Abstract

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Damage caused by the pine weevil, *Hylobius abietis* (L.) (Coleoptera, Curculionidae) feeding on conifer seedlings is a major problem in reforested areas in many parts of Europe. The adult pine weevil feeds on the stem bark of young seedlings, frequently killing a large proportion of newly planted seedlings. Planting beneath a shelterwood has proved to reduce pine weevil damage on conifer seedlings, but the reasons for this are not yet fully understood. One suggestion that has been put forward is that the shelterwood provides alternative food sources, which are not present in clearcuts, for the weevils. The aims of the studies underlying this thesis were to investigate the possibility that additional food supplies could decrease damage to seedlings, to quantify pine weevil feeding on roots in the humus layer and to examine the possibility that increased feeding on roots in the shelterwood could explain the observed difference in feeding damage to planted seedlings. The effect of removing shelter trees on pine weevil damage to seedlings was examined in a survey study.

Pine weevil damage on seedlings was significantly reduced when extra food (fresh branches of Scots pine) was regularly provided close to the seedling. The above ground part of natural field vegetation, mainly bilberry, did not reduce the damage to the same extent.

Roots in the humus layer comprised an important food resource for the pine weevil and during the first year after cutting it was utilised to similar extents in both clearcuts and shelterwoods. Roots from other species, like bilberry, were less abundant but were also utilised by the pine weevil.

After final cutting of shelter trees the area was invaded by immigrating pine weevils in the spring, which damaged the seedlings. Before shelter trees are cut Norway spruce and Scots pine seedlings should have reached diameters of at least 9 and 12 mm, respectively, in order to avoid lethal damage by pine weevil.

Keywords: Curculionidae, conifer seedling, feeding damage, *Hylobius abietis*, large pine weevil, reforestation, shelter trees, shelterwood.

Author's address: Kristina Wallertz, Asa Forest Research Station, Swedish University of Agricultural Sciences, SE 360 30 Lammhult, Sweden, e-mail: Kristina.Wallertz@esf.slu.se

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Appendix

Papers I-III

This thesis is based on the following papers, which will be referred to by their corresponding Roman numerals, I-III.

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.

Wallertz, K., Nordlander, G. & Örlander, G. 2005. Feeding on roots in the humus layer by adult pine weevil, *Hylobius abietis*. Agricultural and Forest Entomology. *Submitted*.

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

Papers I and III are reprinted from Scandinavian Journal of Forest Research (<u>www.tandf.no/forest</u>) by kind permission of Taylor & Francis AS.

Örlander and Nordlander were mainly responsible for writing Paper I and for the inspiration behind it, while Wallertz was responsible for the field work and part of the data processing. Örlander and Nordlander were responsible for the experimental design of study II, and Wallertz undertook the field work and data processing. Wallertz and Nordlander were mainly responsible for writing the paper and for researching the associated literature, assisted by Örlander. In study III, Örlander and Wallertz conceived the study and were responsible for researching the literature and writing the paper. Luoranen and Wallertz both undertook the data processing. Data were collected by Wallertz.

Introduction

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 (Långström & Day, 2004). The major forestry problem caused by pine weevils 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).

Several measures can be used to protect seedlings from pine weevil damage, but the most common approach in Europe since the 1980s has been to use insecticides (Leather *et al.* 1999). However, because of the environmental and health risks associated with insecticides their use has been questioned recently in many countries. The use of feeding barriers that prevent the pine weevil from reaching the seedlings or silvicultural measures that affect the willingness of the weevil to feed on the seedlings are alternative approaches to insecticides. 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. Seedlings in commercial forestry in southern Sweden are normally treated with insecticides (Långström & Day, 2004), however, various kinds of coatings and mechanical devices are also being developed (Lindström *et al.* 1986, Petersson *et al.* 2004).

Silvicultural measures that can reduce pine weevil damage include scarification and planting under shelterwoods (Söderström *et al.* 1978, 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) and for reducing pine weevil damage to conifer seedlings (Söderström 1978, Petersson & Örlander 2003). Planting under shelter trees has proved to reduce damage to conifer seedlings compared to planting on clearcuts (von Sydow & Örlander 1994, Nordlander *et al.* 2003a, 2003b). The main concerns of the studies underlying this thesis were factors affecting the intensity of pine weevil feeding in shelterwoods, therefore more details regarding shelterwood systems are discussed below.

Shelterwoods

General considerations

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 serve a sheltering purpose (Hagner 1962, Karlsson 2000). Shelterwoods are used not only in Scandinavia but also in both other parts of Europe and North America (Smith 1986, Matthew 1991).

Shelter trees provide the additional benefits of reducing the risk for damage by frost and pine weevil, as well as promoting greater diversity of field vegetation

than clearcuts (Langvall & Örlander, 1991, von Sydow & Örlander, 1994, Hannerz & Hånell, 1997). Moreover, in Sweden shelterwood is sometimes used as a method to promote mixed conifer forests. Naturally regenerated pine seedlings derived from the shelter trees grow together with planted seedlings of spruce. In the region where the studies this thesis was based upon were performed, seed trees were left in about 13% of the total area of final cuttings to promote natural regeneration, and shelter trees with planted seedlings in about 22%, giving a combined total of about a third of the area (National Board of Forestry).

Why do seedlings under shelter trees suffer less from damage by pine weevil compared to seedlings on a clearcut?

Pine weevils are attracted to new clearcuts by the odour from fresh stumps and fresh slash (Escherich 1923, Nordenhem & Eidmann 1991, Schlyter 2004). Therefore, the hypothesis that fewer weevils should be attracted to areas with a shelterwood than to clearcuts because there are fewer stumps in the former 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). Thus, differences in the size of pine weevil populations do not explain the difference in damage intensity to seedlings between shelterwoods and clearcuts.

Pine weevils feed mainly on food sources other than conifer seedlings (Örlander *et al.* 1999, Bylund *et al.*, 2004), and the availability of alternative food sources that may be favoured in shelterwoods has been suggested to be an important factor in the lower amounts of pine weevil damage to seedlings observed within them. Pine weevils feed on thin branches in the crowns of shelter trees during a period in spring and early summer when the weevils immigrate into recently cut areas (Örlander *et al.* 2000). However, during the rest of the season the weevils seem to feed close to the ground and, thus, the opportunity to feed in the crown does not appear to be sufficient to suppress feeding on seedlings throughout the entire season.

In a study by Nordlander *et al.* (2003b) pine weevils damaged seedlings close to the centre of a clearcut twice as heavily as seedlings planted near the sun-exposed edge of the clearcut, even though the light conditions and soil temperature were similar. The cited authors suggested that the lower level of damage depended on the greater availability of alternative food sources close to the forest edge rather than differences in the microclimate. The effects of alternative food sources on pine weevil damage to seedlings are examined in Papers I and II.

The pine weevil

Pine weevils migrate by flight in spring or early summer and invade fresh clearcuts, attracted by the odour from newly dead conifer roots, where they can breed (Escherich 1923, Schlyter 2004). Adult weevils can fly long distances

(Solbreck 1980), and in southern Sweden the short average distance between fresh clearcuts implies that most sites are within the reach of swarming pine weevils. Pine weevils build up their flight muscles before leaving the site of emergence (Nordenhem 1989). Some time after immigration to the breeding sites the 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 2 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. These weevils often cause severe damage to seedlings in the autumn before they hibernate in the soil. The time of development depends on the climate and therefore varies between regions and years (Långström, 1982).

Pine weevils feed on woody stems of several tree species (Manlove et al. 1997, Leather et al. 1999, Löf 2004, 2005), but prefer conifers. 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 species of the food source (Christianssen & Bakke 1971, Pohris 1983, Leather et al. 1994, Petersson et al. 2005, Örlander & Nordlander 2003, Wainhouse et al. 2004). In a laboratory experiment the weevils consumed five times as much bark at 20 °C than they did at 10°C, and twice as much on pine compared to spruce at 20 °C (Leather et al. 1994). The optimal temperature for pine weevil activity seem to be somewhere around 20 °C; their activity is reduced at much higher and lower temperatures (Christiansen & Bakke, 1968). Wainhouse et al. 2004 showed that weevil size was 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).

Objectives

The unifying aim of the studies around which this thesis is based, was to obtain a better understanding of factors that determine the intensity of feeding by pine weevils in shelterwoods.

The main objectives were to:

- investigate the possibility that supplying additional food on the ground near seedlings can reduce damage to them (Paper I)
- estimate the consumption of roots in the humus layer by adult pine weevils and test the hypothesis that increased feeding on roots in the shelterwood results in less feeding damage to planted seedlings (Paper II)
- investigate the extent of damage to seedlings that occurs after removal of the shelter trees (Paper III).

Material and methods

General aspects

The experiments were performed in part of the boreo-nemoral zone, the southwest border of which coincides with the natural limit for spruce (Lundmark 1986). In this zone, Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula pendula*) are the most abundant forest tree species. All experimental sites were situated within a radius of 50 km from Asa Experimental Forest, in the county of Kronoberg, where around 75% of the total land area is classified as forest land (Figure 1). The volume proportion of the most common species Norway spruce, Scots pine and birch is 57, 28 and 10% respectively (National Board of Forestry).



Figure 1. Map of Sweden, the county of Kronoberg coloured in dark grey.

Age of clearcut

The experiments described in Papers I and II were performed on fresh clearcuts *i.e.* the first season after cutting. The first year after removal of shelterwood trees (paper III) the area attracted weevils in a similar way as a fresh clearcut (Paper

III). Therefore, all studied sites can be considered as fresh clearcuts that populations of weevils invaded in early spring or the following summer. In the study in which the effects of removing shelter trees were examined (Paper III), inventories were made over two years. In the second year, damage on seedlings during spring and summer was caused by weevils remaining from the first year. However, in southern Sweden a new generation of weevils usually emerges in the autumn of the second year, so weevils from two different generations may have caused damage to the seedlings at the time of inventory in late autumn. However, most of the feeding on the seedlings recorded in Paper III occurred in the first year when the pine weevils invaded the area.

Methods

The experiments described in Paper I were designed using randomized blocks with four replicates and two treatments and measurements were conducted on seedlings and branches (Table 1). In Paper II the seedlings and roots were exposed to one of two treatments and were measured at four different times. In the investigations reported in Papers I and II the mean of debarked area (\pm SE) attributable to pine weevils was determined for seedlings, branches and roots in each plot. The results were compared using analysis of variance and differences were considered to be significant when *p*<0.05.

In the study described in Paper III, 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 area (\pm SE) was calculated for pine and spruce in 2 mm diameter classes. This data was 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 of being damaged by pine weevil were tested using nonlinear regression.

Pine weevil feeding on seedlings was recorded in the same way in all experiments. The area debarked on the main stem was estimated to within 0.1 cm^2 , and damage severity was recorded on a six-level scale from undamaged to dead. The debarked area was estimated in the same way on roots (Paper II) and branches (Paper I).

Latitude	Plots	Seedlings	Root bark area $(m^2 ha^{-1})$
57°10′N	4	392	
56°50′N	4	392	
57°10′N, 57°15′N	160	1280	3741
56°55′N -57°30′N	60	976	
	Latitude 57°10′N 56°50′N 57°10′N, 57°15′N 56°55′N -57°30′N	Latitude Plots 57°10'N 4 56°50'N 4 57°10'N, 57°15'N 160 56°55'N -57°30'N 60	LatitudePlotsSeedlings57°10'N439256°50'N439257°10'N, 57°15'N160128056°55'N -57°30'N60976

Table 1. Data from the three papers, location, number of plots and seedlings and mean bark area per hectare

Paper I

Two field experiments were designed to investigate whether damage to seedlings by pine weevil can be reduced by supplying alternative food sources. In Experiment 1, which was performed on a clearcut, fresh branches of Scots pine were placed close to sets of Norway spruce seedlings every week, but not around control seedlings, which were left without any additional food supply. New branches were spread out every week and a sample of five branches per plot that had been spread the previous week was collected at the same time. At the end of the experiment, an additional branch from each of the six spreading dates was collected from each plot. The length, diameter and area debarked by pine weevils of each branch were then estimated.

The second experiment was conducted in a Scots pine shelterwood. In the shelterwood, the extra food, bilberry, (*Vaccinum myrtillus*) was already growing at the site. Therefore, bilberry and other field vegetation was removed from treated plots and retained in control plots.

Paper II

It has been suggested that the additional food supply in the form of fresh roots of shelter trees and stumps in the shelterwood might be one reason why the seedlings are damaged less in shelterwoods than in clearcuts. To test this hypothesis, and to obtain a more general understanding of the extent of adult pine weevil feeding on different kinds of roots, the amount of pine weevil feeding on the bark of roots in the humus layer was assessed in adjacent shelterwood and clearcut areas. The root bark area, length and mid-point diameter of each root and the area debarked by pine weevil (to the nearest 0.1 cm²) were all measured in both clearcuts and shelterwoods. The vitality of the roots was classified in four classes, from fresh roots with firm bark to roots where the bark and wood were clearly affected by decay. Furthermore, to examine possible correlations between feeding on seedlings and roots, Norway spruce seedlings were planted at all sites and the debarked area was estimated and compared to the debarked area on the roots.

Paper III

A survey was conducted in five shelterwoods in which the shelter trees were dominated by Scots pine and one in which the shelter trees were mainly Norway spruce. Measurements on the shelter trees were made before cutting in order to calculate the initial basal area for each plot. Surveyed seedlings were followed individually for two years. Most of the seedlings selected for this purpose were conifers, but where no conifers could be found, birch or other tree species were chosen. Seedlings of various tree species were also counted every year to obtain estimates of the numbers of seedlings at each site each year.

Results

Effects of additional food on damage by pine weevil *Hylobius abietis* (Paper I)

The results from the first experiment showed that it is possible to reduce damage to seedlings by supplying the pine weevils with additional fresh food. On plots where branches were supplied as additional food sources the weevils fed heavily on them (mean weekly total debarked area on sampled branches was 150 mm²), and the mean debarked area on seedlings was significantly lower than in the control plots (54 and 140 mm², respectively). Furthermore, the accumulated feeding area was three times higher on the branches sampled at the end of the experiment than on branches sampled after a week, indicating that the branches were used as food sources for more than a week.

In the second experiment there was a tendency for the number of dead and severely damaged seedlings to be higher on the plots where the field vegetation had been removed compared to plots where the field vegetation was left undisturbed, but the difference was not significant.

Feeding on roots in the humus layer by adult pine weevil, *Hylobius abietis* (Paper II)

On average, 3741 m² root bark area per hectare was available as a food source for the pine weevil, and no significant differences in this respect were found between clearcut and shelterwood. Most of the roots were fresh conifer roots and only around 4% of them were from bilberry or broadleaved trees. The debarked area was estimated to amount to 2.9 m² per hectare, which is more than the total available area of seedling bark in a standard plantation with 2500 containerized seedlings per hectare (Bylund *et al.* 2004). The study did not reveal why seedlings growing under a shelterwood are damaged less than seedlings on clearcuts, since no difference in the amount of debarked area between the two treatments was found.

Surprisingly, the feeding area was lower in September than in July during both years of the study. The expectation was that the bark area consumed would be greater, or at least as great, in the autumn than in the summer, since the roots had then been exposed to the weevils for a longer time. A complementary experiment was therefore conducted to assess the possibility that feeding scars may heal during the season. However, this experiment showed no healing of feeding scars that could explain why the debarked areas were lower in September than in July.

Damage by pine weevil *Hylobius abietis* to conifer seedlings after shelterwood removal (Paper III)

This study showed that after the final cutting of shelter trees, conifer seedlings are likely to be damaged by pine weevil. The size of the seedling (root collar diameter) had a strong impact on the risk for damage by pine weevil; small seedlings being more vulnerable to feeding than larger seedlings. Most feeding occurred during the first year after cutting, and both spruce and pine were damaged. The debarked area was significantly higher for Scots pine than for Norway spruce. Vitality (growth of the leading shoot before final cutting) also proved to be an important variable. Vital seedlings were less likely to be damaged by pine weevil than seedlings with low vitality.

Discussion

Damage caused by pine weevil is a major problem across much of Europe, including Scandinavia, in areas being reforested using conifer seedlings. The use of insecticides, the currently most common way to protect the seedlings, is questionable because of health and environmental risks. It is, therefore, very important to find alternative methods for preventing damage to seedlings. Planting seedlings beneath a shelterwood is one way of reducing such damage, but the success of this technique has not yet been fully explained. The studies upon which this thesis is based contribute important new data relating to the key factors influencing pine weevil feeding in shelterwoods. The thesis also increases our overall knowledge of pine weevil feeding behaviour.

All the experimental sites were situated in a limited area within a 50 km radius of the Asa Experimental Forest. The geographical distribution of the experiments may restrict the applicability of the results to other areas. However, the life cycle of the pine weevil and its occurrence in clearcuts does not vary across southern Scandinavia (Petersson, 2004), indicating the potential for wider application of the conclusions presented in this thesis.

Available food sources (I, II)

Supplying fresh Scots pine branches close to the seedlings proved to be an effective way of reducing damage caused by pine weevils, thus showing that the total amount of food resources influences the extent to which they feed on planted seedlings. A similar potential food source for the weevils is the slash, consisting of branches and tops from trees after final cutting. Selander (1993) showed that seedlings surrounded with slash had a better chance of surviving weevil attacks than seedlings planted in spots were slash was removed. However, this is not in accordance with the results of Örlander & Nilsson (1999), which suggest that slash may serve as food for the weevils, but only for a short period before it dries

out. In addition, Wainhouse *et al.* (2004) found that the concentration of carbohydrates decreases rapidly in logs. Thus, these findings indicate that alternative food sources for the pine weevil must be fresh, *i.e.* suitable fresh vegetation must either grow or be regularly supplied close to the seedlings.

Bilberry was chosen as a natural potential food source because it commonly dominates the field layer under shelterwood trees, whereas it often disappears on clearcuts (Paper I). Another fresh food source is available in the crowns of mature Scots pine trees, and the bark from twigs of shelter trees and trees adjacent to fresh clearcuts is utilised during the period immediately after migration (Örlander *et al.* 2000). The results presented in Paper II show that roots in the humus layer comprise an enormous food resource that can be utilised by the weevils. The total available bark area from newly planted containerized seedlings, planted at normal spacing with 2500 seedlings per hectare, provide a considerably less abundant food resource than the other food sources mentioned here (Bylund *et al.* 2004).

Pine weevil feeding (I, II, III)

In all experiments, the area debarked by pine weevils on conifer seedlings was measured. In studies I and II planted containerized seedlings of Norway spruce were used, whereas in study III both planted and naturally regenerated seedlings, mainly of Norway spruce and Scots pine, were included. In the study described in Paper III, where the variation in size of the seedlings was high, the root collar diameter at the time of cutting proved to be the most important factor affecting their risk of being severely injured by pine weevil feeding. The vitality of the seedlings was also an important factor; seedlings that had grown more than 10 cm were less severely damaged by pine weevils than seedlings that had grown poorly (< 10 cm).

Damage to seedlings by pine weevil was considerably reduced when fresh Scots pine branches were repeatedly provided close to the seedlings (Paper I). The accumulated debarked area on branches collected at the end of the experiment was higher than the mean debarked area on branches collected once a week, showing that the branches were used for a longer period than just a week. The results show that access to extra food that is attractive to the weevils during the main part of the season can suppress damage to planted seedlings. However, bilberry growing close to the seedlings in a shelterwood did not affect damage to seedlings (Paper I). Fewer seedlings tended to be dead or severely damaged by pine weevil in plots where the field vegetation was left undisturbed, but the difference between these and other plots was not significant. A weakly negative correlation between feeding area on roots and seedlings was found, indicating that feeding on other food sources may reduce the feeding on seedlings.

The debarked area on roots was estimated to amount, on average, to 2.9 m^2 per hectare; the heaviest utilisation of any pine weevil food source that has been recorded to date. Pine weevil feeding on seedlings in the studies presented here was considerably lower, averaging 0.5 m^2 bark area per hectare. Örlander *et al.*

(2000) estimated the amount of debarked area in the crowns of shelter trees and trees at the edge of a clearcut to be 0.6 and ca 2 m^2 per hectare, respectively. However, estimates of feeding in trees at the forest edge are highly dependent on various factors, such as the number of trees, the size of the trees, and the tree species involved.

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 not so ideal (Bylund *et al.* 2004). The weevil density after immigration in the spring has been estimated to be approximately 14000 per hectare (Nordlander *et al.* 2003a). Based on these calculations 20-30 m² of bark per hectare would be consumed by pine weevils during a season of 2-3 months; 3-5 times more than the amounts found in the studies underlying this thesis. However, several factors may affect the areas debarked in specific times and places, such as the density of the population, the nutrient quality of the food, weather conditions and tree species.

The nitrogen concentration in seedling bark is around three times higher than that of logs, and there are also differences between tree species (Wainhouse *et al.* 2004). The consumption of seedling bark may be lower, in absolute terms, than that of root bark, but the fertilized newly planted seedlings may offer higher quality food. Moreover, feeding is dependent on tree species and several studies have shown that pine weevils prefer bark of Scots pine to Norway spruce (Långström 1982, Leather *et al.* 1994, Manlove, 1997). We found that the debarked area was larger on Scots pine seedlings than Norway spruce seedlings, especially for large seedlings with a root collar diameter greater than about 10 mm bark (Paper III). Moreover, three times more bark was consumed in the crowns of mature Scots pine trees than in those of mature Norway spruce trees in a study by Örlander *et al.* (2000). No information about feeding preferences between roots of Scots pine and Norway spruce was provided by our root feeding study (Paper II), since roots of the two conifer species were not separated.

Feeding environment (I, II)

On fresh clearcuts and shelterwoods, the pine weevils seem to feed mainly on the lower part of seedlings stems (Petersson *et al.* 2004). Part of the stem is normally planted below ground and weevils may find hiding places close to the base of the seedlings, especially when they are planted directly in humus (Nordlander *et al.* 2005). Furthermore, Nordlander *et al.* (2003b) suggested that feeding below ground is preferred by the pine weevil because there is more shelter below ground.

Roots in the humus layer and, to some extent, branches on the ground, provide the pine weevil opportunities to feed in sheltered conditions (Papers I, II). Roots can provide moist and hidden places when the temperature or other factors prevent the pine weevil from eating in more exposed places. In support of this hypothesis, in a study of pine weevil feeding on partially buried stem sections 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 influences the feeding behaviour of the pine weevil. Such temperature effects may also explain why we found considerably less feeding on roots in 1998 than in 2002, when the weather was extremely warm and dry during the summer (Paper II).

The pine weevil prefers to feed below ground if the food source is placed on bare soil without shelter above ground (Nordlander *et al.* 2005). Under natural conditions, as in Paper II, the undisturbed ground vegetation may provide shelter for the weevils above ground but below ground food sources still accounted for most of the food consumed by the pine weevil.

Conclusions

It is possible to reduce damage to seedlings if fresh food that is attractive to the pine weevil is supplied close to them.

Conifer roots in the humus layer constitute a large food source for the pine weevil. During the first year after cutting it is used to approximately the same extent in clearcuts and shelterwoods. Roots from other species, like bilberry, are not as abundant as conifer roots but are still utilised by the pine weevil.

After final cutting of shelter trees the area is invaded by immigrating pine weevils in the spring. Before removal of shelter trees, seedlings should have reached a diameter of at least 9 mm for Norway spruce and 12 mm for Scots pine, to avoid serious damage by pine weevil. Low vitality of the seedlings increases the risk of being damaged by pine weevil.

The debarked area is larger on Scots pine seedlings compared to seedlings of Norway spruce. It seems that the bark of Scots pine is more attractive to pine weevils regardless of whether it comes from branches of mature trees or stems of seedlings.

Further research is needed to establish the feeding budget of the pine weevil and to identify the factors that influence pine weevil feeding. Such studies may also elucidate why pine weevils cause less damage to seedlings planted in shelterwoods than seedlings planted in clearcuts.

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