmann 1991, Schlyter 2004). The hypothesis that fewer weevils should be attracted to areas with a shelterwood than to clear-cuts, because there are fewer stumps in the former, therefore seems plausible. However, trap catches of pine weevils have shown the sizes of pine weevil populations in shelterwoods and clearcuts to be similar, although the damage to seedlings was considerably more intense in the latter (von Sydow & Örlander 1994, Nordlander et al. 2003a). Similarly, Pitkänen et al. (2008) caught higher numbers of pine weevils among groups of retained trees than in open areas. Thus, reasons other than differences in the size of populations have to be found to explain the reduction in pine weevil damage.

In Canada, damage from *H. congener* decreased as shade increased from over-story trees (Swift 2000, Lyver 2001). Moreover, shelterwood systems are frequently recommended for regeneration of white pine (*Pinus strobi*) in north-eastern North America, because of the protection shelter trees offer against the white pine weevil, *Pissodes strobus* (Major et al. 2009). In a study by Heiskanen (2004), the provision of shade after planting reduced solar radiation, enhanced shoot growth, and reduced pine weevil damage for at least a few years after planting. However, Nordlander et al. (2003b) argued that reasons other than light reduction are involved in the decrease of pine weevil damage on seedlings planted underneath shelter trees. The authors found that, even with the same conditions of light and temperature, seedlings planted near the edge of a clearcut were less damaged by pine weevil compared to seedlings far from the edge. They suggested that the greater availability of alternative food sources for the weevil close to the forest edge may be the cause of lower levels of damage there, rather than microclimatic differences between the edge and centre of a clearcut. The effects of alternative food sources on pine weevil damage to seedlings are examined in Paper I, II and IV. The theory was that access to extra food sources should be greater in shelterwoods compared to open clear-cuttings and at least to some extent explain the differences in pine weevil damage to seedlings.

After removal of shelter trees the odour from new stumps attracts weevils such that they are likely to invade the area (Sundkvist 1994, Örlander & Karlsson 2000). The severity of pine weevil damage to seedlings beneath shelter trees might be influenced by seedling size, tree species and seedling vitality; factors that were examined in Paper III.

1.8 Seedling quality

The risk of severe damage to seedlings depends not only on feeding activity and the environment, but also on seedling size (Örlander & Nilsson 1999, Thorsén et al. 2001). Thorsén et al. indicated that to ensure more than 80% survival of Norway spruce seedlings, the root collar diameter should be at least 8 mm for seedlings planted in scarified plots. Wainhouse (2009) calculated minimum diameters for Sitka spruce and Corsican pine to be 10.3 mm and 7 mm, respectively, in order for them to be relatively resistant to pine weevil feeding.

One possible way to increase growth in order to quickly achieve a seedling size that is more resistant to weevil attack, is to fertilize seedlings before or after planting. Seedling performance in response to field fertilization is variable (Grossnickle 2000), and field fertilization generally increases the amount of ground vegetation (Nordborg & Nilsson 2003). Moreover, Nilsson & Örlander (2003) found that field fertilization enhances growth when combined with a herbicide treatment, but not without, suggesting that the ground vegetation is more efficient in the uptake of nutrients than Norway spruce seedlings.

Loading the seedlings with fertilizer during the autumn before planting has proved to increase shoot growth after plantation (Grossnickle 2000, Rikala et al. 2004). However, fertilizing seedlings has also increased pine weevil damage to them (Selander & Immonen 1992, Zas et al. 2006). The effect of nutrient loading, in combination with other measures to enhance growth and tolerance to pine weevil damage, are investigated in Paper V.

The amount of resources available to seedlings could modify their defense mechanisms which might, in turn, lead to changes in their resistance to insect feeding (van Akker 2004, Herms & Mattsson 1992). Carbon nutrient balance and growth differentiation balance are two hypotheses among several others, that attempt to describe a plant's strategic dilemma of whether to grow or defend itself (Herms & Mattson 1992). In conifers, resin within ducts in the bark constitutes an important quantitative defence (Wainhouse 2009). Reduced feeding by weevils is probably caused by the higher concentrations of resin acids found in the wounded area (Gref & Ericsson 1985). Fertilization significantly increased growth and reduced the resin canal density in the phloem of *Pinus pinaster* (Moreira et al. 2008). The authors suggested that general tracheid enlargement which pushes the resin canals farther apart explains, at least to some extent, the decline in resin canal density and also the lower defensive function in fertilized compared to unfertilized seedlings. By contrast, Wainhouse et al. (2009) showed there to be a positive correlation between growth and resin-based quantitative defence in young Corsican pine and Sitka spruce. Thus the effect of fertilization on seedlings' defences against and tolerance to pine weevil damage, appear to be inconclusive at present.

1.9 Aims of this thesis

The work described in this thesis was designed to investigate how additional food sources affect pine weevil feeding on conifer seedlings, and to determine whether access to these food sources may explain the reduction of pine weevil damage to seedlings in shelterwood systems. Another important issue with implications for forest regeneration management was to study the effect that removing shelter trees has on the level of damage pine weevils cause to seedlings. How factors like nutrient-loading, plant establishment, and soil scarification affect growth and tolerance to pine weevil feeding were also essential parts of the studies.

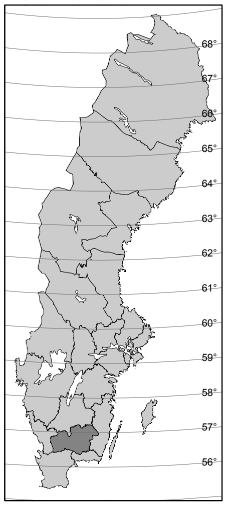
The main objectives were *i)* to obtain a better understanding of factors that determine the intensity of feeding by pine weevils in shelter-woods and on clear-cuttings, and *ii)* to investigate how seedling establishment affects conifer seedlings´ tolerance to pine weevil feeding.

2 Materials and methods

2.1 General aspects

The experiments were performed in the south-west border of the boreo-nemoral zone, which coincides with the natural limit for Norway spruce (Lundmark 1986). In this zone, Norway spruce (*Picea abies* L. Karst.), Scots pine (*Pinus sylvestris* L.) and silverbirch (*Betula pendula*) are the most abundant forest tree species. All experimental sites were situated within a radius of 50 km from the Asa Forest Research Station, in the county of Kronoberg, where around 75% of the total land area is classified as forest land (Figure 1). The proportion by volume of the most common species in this area is: Norway spruce 56%, Scots pine 25%, and birch 11% (Swedish Forest Agency).

Figure 1. Map of Sweden with the county of Kronoberg highlighted in dark grey.



Most of the inventories of feeding on seedlings or other food sources were performed on fresh clear-cuts i.e. those in the first season after cutting. This means that adult pine weevils that had recently migrated into the clearcuts were the main cause of feeding damage. In the studies reported in papers III and V, seedlings were measured in both the first and second years after felling, which means that both colonizing weevils and weevils from the new generation emerging in the autumn of the second year, may have caused damage to the seedlings at the time of the inventory.

All examined food sources in the experiments, including the seedlings, were untreated, i.e. no insecticides or other chemicals had been used on them. Due to the experimental design of study V, some of the seedlings were protected against pine weevil by a plastic shield covered with Fluon® for different lengths of time. Containerized seedlings of Norway spruce were used in all experiments where planting of new seedlings was conducted. In the survey where damage was investigated after the removal of shelter trees, the seedlings originated from planted or naturally regenerated seedlings of Norway spruce and Scots pine.

In studies I, II and IV, experiments were designed to investigate how food sources other than seedlings (branches of Scots pine and roots in the humus layer) might affect pine weevil feeding. The overall question was whether the availability of an extra food supply might be the reason for a reduced level of pine weevil damage to seedlings beneath shelter trees.

Mean values (±SE) of numbers of pine weevils caught, levels of pine weevil feeding on branches in the crowns, branches on the ground (Papers I, II), on roots (Paper IV), and on seedlings (Papers II, IV, V) were calculated. When analysis of variance was performed the SAS GLM (SAS Institute, Inc., Cary, NC, USA) procedure was used. Frequency data were used for calculating the level of pine weevil damage and, because the requirements for normally distributed data were not fulfilled, the data were Arc-sin square root transformed before being tested (Zar 1984). The SAS Univariate procedure was used to test for normal distribution.

In study III, damage to seedlings was investigated after shelterwood removal. Before the shelter trees were cut, 10 circular plots were laid out at six different sites (Table 1). The shelter trees and seedlings were measured. Mean debarked seedling stem areas (±SE) were calculated for pine and spruce seedling diameter and recorded in 2 mm classes. These data were then pooled into four diameter-classes to calculate differences in the extent of feeding between pine and spruce. The differences in the risk of seedlings being damaged by pine weevil were tested using non linear regression. Since the assumptions for using t-tests were not met when estimating differences in the amount of feeding area between tree species and between basal area Wilcoxon rank-sum tests were used.

The experimental design of the study described in Paper V was randomized blocks with four blocks on each of three sites. The general linear model (GLM) procedure of the SAS software for randomised block designs was used to perform the statistical tests. Different hypotheses regarding the effect of nutrient-loading and establishment (protection against pine weevil for shorter or longer periods) were analysed for seedlings planted in humus or mineral soil. In the analyses only comparisons that were relevant for testing each hypothesis were performed.

Pine weevil feeding on seedlings was recorded in the same way in all experiments. Damage severity was recorded using a six-level scale ranging from undamaged to dead (Papers II,III,IV and V). The debarked area on the main stem of the seedlings was estimated to within 0.1 cm^2. The same technique was used to estimate debarking of roots (Paper IV) and branches (Papers I,II).

3 Results and discussion

3.1 Feeding on different kinds of food source (I, II, IV)

Pine weevils have been observed feeding on several types of food source, both coniferous and broad-leaved tree species, as well as sprigs and shrubs of different species (Munroe 1927, Leather 1994, Manlove 1997, Örlander et al. 1999, Månsson & Schlyter 2004, Bylund et al. 2004, Wainhouse 2004). The availability of alternative food sources may be greater in shelterwoods than clear-cuts, and could be an important factor accounting for the lower amounts of pine weevil damage to seedlings observed in shelterwoods (Nordlander et al. 2003a, 2003b).

The first question that has to be answered is whether additional food supply relieves feeding pressure on seedlings. On plots where branches were supplied as additional food sources, the weevils fed extensively on them (Paper II) which resulted in decreased feeding on the planted seedlings. The mean debarked area on seedlings was significantly lower in plots with the extra food supply than in the control plots, standing at 54 mm^2 and 140 mm^2, respectively. The results indicate an affirmative answer to the initial question.

Furthermore, the accumulated feeding area was three times higher on branches sampled at the end of the experiment than on branches sampled after one week, indicating that the branches served as a food source for more than one week. Therefore, planting in fresh slash consisting of branches and tops of trees, after final cutting, could be a practical and effective measure to reduce damage to seedlings (Selander 1993). Örlander & Nilsson (1999) suggested that slash might serve as food for the weevils, but only for a short period before it dries out, which is in accordance with another study conducted by Axelsson (1987). Wainhouse et al. (2004) demonstrated a rapid decline in the carbohydrate content of logs after felling, suggesting that the nutritional quality of such material is likely to change over time and that it therefore represents a relatively poor food source for adult weevils. Thus, extra food can relieve seedlings from pine weevil damage, but it has to be fresh, which means that suitable vegetation must either grow or be regularly supplied close to the seedlings. In practice the latter option seems hard to achieve.

Bilberry is a natural potential food source and is commonly abundant in the ground vegetation beneath shelter trees. However, bilberry growing close to the seedlings in a shelterwood did not significantly affect pine weevil feeding on planted seedlings (Paper II). The mean debarked area of roots in the humus layer by pine weevils was estimated to 2.9 m^2, per hectare: 2.6 m^2 of conifer roots and 0.3 m^2 of bilberry roots (Paper IV). Bilberry is probably one of many additional food sources utilized by the pine weevil, but the study indicate that roots from conifer trees are preferred.

Bark on branches of large trees is another potential food source that is utilized by pine weevils. As early as 1923, Escherich mentioned that pine weevils may feed in the crowns of mature trees. Most of the feeding in the crowns occurred in the spring or early summer on trees at the edge of fresh clear-cuts (Paper I). The number of weevils collected from trees provided with a Fluon®-coated plastic band was similar to those that had no such obstacle, which proves that many weevils reach the crowns by flying. The weevils consumed, on average, 200 cm^2 bark per tree and calculations show that this amount of feeding on Scots pine surrounding a normal sized clearcut represents a food intake large enough to meet the needs of maturation-feeding pine weevils. This does not exclude the fact that other food sources are also used during this period. The average area of bark consumed on shelter trees from four fresh shelterwoods was 50 cm^2 which is much lower than for trees at the edges of clear-cuts. This accords with the results of pine weevil catches, where the number of weevils collected at the edge of the clearcut was significantly higher than the number collected 5-10 m away from the edge. Branches in the crowns of Scots pine trees represent a large food source that is predominantly utilized only during a short period in the spring and early summer. Thus, feeding in the crown can only relieve seedlings from feeding pressure during that part of the season.

Roots in the humus layer are yet another food source utilized by *H. abietis*. On average, 3 741 m^2 per hectare of root bark was available in the humus layer and there was no difference in mean root areas of the clear-cut and the shelterwood the first year after cutting (Paper IV). The mean area debarked by pine weevils was 2.9 m^2, indicating that roots are a major food resource for them. The frequency of seedlings that were killed or severely damaged by pine weevil was higher in the clearcuts than in the shelter-woods in 1998; no difference was found in 2002. However, although the pattern of feeding was not consistent when comparing shelterwoods and clear-cuts, a weak negative correlation was found between the debarked areas on roots and seedlings, indicating that feeding on roots decreases damage to seedlings, at least to some extent.

Bylund et al. (2004) calculated that a normal plantation of 2 500 seedlings per hectare would provide pine weevils with approximately 2.5 m^2 of seedling bark per hectare. Pine weevils eat around 0.2 cm^2 of bark tissue per day under semi-natural conditions; however, they may eat less in situations where conditions are less ideal (Bylund et al. 2004). The population density after immigration in the spring has been estimated to be approximately 14 000 weevils per hectare (Nordlander et al. 2003a). Based on these calculations 20-30 m^2 of bark per hectare would be consumed by pine weevils during a season of two to three months; i.e. three to five times more than the amounts consumed in the studies underlying this thesis. Several factors may affect the debarked areas at specific times and places, including population density, nutritional quality of the food, weather conditions, tree species and vitality of the seedlings. In laboratory conditions the weevils fed on all non-host species except P*opulus*, indicating that the pine weevil is able to feed on species other than Scots pine or Norway spruce when these are absent (Månsson & Schlyter, 2004).

The reported findings provided knowledge about pine weevil feeding on seedlings and on other food sources. However, to make a complete feeding budget for the pine weevil we need to recognize and quantify the other sources that are fed upon.

3.2 Tree species (I, III)

The relative area of bark consumed from branches in the crowns of mature Scots pine was three times that of Norway spruce (Paper I). In the study presented in Paper III, the debarked area was significantly higher in all diameter classes for Scots pine seedlings than for Norway spruce seedlings. This agrees well with some earlier studies (Långström 1982, Leather et al.

1994, Manlove 1997) but conflicts with others (von Sydow & Örlander, 1994). Large Scots pine seedlings (10-14 mm in root collar diameter) were more attractive to weevils than Norway spruce seedlings of the same size. Scots pine twigs with a diameter between 10-12 mm had the highest proportion of their area consumed by weevils, while twigs thinner than 3 mm and thicker than 20 mm were seldom utilized. These results indicate that, even within the same species, bark varies in its suitability as a food, depending on twig diameter, bark structure, age, or other reasons.

Evidence of variation between species in their ability to tolerate pine weevil attack was demonstrated in laboratory experiments comparing seedlings of Scots pine and Norway spruce (Långström & Hellqvist 1989). They showed that mechanically wounding the two species to the same extent resulted in a higher mortality rate among spruce than pine. Wainhouse et al. (2009) showed that the number of resin ducts in Norway spruce was similar to Scots pine, but that the rate of resin production was generally lower, resulting in a greater susceptibility of Norway spruce seedlings to feeding by pine weevil. After shelter-wood removal (Paper III) the mean debarked area among Scots pine seedlings was twice that of Norway spruce; thus it is not possible to determine conclusively any difference in tolerance between the two tree species by this study.

3.3 Seedling properties (III, V)

The study presented in Paper III showed that after shelter tree removal, the risk of severe damage to seedlings increases, which is in accordance with several other studies (Karlsson 2000, Karlsson & Örlander 2004). The risk of damage was strongly correlated to seedling size before cutting, with small seedlings being more vulnerable compared to larger seedlings. Seedling size is well documented to be an important factor in seedling tolerance to pine weevil feeding (Thorsén et al. 2001, Långström & Day 2004). The results from the study in Paper III show that before removal of shelter trees, Norway spruce and Scots pine seedlings need to have reached a stem base diameter of at least 10-12 mm in order to avoid severe damage by pine weevil.

The vitality of the seedlings, assessed as leading shoot growth during the year before cutting, also influenced the risk of severe damage by pine weevil; better vitality resulted in less damage. This finding is in accord with Örlander & Karlsson (2000) who showed that height, and top-shoot length, in the year before release cutting, correlated with survival and growth in height of advance grown seedlings. Vitality and seedling height were suggested to be fairly good predictors of post-release growth and survival (Glöde 2002).

In the study presented in Paper V, the lowest dry weight of new roots was from nutritionally unloaded seedlings planted in unscarified humus. Loaded seedlings in humus had about the same dry weight of roots as both unloaded and loaded seedlings in mineral soil. This indicates that loading might have had some effect on seedling performance even though it did not show in any of the analyses performed on growth. The similarity between the average dry mass of new roots of loaded and unloaded seedlings planted in scarified plots, is probably because seedling establishment and especially root growth, are known to be enhanced by soil scarification (Örlander et .al. 1990, Nordborg, 2003). Nutrient loading in the nursery is one way to build up plant nutrient reserves when shoot growth in the nursery has ceased. These reserves are then available to seedlings after planting and might thus improve field performance, growth and vitality (Grossnickle 2000).

In several studies, fertilized seedlings have been attacked by pine weevil more frequently than unfertilized seedlings (Selander & Immonen 1992, Selander & Immonen 1991, Zas et al. 2006, Zas et al. 2008). Loading increases the nutrient content of the seedlings, which might make seedlings more attractive to weevils immediately after planting. However, nutrient loaded spruce seedlings in Paper V were not fed upon any more than were unloaded seedlings . Laboratory studies also confirmed this finding, which contradicts those of several other studies mentioned above. The reason for this discrepancy is, however, not fully understood. In the present study, pine weevil feeding on unprotected seedlings planted in humus was very intense, causing 90 % mortality after one season. This indicates that the pine weevil pressure was very high and therefore differences between treatments might have been hard to detect. Other factors that may have influenced the results of the different studies are the composition and amount of fertilizer applied and how and when the application occurred.

Seedlings that were physically protected from pine weevils during a short period after planting, were fed upon to the same extent (in terms of debarked area) as those without protection, but the mortality rate of the former was significantly lower after one season (Paper V). For those seedlings that were protected for the whole first season, the debarked area was even higher compared to those seedlings protected for only a short period, yet still the mortality rate among them was lower. The results indicate that protection of the seedlings during the time of establishment enhances tolerance to pine weevil damage to seedlings.

It is possible that factors collectively termed "planting stress" could influence seedling susceptibility to attacks of pine weevil (Wainhouse 2004). Growth of new roots is known to be critical for newly planted seedlings, in order that they might reach water and nutrients in the soil quickly (Nordborg & Nilsson 2003). Seedlings stressed of draught are known to suffer greater damage from pine weevils than well-watered ones (Selander & Immonen 1991). Selander et al.(1990) suggested that well established seedlings are more tolerant to feeding by pine weevil than newly planted. Treatments that postpone the start of pine weevil feeding may increase root growth and reduce stress factors and thus enhance their ability to sustain damage.

Månsson & Schlyter (2004) found that in 35 out of 38 species selected from 25 plant families, the outer bark was contacted and removed by pine weevil but not always consumed, probably because of repellent qualities in the plant. Alpha-pinene has been reported as an attractant in several studies (Selander et al. 1974, Nordlander 1990). Other terpenoids emitted from conifer seedlings have been found to inhibit attraction, for example limonene (Nordlander 1990, 1991), verbenone (Lindgren et al. 1996) and carvone (Klepzig & Schlyter 1999). In the present study the analyses of monoterpenes in nutrient loaded and unloaded seedlings indicated that they might exist in higher concentrations in unloaded seedlings. However no differences were found in feeding pattern between the differently fertilized seedlings, indicating that other factors may influence feeding more than the monoterpene content.

3.4 Finding and consuming the food (I,II,IV,V)

Other interesting questions concern how weevils find their food, and what other factors may influence their feeding behaviour. In Paper I the weevils were actually observed flying to or from the crowns of mature Scots pine trees. Some weevils were also seen taking off from the ground and flying up to large trees. Visual orientation appeared to be important in finding suitable trees to feed on, the highest number of weevils was also found in the most exposed trees at the forest edge.

In Paper V, the effect of scarification on reducing the level of damage to seedlings was distinct and confirms the findings of several previous studies

(Söderström et al. 1978, Örlander & Nilsson 1999, Petersson & Örlander 2003). The presence of hiding places may affect the amount of time weevils spend in an area and hence the time spent on the direct consumption of bark. Björklund et al. (2003) found that traps set in patches of mineral soil caught no fewer weevils than traps placed in humus, although the likelihood that an approaching weevil would feed on the seedlings was reduced. Pine weevils prefer to feed below ground if the food source is on bare soil with no shelter above ground (Nordlander et al. 2005). Mineral soil offers fewer hiding places than humus and this is probably one reason for the decreased tendency of weevils to spend long periods of time on scarified plots.

Roots in the humus layer, and to some extent branches on the ground, provide the pine weevil sheltered conditions for feeding (Papers II, IV). Bylund et al. (2004) found that feeding on the buried sides of the stems accounted for 70% of the total feeding in relatively warm conditions indoors, compared to just 30% outdoors. This indicates that temperature does influence the feeding behaviour of pine weevils. Such temperature effects may also explain why we found considerably less feeding on roots in 1998 compared to the summer 2002, when the weather was extremely warm and dry during the summer (Paper IV).

4 Conclusions

4.1 Conclusions of this study

It is possible to reduce damage to seedlings if fresh, attractive food is regularly supplied in the vicinity of the planted seedlings.

Most of the feeding by pine weevils in the crowns of large trees occurs during a short period after the migration flight in the spring or early summer.

Conifer roots in the humus layer constitute a large food source for the pine weevil. Roots from other species, like bilberry, are also utilized by the pine weevil although the results indicate that conifer roots are preferred.

After final cutting of shelter trees, the area is most likely invaded by immigrating pine weevils in the spring. Important factors that influence the severity of pine weevil damage to seedlings beneath shelter trees include seedling size and vitality.

Loading seedlings with nutrients in the autumn before plantation did not lead to more feeding by the pine weevil. Seedling establishment seemed to be an important factor for tolerance to pine weevil damage.

The findings reported provided valuable new knowledge about pine weevil feeding on seedlings and on other food sources that might be useful for future research.

4.2 Practical use and future research

The use of insecticides to protect seedlings is increasingly questioned because of the associated environmental and health risks. Alternative methods that reduce pine weevil damage are therefore of great importance. Planting beneath shelter trees is one way of reducing pine weevil damage, although the method needs to be combined with other measures in order to achieve an adequate level of protection (Petersson & Örlander 2003). In stands of Scots pine or a mixture of Scots pine and Norway spruce, leaving shelter trees in combination with scarification, or providing seedlings with some kind of feeding barrier seem to be a good option. Shelter trees also reduce the risk of frost damage to seedlings and at the same time promote greater diversity of ground vegetation (Langvall & Örlander 1991, Karlsson & Örlander 2004). Leaving shelter trees also enhances the aesthetic value of forestry, giving plantations an appearance more resembling to that of the original forest.

An additional alternative supply of fresh food for weevils, regularly provided close to the seedlings, was proven to relieve feeding pressure on seedlings. It has been suggested that the lower level of damage that occurs beneath shelter trees is due to the greater availability of alternative food found there. However, although the study of pine weevil feeding on roots in the humus layer and on branches of large Scots pine trees has contributed to new and valuable knowledge, the results could not explain the observed reduction in the level of damage caused by pine weevils to seedlings beneath shelter trees. Trying to complete a feeding budget for the pine weevil could stimulate the generation of new hypotheses and suggest alternative and novel methods that could be implemented to protect conifer seedlings from the damage caused by pine weevil feeding.

Several studies have shown that loading seedlings with nutrients before planting positively affects root growth and hence nutrient and water uptake. These factors affect the vitality and establishment of seedlings and their ability to tolerate pine weevil attack. Nutrient loading did not affect pine weevil feeding on seedlings, but it did have a weak positive impact on root growth. It could, therefore, if combined with other measures, be a useful tool to improve seedling establishment. Treatments that postpone the start of pine weevil feeding enhanced the ability of seedlings to sustain damage later on, probably due to increased root growth and reduced stress factors during their establishment. It would be desirable to find methods to facilitate and hasten seedling establishment in order to create a seedling that can better sustain damage by pine weevil.

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