

Regeneration Methods to Reduce Pine Weevil Damage to Conifer Seedlings

Magnus Petersson

*Southern Swedish Forest Research Centre
Alnarp*

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Abstract

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Damage caused by the adult pine weevil *Hylobius abietis* (L.) (Coleoptera, Curculionidae) can be a major problem when regenerating with conifer seedlings in large parts of Europe. Weevils feeding on the stem bark of newly planted seedlings often cause high mortality in the first three to five years after planting following clear-cutting. The aims of the work underlying this thesis were to obtain more knowledge about the effects of selected regeneration methods (scarification, shelterwoods, and feeding barriers) that can reduce pine weevil damage to enable more effective counter-measures to be designed. Field experiments were performed in south central Sweden to study pine weevil damage amongst planted Norway spruce (*Picea abies* (L.) H. Karst.) seedlings.

The reduction of pine weevil damage by scarification, shelterwood and feeding barriers can be combined to obtain an additive effect. When all three methods were used simultaneously, mortality due to pine weevil damage was reduced to less than 10%.

Two main types of feeding barriers were studied: coatings applied directly to the bark of the seedlings, and shields preventing the pine weevil from reaching the seedlings. It was concluded that the most efficient type of feeding barrier, reduced mortality caused by pine weevil about equally well as insecticide treatment, whereas other types were less effective.

Soil scarification reduces feeding by pine weevil, but different soil features associated with type and cultivation strongly influences the results. In our experiments, mortality was highest in undisturbed humus and lowest in pure mineral soil. Pine weevil damage was reduced somewhat when the humus was cultivated, and feeding levels were lower than on pure humus when humus and mineral soil were mixed. The results indicate that pine weevils are more willing to stop and feed when suitable places for hiding are available close to the seedling.

When grass vegetation surrounded a mineral patch pine weevil feeding increased significantly, but the pine weevils did not use vegetation as a "bridge" to reach the seedling. The most probable explanation for the increase in feeding is that pine weevils perceived the vegetation as a shelter.

Keywords: *Deschampsia flexuosa*, Feeding barrier, *Hylobius abietis*, micro climate, *Picea abies*, reforestation, seedling damage, shelterwood, soil treatment, vegetation.

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

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Appendix

Papers I-IV

This thesis is based on the following papers, which are referred to in the text by the corresponding Roman numerals, I-IV.

- I. Petersson, M. & Örlander, G. 2003. Effectiveness of combinations of shelterwood, scarification, and feeding barriers to reduce pine weevil damage. *Canadian Journal of Forest Research* 33: 64-73.
- II. Petersson, M., Örlander, G. & Nilsson, U. 2004. Feeding barriers to reduce damage by pine weevil (*Hylobius abietis*). *Scandinavian Journal of Forest Research* 19: 48-59.
- III. Petersson, M., Örlander, G. & Nordlander, G. Soil features affecting damage to conifer seedlings by the pine weevil *Hylobius abietis*. *Forestry* 78 (1) 2005. *Accepted*.
- IV. Petersson, M., Nordlander, G. & Örlander, G. Why vegetation increases pine weevil damage: bridge or shelter? *Manuscript*.

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Introduction

To regenerate stands successfully by planting seedlings after clear-cutting several factors must be considered. The environment on the new clear-cutting area will favour seedlings in several respects, such as the increase in global radiation, available soil water and nutrients and the reduction of competitive vegetation (Davis, 1987; Örlander *et al.*, 1996; Nilsson & Örlander, 1995). On the other hand, this radical change to the ecosystem also creates favourable environments for other species, e.g. the pine weevil (*Hylobius abietis* (L.)), that can harm seedlings (Day & Leather, 1997). The pine weevil is attracted to clear-cuttings, where it uses roots of recently dead trees as a breeding substrate (Eidmann, 1974; Nordlander *et al.*, 1986; Nordenhem & Eidmann, 1991). The associated forestry problem is that the adult pine weevil feeds on the bark of planted conifer seedlings (Christiansen, 1971; Eidmann, 1974; von Sydow, 1997; Örlander & Nilsson, 1999).

Importance of pine weevil damage

In recent decades the problems of reforestation caused by pine weevil damage has been most pronounced in Scandinavia, the UK and parts of central Europe, where clear-cutting methods are widely used (Långström & Day, 2004). In contrast, countries like Germany and Switzerland use other harvesting systems to some degree, e.g. selection cutting, which are probably much less favourable for the development of the pine weevil, and consequently pine weevil damage is less problematic (Långström & Day, 2004; Petersen & Guericke, 2004). However, selection cutting is not seriously discussed (mainly for economic reasons) as a way of reducing pine weevil damage in most of the Nordic countries or the UK.

In recent years (1995-2003) the annual clear-cutting area in southern and central Sweden has been approximately 97000 ha (Figure 1, part I-II), and approximately 60% of this area has been regenerated by planting (Anon., 2004). In this part of Sweden seedlings often need to be protected against pine weevil damage (Lindström *et al.*, 1986; von Sydow, 1997, Örlander & Nilsson, 1999; Thorsén *et al.*, 2001) and insecticide treatment is frequently used. The number of planted seedlings amounts to approximately 300 million per year in Sweden, about 100 million of which are protected with insecticides (von Hofsten, 2004).

Synthetic pyrethroids e.g. permethrin, have been widely used to protect forest seedlings in Europe since the 1980s (Leather *et al.*, 1999). Treatment with permethrin often reduces damage to an acceptable level (Örlander & Nilsson, 1999; Petersson, 2000; Thorsén *et al.*, 2001; Thacker & Carroll, 2004). However, from 2004 permethrin is prohibited in all countries in the European Union (Anon., 2000b). Currently, other insecticides are allowed for use within the EU (e.g. other pyrethroids and carbamates, Långström & Day, 2004). However, the use of insecticides has been questioned because of the environmental and health hazards they pose. The negative effects of synthetic pyrethroids include their toxicity to

aquatic organisms (Bergkvist, 1997; Roberntz, 2002) and working with insecticides may also be hazardous to health (Hagberg, 1990; Tuomainen *et al.*, 2003).

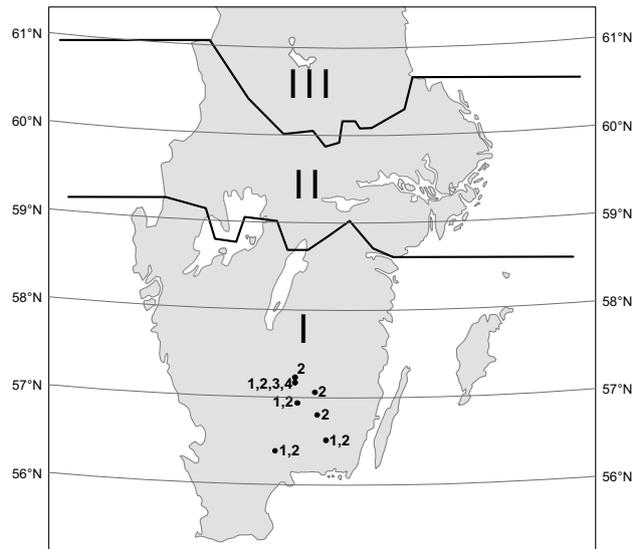


Figure 1. Location of the three parts of Sweden (I-III) and location of the experimental sites (figures from 1-4 corresponds to the number of the Papers I-IV).

Without access to effective methods for reducing pine weevil damage the consequences for the forest sector may be considerable. In Sweden the costs of prohibiting insecticides has been estimated to be 400 million SEK per year, based on the expected increase in mortality of seedlings, decreased height growth of seedlings damaged by pine weevil, decreased increment etc. (Thuresson *et al.*, 2003). In the UK the economic losses to this pest are estimated to be approximately £8 million per year, even with the access to insecticides (Anon., 2000a). Therefore, it is important for the forest sector that efficient methods are developed.

The pine weevil

In addition to the pine weevil *Hylobius abietis*, its close relative *Hylobius pinastri* Gyll. also occurs in the northern Europe and causes similar damage. The latter species is more frequent on moist sites and may constitute about 10-30% of the total *Hylobius* population (Långström, 1982; Nordlander, 1990). However, in clear-cuttings in southern Sweden and in Estonia *Hylobius pinastri* only accounts for 0-3% of the *Hylobius* weevils (Örlander *et al.*, 1997; Voolma *et al.*, 2001).

In order to understand why some management methods are effective while others are not as good, knowledge of the life cycle of the pine weevil is essential

(Figure 2). Furthermore, knowledge of its life cycle may be useful when seeking new and efficient counter-measures, and for optimising their timing.

Migration

The adult insect migrates in the spring and early summer when air temperature reach approximately 18 °C (Solbreck & Gyldberg, 1979). The insect is attracted by volatiles emitted from suitable breeding substrates, e.g. newly dead conifer roots (Escherich, 1923; Nordenhem & Eidmann, 1991; Schlyter, 2004). After immigrating into an area with suitable breeding substrate the flight muscles regress. After that the weevils move around by walking on the ground to find oviposition sites and food. The adult weevils of the parent generation hibernate in the soil and appear again the following spring (A+1). The weevils resume mating and ovipositing during this second season. Some of them will migrate to fresh breeding substrate while others will stay (Nordenhem, 1989).

The distance dispersed in one season might be as far as 80 km, and a majority of the weevils probably migrate more than 10 km (Solbreck, 1980). In southern Sweden (Figure 1, part I) the number of new clear-cuttings made each year is approximately 17000, based on official statistics from the Swedish National Board of Forestry for the period 1995-2004. The average distance between fresh clear-cuttings in this area was calculated to be 2.3 km. Thus, it is likely that almost all clear-cuttings will be colonised by immigrating weevils.

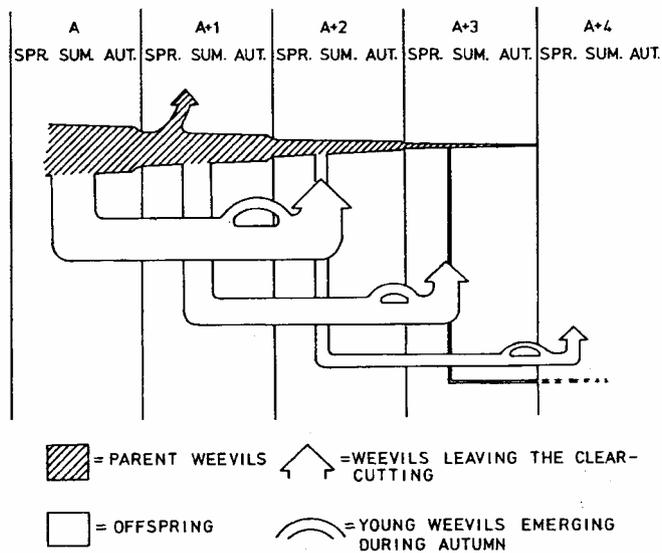


Figure 2. Schematic diagram of pine weevil population dynamics on a clear-cut during successive years after cutting, based on the assumption that all weevils have a two-year generation time (presented by Nordenhem, 1989).

Life cycle

Soon after immigration to fresh clear-cuttings (in year A, Figure 2), or other sites with breeding substrate, the females are ready to start laying their eggs (Nordenhem, 1989). Suitable substrates for oviposition, such as conifer roots, are located by odours diffusing through the soil and the strength of attraction depends on the physiological phase of the adult (Nordlander *et al.*, 1986; Nordenhem & Eidmann, 1991). Scots pine is generally more favourable for larval development than e.g. Norway spruce and Sitka spruce (Wainhouse, 2004). The weevils burrow into the soil and oviposit in the vicinity of conifer roots or directly in the inner bark of the roots (Nordenhem & Nordlander, 1994; Nordlander *et al.*, 1997). The eggs hatch after some weeks and the larvae feed on the bark and wood of the roots. The time for development from egg to adult depends on the climate, and in Scandinavia it varies between 14 months to 4 years from the south to the north (Bejer-Petersen *et al.* 1962; Långström, 1982). The following section describes the life cycle of pine weevils with a 2-year generation time: the standard generation time in southern Sweden (Bejer-Petersen *et al.*, 1962; Nordenhem, 1989; Örlander *et al.*, 1997; Day *et al.*, 2004).

The larvae go through five larval instars before pupation in June of the second year (A+1) (Bejer-Petersen *et al.*, 1962). Some, but not all, adults emerge from the pupal chamber later during the summer and feed for a period before hibernating in the soil. This late summer and autumn feeding may cause serious damage to seedlings (Nordenhem, 1989; von Sydow, 1997; Örlander & Nilsson, 1999). The rest of the new generation of weevils remain in underground pupal chambers until the following year (A+2, Figure 2). In the spring of the third year (A+2), both those that have had a period of feeding in the previous autumn and those that have remained in the pupal chamber appear and start feeding (Örlander *et al.*, 1997; Örlander & Nilsson, 1999). The maturation feeding often causes severe damage to seedlings in A+2 clear-cuttings (von Sydow, 1997; Örlander & Nilsson, 1999). The size of the population increases from approximately 1 weevil/m² at the fresh clear-cutting (A) to 10 weevils/m² in the third season (A+2) (Bylund *et al.*, 2004; Moore *et al.*, 2004). The flight muscles develop after some time of feeding and the weevils migrate to find a suitable breeding substrate (Nordenhem, 1989). This process is also repeated in the fourth year (A+3), when the number of emerging weevils is still high and may constitute a third of the new generation (Nordenhem, 1998; Moore *et al.*, 2004). This rather high number of weevils in the fourth year (A+3) is probably due to two factors: females of the previous generation also oviposit in the second year (A+1) and the time of development from larvae to adult can be delayed for a year (Bejer-Petersen *et al.*, 1962; Nordlander, 1987; Nordenhem, 1989).

Food

Pine weevils orientate to seedlings by responding to host odour and visual stimuli (Björklund *et al.*, 2003). Several food sources are utilized, including shrubs and trees of several species, but woody seedlings are preferred, especially of conifer

species (Munroe, 1927; Leather *et al.*, 1994; Löf *et al.*, 2004; Månsson & Schlyter, 2004; Wainhouse *et al.*, 2004). The weevils also feed on branches and roots of large Scots pine (*Pinus silvestris* L.) and Norway spruce trees (Örlander *et al.*, 2000, Nordlander *et al.*, 2000, 2003b). The quantity of food needed for one day has been estimated to be approximately 20 mm² Scots pine bark per weevil (Bylund *et al.*, 2004). The cited authors concluded that planted conifer seedlings only constitute a small part of the food needed for a pine weevil population of common size. In accordance with this conclusion Wainhouse *et al.* (2004) estimated that 2500 sitka spruce (*Picea sitchensis* (Bong) Carrière) seedlings per ha⁻¹ would provide 12500 weevils with enough food to complete their initial maturation feeding.

Other Hylobius species

In North America there are two *Hylobius* species that cause similar damage to conifer seedlings to that caused by *Hylobius abietis*. *Hylobius pales* (Herbst) occurs in eastern North America and causes severe damage to pine plantations and Christmas tree plantations (Peirson, 1921; Fox & Hill, 1973; Lynch, 1984). Severe damage can be avoided if planting is delayed until the weevil has disappeared from the clear-cutting. In the south of the region, one year is enough and in the north 2-4 years is recommended (Walstad, 1976; Lynch, 1984). Several methods to reduce damage have been used e.g. chemical treatment of the seedling, reduction of the insect population with traps, site preparation and stump removal (Lynch, 1984; Salom, 1998). *Hylobius congener* Dalla Torre (Schenkling & Marshall) is common in large parts of North America from North Carolina to the Canadian east coast, and west to Alaska (Welty & Houseweart, 1985). The length of generation is reported to be two years (Welty & Houseweart, 1985; Lyver, 2001). Methods to reduce damage to planted seedlings include chemical treatment, delayed planting, removing duff before planting, planting under shelter trees and using large seedlings (Welty & Houseweart, 1985; Swift *et al.*, 2000; Lyver, 2001).

Orientation to hosts and seedling response

Orientation by the pine weevil can be seen as a series of behavioural steps at different scales, from finding a suitable habitat (e.g. a fresh clear-cutting) to orientation to a seedling for feeding (Schlyter, 2004). Insects normally find a host by attraction from a distance that may involve odour or vision, or both (Bernays & Chapman, 2004) and for pine weevils both vision and odour are involved (Björklund *et al.*, 2004). Odour comes from monoterpenes that are released from conifer seedlings, e.g. α -pinene, and attract weevils (Nordlander, 1991). Conifer seedlings may also contain monoterpenes that are repellent or inhibit attraction, e.g. limonene (Nordlander, 1990, 1991). Once the insect has reached the seedling it makes the decision whether or not to feed (host acceptance), and olfaction may still be important at this stage. All seedlings contain compounds like carbohydrates that are nutrients for pine weevils and are perceived as host volatiles (Bernays &

Chapman, 1994). The balance between the stimulants and deterrents may affect whether or not, and how much of, the seedling is eaten.

Resistance to attacks

Large and vital seedlings which establish a root system quickly seem to have the highest capacity to survive pine weevil attacks. The status of the seedling concerning nutrition and defence affect the feeding of the pine weevil (Wainhouse, 2004). The resin flow, which is important for defence, is affected by the sap flow, and therefore seedlings with an established root system will produce more resin and resist attacks by pine weevils more effectively than newly planted seedlings (Örlander *et al.*, 1991). Water-stressed seedlings are fed upon more intensively than well-watered ones (Selander & Immonen, 1992) and naturally regenerated seedlings appear to be less susceptible to pine weevil damage during the first year, compared to planted seedlings of the same size (Selander *et al.*, 1990). This difference decreased during the following two years in a study by Selander *et al.* (1990), indicating that the planted seedlings they examined were affected by water stress, due to disturbance to their root systems. High nitrogen levels in the bark of the seedling, due to high levels of N fertilization in the nursery, tend to increase attack rates and the susceptibility of the seedlings (Selander & Immonen, 1991).

Wound repair and tolerance to moderate attacks by pine weevil may be of importance for the survival of seedlings Wainhouse (2004). Non-lethal attacks by pine weevil cause an increase in the concentration of resin acid in the area immediately adjacent to the wound (Gref & Ericsson, 1985). The callus tissue thus formed is avoided by pine weevils, probably due to the elevated concentration of resin acid (Ericsson *et al.*, 1988). However, wounded seedlings are preferred to unwounded ones for new attacks, probably because they release higher amounts of monoterpenes (Ericsson *et al.*, 1988; Nordlander, 1991). In fact, the risk of additional attacks may be up to five times higher for previously wounded seedlings (Nordlander, 1991).

Growth may be affected in various ways amongst seedlings surviving pine weevil attacks. In a field experiment described by Örlander & Nilsson (1999), planted Norway spruce seedlings given intensive insecticide treatments were compared with untreated seedlings, which were repeatedly attacked. After four years, the stem volume was significantly higher for the seedlings that had not been attacked than for those that had been attacked. Långström & Hellquist (1989) also found that root growth decreased when mechanical scars were made in the bark.

Regeneration method affecting pine weevil damage

When clear-cutting was introduced in Germany in the 19th century severe pine weevil damage to the newly planted seedlings soon followed (Ratzeburg, 1839). In Scandinavia the pine weevil was reported as a problem by Holmgren in 1856. Since then methods to reduce damage by this pest have been important research

subjects, and the approaches adopted have changed with various economic and technical developments.

The different measures that can be used to reduce damage to planted seedlings, singly or in combination, are listed below and shown schematically in Figure 3. The papers appended to this thesis deal with methods involving delayed planting, silvicultural methods affecting weevil behaviour, and protection of seedlings (approaches 2, 3 and 5, see below).

1. Population reduction

This can be achieved by measures such as trapping weevils to suppress damage to seedlings. The technique is often labour-consuming and has been used for 100 years with variable results (Escherich, 1923; Munro, 1929; Eidmann, 1974; Långström & Day 2004). The use of natural enemies like parasitic insects (Gerdin, 1984; Henry & Day, 2001) or nematodes (Pye & Pye, 1985; Armendariz *et al.*, 2002) have been studied, but their capacity to reduce pine weevil populations remains unclear (Kenis *et al.*, 2004).

2. Delayed planting

Two important factors influencing regeneration results are connected to the clear-cut age, firstly the population of pine weevils (Nordenhem, 1989; Örlander *et al.*, 1997; Nordlander *et al.*, 2003a) and secondly the cover and composition of ground vegetation (Bergquist & Örlander, 1998; Uotila, 2004).

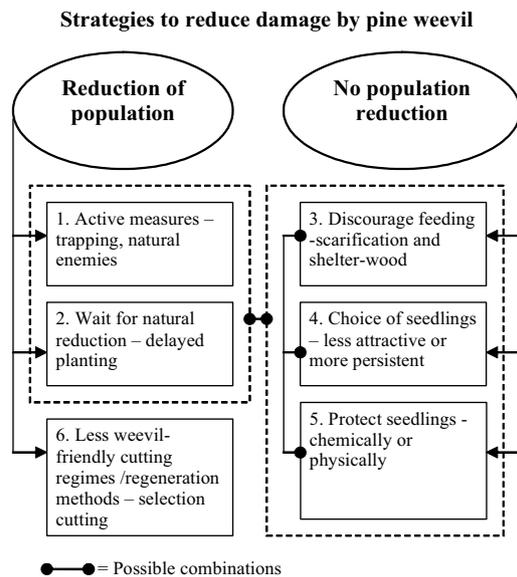


Figure 3. Scheme showing different strategies to reduce damage by pine weevil on seedlings planted after cutting.

In the southern part of Sweden and probably large parts of northern Europe, damage to newly planted seedlings is often severe in the first three years after clear-cutting (A, A+1 and A+2) (Långström, 1982; Nordenhem, 1989; von Sydow, 1997; Moore *et al.*, 2004) (Figure 2). The extensive damage is mainly due to the high population of pine weevils (Bejer-Petersen *et al.*, 1962, Nordenhem, 1989; Örlander *et al.*, 1997; Moore *et al.*, 2004). In the third year (A+2), the size of the population is probably at its highest level in the spring and then rapidly decreases during the summer (Nordenhem, 1989; Örlander *et al.*, 1997). By planting in the middle of June in the third year (A+2), the high pine weevil population levels could be avoided while still using this season for seedling growth (Bejer-Petersen *et al.*, 1962; Nordenhem, 1989; Örlander & Nilsson, 1999). However, during dry years or in regions with low precipitation during early summer, drought may cause high levels of mortality amongst late planted seedlings. (Nilsson & Örlander, 1995). Seedlings planted after four years (A+4) show insignificant damage (Örlander & Nilsson, 1999), which is consistent with general estimates of weevil population dynamics (Nordenhem, 1989, Örlander *et al.*, 1997, Moore 2004). However, the fallow time needed varies with latitude, and will be longer further to the north because the development of the larvae will be slower (Bejer-Petersen *et al.*, 1962; Långström, 1982).

The vegetation cover also influences damage caused by pine weevils. The clear-cutting age is important in this respect too, since the vegetation cover is often low in the old forest and in clear-cuts in the year following cutting (Ingelög, 1974; Bergquist & Örlander, 1998). Ground vegetation affects damage by pine weevil in at least two different ways. Firstly, soil scarification decreases damage, but when ingrowth of vegetation in the scarified patches starts, the effect is reduced (Örlander & Nordlander, 2004). Secondly, competition from vegetation for soil water, global radiation & nutrients affect the vitality of the planted seedlings, reducing their resistance to pine weevil feeding (Örlander *et al.*, 1990, 1996, Nilsson & Örlander, 1999; Norberg & Dolling, 2003). The stimulatory effect on pine weevil damage of high-growing vegetation surrounding the seedlings has also been a matter of concern, and this issue was examined in Paper IV.

The most obvious negative aspect of delayed planting is that field vegetation and naturally regenerated broadleaf species will establish during the fallow period and compete with the planted seedlings, leading to decreased growth and higher mortality (Sands & Nambiar, 1984; Nilsson & Örlander, 1995, 1999). The fallow period also represents lost years with respect to the growth of the conifer trees that will constitute the new stand.

3. Affecting weevil behaviour

Two methods can be mentioned here; planting under a shelterwood of conifer trees (von Sydow & Örlander, 1994; Nordlander *et al.*, 2003a; Paper I) or planting in scarified soil (Söderström *et al.*, 1978; Örlander & Nilsson, 1999; Björklund 2004; Nordlander *et al.*, 2005; Paper II).

Shelterwood

When the old forest is harvested some trees can be left as seed trees (Hagner, 1962; Karlsson, 2000) or a shelterwood can be retained in order to optimise environmental factors like the micro-climate (Langvall & Örlander, 2001). When planting under a shelterwood of Scots pine the damage caused by pine weevils is reduced significantly, and the reduction is correlated to the density of the shelter trees (von Sydow & Örlander, 1994). The reason for this reduction is not yet fully understood, but several hypotheses have been put forward. The reduced damage to seedlings under a shelterwood is not due to a reduction in the insect population, since the number of pine weevils was approximately the same in a shelterwood compared to a clear-cutting studied by Nordlander *et al.* (2003a). Pine weevils feed on thin branches in the crowns of shelter trees when they immigrate to a fresh shelterwood, but estimates of the debarked area have shown that such feeding could only partly explain the reduction in seedling damage, and it mainly occurs in the spring of the first year after cutting. (Örlander *et al.*, 2000).

Micro-climatic factors do not seem to provide an obvious explanation either, since changes in global radiation and temperature were not correlated to seedling damage in a study by Nordlander *et al.* (2003b). The hypothesis that damage to the seedlings is reduced because roots from the shelter-trees and a high abundance of woody vegetation provide the pine weevils with a rich food supply remains to be proven (Örlander *et al.*, 2001; Nordlander *et al.*, 2003a, 2003b). How the damage-reducing effect of a shelterwood interacts with scarification and protection of seedlings was investigated in Paper I.

Soil scarification

Scarification is defined as a measure to create a favourable environment for seeds to germinate or for seedlings to grow. The aim is normally to remove the humus layer, vegetation and dead parts of vegetation in order to expose mineral soil (Anon., 2000c). Humus is defined as organic material in different phases of breakdown and together with fine roots and living smaller organisms it forms the humus layer (Lundmark, 1986)

Soil scarification reduces pine weevil damage to planted conifer seedlings and in the late 1970s the method was taken up by Söderström *et al.* (1978), and the effect has been confirmed in more recent studies (Lindström *et al.*, 1986; Thorsén *et al.*, 2001 and Örlander & Nilsson, 1999).

Debarked stem area seems to be correlated to the size of the mineral patch up to a size of approximately 40x40 cm, at which point almost the full effect may be reached (Nordlander *et al.* 2000). The topography in the scarified patches has also been shown to affect the damage to the planted seedlings significantly, in investigations by Nordlander *et al.* (2005), since considerably less bark was consumed on seedlings planted on mounds compared to flat spots or in depressions.

The time that pine weevils spend on mineral soil is minimised because they increase their walking speed and have a tendency to walk in straighter lines when they encounter it (Kindvall *et al.*, 2000). However, although seedlings on scarified patches are found by pine weevils to the same extent as seedlings planted in undisturbed soil, it is less likely that the weevils will decide to stop and feed on seedlings on bare mineral soil (Björklund *et al.*, 2003). The cited authors suggested that this was due to the lack of hiding places or shelter in the mineral soil. The variation in effectiveness of scarification between different sites is sometimes large (Örlander & Nilsson, 1999). Several factors concerning scarification seem to be important. In order to investigate some of these factors, an experiment was established to determine the importance of soil type and the presence of hiding places created by scarification (Paper III).

4. Seedling variables such as species, size and type

Seedlings of some tree species are only slightly damaged by the pine weevil, e.g. several broadleaf species (Löf *et al.*, 2004; Månsson & Schlyter, 2004; Schlyter, 2004). Large seedlings resist the feeding better, and their bark may also be less suitable for pine weevil feeding (Thorsén *et al.*, 2001; Örlander & Nilsson, 1999; Långström & Day, 2004). Differences in bark structure may also explain the observed reduction in feeding amongst cuttings compared to normal seedlings (Hannerz *et al.*, 2002).

When the feeding by pine weevils leads to girdling of the stem below the lowest living branch, the seedling will die. More scattered feeding can also lead to severe damage or death, and Norway spruce seems to be more sensitive than Scots pine (Långström & Hellqvist, 1989). Seedling size, especially the stem base diameter, is significantly related to mortality caused by pine weevil (Lekander & Söderström, 1969; Örlander & Nilsson, 1999; Thorsén *et al.* 2001). Bare-rooted seedlings have somewhat lower mortality than containerized seedlings because of their larger stem base diameter (Eidmann, 1969; Selander *et al.*, 1990; Örlander & Nilsson 1999). Older seedlings with larger stem base diameters also tend to have thicker bark, which probably helps reduce the bark area consumed. Cuttings are reported to have lower mortality than normal seedlings with the same initial stem base diameter (Hannerz *et al.*, 2000). Naturally regenerated seedlings seem to be more resistant to feeding compared to planted seedlings of the same size (Selander *et al.*, 1990). Little is known about genetically based differences among seedlings with regard to defence and resistance to damage.

5. Protecting seedlings with insecticides, anti-feedants or barriers.

Insecticides will kill or harm the weevil (Heritage *et al.*, 1989; Örlander&Nilsson, 1999), while feeding barriers will protect the bark physically (Lindström *et al.*, 1986; Hagner & Jonsson, 1995; Eidmann *et al.*, 1996, Paper II). Anti-feedants will make the pine weevil avoid feeding by the smell or taste (Klepzig & Schlyter, 1999; Bratt *et al.*, 2001).

Feeding barriers to protect individual seedlings were tested in Germany in the beginning of the 20th century (Escherich, 1923). Experiments were re-started in the middle of the 1970s when DDT and other insecticides were questioned. In Sweden, a plastic collar for bare-rooted seedlings was developed and commercially used (Lindström *et al.*, 1986), but the development was interrupted because of the introduction of synthetic pyrethroids in the late 1970s. Interest in alternative methods to reduce pine weevil damage was low until the use of insecticides was questioned again in the 1980s. This situation led to the development of several new shields (Eidmann & von Sydow, 1989; Hagner & Jonsson, 1995; Eidmann *et al.*, 1996). In the beginning of the 1990s another type of protective barrier for seedlings was tested, i.e. coatings applied directly to their stem bark. During the 1990s there was extensive activity in Sweden related to the development and evaluation of feeding barriers (Paper II).

Methods for reducing damage radically changed when insecticides like DDT and Lindane were introduced in the late 1950s. They can be applied either in the nursery before planting or immediately after planting in the field. It is also possible to apply a second treatment to the seedlings in the field. The effect of pyrethroids usually lasts for at most one season (Torstensson *et al.*, 1999; Tuomainen *et al.*, 2003), although some studies have reported more long-lasting effects (Örlander & Petersson, 1998). The treatment of seedlings with pyrethroids usually reduces damage substantially, but with high pine weevil pressure mortality rates of 20% are common (Papers I-II).

6. Alternative cutting regimes

Some cutting practices, e.g. selection cutting instead of clear-cutting, reduce the amount of breeding substrate, and thus the pine weevil population, on the regeneration area (Långström & Day, 2004). This method also results in living trees being close to the fresh stumps, which may influence damage in the same way as shelter trees (see point 3, above). Normally this method involves the use of natural regeneration instead of planting and, thus there will be less concern about pine weevil damage. Harvesting at appropriate times during the season to avoid immigrations of pine weevils may also reduce damage. This method has not been thoroughly investigated, but recent studies suggest that the effects of varying the timing of clear-cutting are not consistent (Örlander & Wallertz, 1999, Moore *et al.*, 2004).

Aims

The unifying aim of the work underlying this thesis was to gain more knowledge about the effects of different regeneration methods on the extent of damage amongst Norway spruce seedlings caused by pine weevil feeding. It was also essential to obtain a better understanding of the effects of combining different silvicultural methods and the way they interact. From a practical perspective, another important goal was to evaluate the effect of various regeneration methods quantitatively, and to gain potentially useful knowledge for the future development of these methods.

The main objectives were to investigate:

- the effect of combinations of shelterwood, soil scarification and feeding barriers on pine weevil damage
- the main factors that control the efficiency of feeding barriers to protect seedlings from pine weevil damage, and the mechanisms involved
- how different soil types (humus and mineral soil) and different types of soil cultivation affect feeding by the pine weevil
- how pine weevil feeding is influenced by vegetation surrounding seedlings, and the cause of any such influence.

Materials and methods

All experiments were conducted in the interior of southern Sweden. Experiments reported in Papers I and II were dispersed from latitude 56°30' to 57°10' N. Experiments described in Papers III and IV were all located at latitude 57°10' N (Asa Forest Research Station).

Untreated seedlings and seedlings protected with permethrin were used as reference groups for seedlings equipped with feeding barriers (Papers I-II). Insecticide-treated seedlings were dipped into a permethrin emulsion of 0.75% active ingredient before planting and usually a solution of the same concentration was sprayed on the seedlings in the spring of the following year.

Feeding barriers were divided into three groups according to the design, i.e. coatings and two types of shields. Shields were defined as feeding barriers placed around the seedling (with a gap between them and the stem bark) and coatings as liquids that were sprayed or painted on the stem, forming a thin layer on the bark. Shields were divided into two types: those with and those without a collar at the top.

In the studies described in Papers I and II a randomised split plot design was used with sites as replicates. Frequencies or means of all the measurements were calculated for each plot. Since frequencies were often not normally distributed they were Arc-sin square root transformed (Zar, 1984) before statistical tests.

In the investigations reported in Papers III and IV a design with single-seedling plots was used. In Paper III, control (undisturbed humus layer) and pure mineral soil (a treatment considered as ideal) were compared with the other treatments. Frequencies were analysed pair-wise, comparing all treatments with control and pure mineral soil. In Paper IV, different hypotheses concerning the effect of vegetation on debarked area were analysed, via several pair-wise comparisons

designed to elucidate why the debarked area increased when vegetation of various densities surrounded the seedlings.

The severity of seedling damage was recorded on a 6-level scale from undamaged to dead (Papers I and II), or a simple 2-level scale with the classes dead or not dead (Papers III and IV). In Papers I and II the area debarked by pine weevil feeding was measured separately for the lower and upper parts of the stem. The lower part was defined as the part that was covered by a feeding barrier. For untreated seedlings or seedlings treated with insecticides it was defined as the part from the ground to a height of 10 cm. The debarked area was defined in six classes, ranging from 0 to 100% debarked area, for each part of the stem. The measurements of debarked area reported in Papers III and IV had an accuracy of 1/10 cm².

Methodological considerations

The definition additive means, in strictly statistical terms, that when performing an ANOVA each factor should be significant and there should be no significant interactions between the additive factors. However, a less strict interpretation of additive was used in Paper I. The effects on damage by pine weevil were significant (ANOVA, Table 3), but significant interactions occurred. This may have been because insecticide treated seedlings were almost not affected (in absolute numbers) by damage reducing factors like cutting regime and soil treatment.

The experimental design with single-seedling plots was used in two of the experiments (Papers III and IV). The advantage of this design is that there are many replicates for a given number of seedlings, so the number of seedlings required can be minimised. This is an important consideration in the experimental planning, especially when complex and labour consuming treatments and registrations are involved, as in Paper III (soil treatment) and IV (artificial vegetation cover). However, compared to a design with larger plots, there are statistical disadvantages with single-seedling plots. When frequencies are statistically analysed, there are only two values, 0 or 1. Consequently, the comparison between treatments is more complex, since ANOVA cannot be used. In Papers III and IV, only the hypotheses that were specifically addressed in the study were tested, and effects irrelevant to the hypothesis were not analysed. When one treatment was tested against several other treatments, a Bonferroni adjustment was made in Paper IV at the 0.05 α -level.

Pine weevil damage should always be assessed after the activity of the pine weevil has stopped in the autumn. When seedlings are planted on a fresh clear-cutting, feeding will often start in May and proceed throughout the whole vegetation period, with a decrease in the second half of the season (Nordenhem, 1989; Örlander & Nilsson, 1999). Consequently, pine weevil damage can be assessed in September or October on fresh clear-cuttings. Therefore, there may be a considerable time lag between the main part of the feeding and the recording,

which facilitates accurate assessment, since it gives the seedling time to react to the damage, i.e. either to survive or to die.

However, on a one-year-old clear-cutting (A+1, Figure 2) much of the feeding occurs during late summer or autumn by the new generation of weevils that emerges. Thus, the time between damage and recording is short, making it difficult to estimate the consequences of the damage, because even a severely damaged seedling may still appear vital in the late autumn. The same problem can also occur on two-year-old clear-cuttings (A+2, Figure 2), because some new weevils also emerge in the late summer of this year (Nordenhem, 1989; Örlander & Nilsson, 1999). In contrast to the assessment of damage class, it is easier to assess the true debarked area on A+1 and A+2 clear-cuttings because no healing processes will have started yet.

Results and discussion

Protection of seedlings (I, II, IV)

The variation in the protective effect of the different types of feeding barriers was considerable. The most effective feeding barriers reduced damage to the same level as insecticide treatments, whereas others had no significant effect compared to untreated. Feeding barriers could be divided into three groups depending on whether the mortality caused by pine weevil after three years in their presence was: not different from that of controls; significantly lower than in controls but higher than in permethrin-treated seedlings (coatings and shield without collar); or not significantly different from that of permethrin-treated seedlings (shield with a collar).

The area debarked by pine weevil was significantly reduced in the first year for seedlings protected with feeding barriers compared to unprotected seedlings. In the second year after planting the mean debarked area increased for seedlings protected with feeding barriers. There was a tendency for the lower part of the stem to be fed upon more than the upper part by pine weevil in the first two years after planting, irrespective of treatments. However, in the third year (A+2) the debarked area was similar for the different parts of the stem.

The durability of the feeding barriers varied with their type, and the coatings were least durable. It is likely that increasing the durability of the coatings and some shields would increase their capacity to reduce damage by pine weevil. For coatings several factors may affect the degradation, including the growth of the stem diameter and monoterpene emission from the bark, both of which may accelerate the degradation. As reported in Paper I, there was a tendency for degradation to be slower in the shelterwood with semi-shaded conditions than in the clear-cutting. Thus, UV-radiation probably increases degradation. One characteristic of a coating that is of great importance is its flexibility, because

during the first two years the stem base diameter often more than doubles (Örlander & Nilsson, 1999).

The durability of shields made of plastics (polypropylene) was significantly higher than that of coatings (Paper II). This is not necessarily entirely advantageous, since shields may hinder the development of the seedlings if they are too persistent or rigid. In a study by von Hofsten *et al.* (2001) it was found that shields may affect the growth of both the stem and root system. To facilitate their breakdown, the shields made of plastics were provided with weak zones (slits). Constructions with two types of material, one that will degrade rapidly and one with a higher durability, have also been tested, e.g. Hylostop (Eidmann *et al.*, 1996, Paper II).

Undefined damage occurred significantly more often amongst seedlings treated with coatings, so it is likely that the treatment *per se* caused damage to some seedlings. Possible explanations for this finding are that the coating may be toxic to the seedlings, or that an almost air-tight coating reduces gas exchange and thus damages them.

Mammals and birds also negatively affected the seedlings with feeding barriers, especially shields, since they occasionally pulled the barriers up or put them in positions where their protective effect was lost. This phenomenon occurred in almost every experiment involving feeding barriers, and thus seems to be a factor that must be considered (Papers I and II).

Vegetation surrounding the feeding barriers increased damage by pine weevil significantly, especially for Shields (Paper II). A hypothesis tested was that vegetation is used as a bridge by weevils to walk across. This was contradicted by the results in Paper IV. At least two other explanations are possible; vegetation may change the microclimate in a favourable way for pine weevils or it may provide shelter for the weevils from threats such as predators or intense solar radiation. Irrespective of which of these effects is most important, the presence of vegetation may lead to pine weevils spending more time close to the feeding barrier and thus (probably) more weevils successfully crossing the feeding barrier. The idea that insects use shelter has been suggested in several previous studies. Danks (2002) showed that insects use shelter for protection against physical factors and predators. Insects often eat in discrete meals and between the meals they seek shelter, (Chapman, 2002; Björklund, 2004).

Seedling height in year 3 was significantly higher for seedlings treated with insecticides compared to unprotected seedlings, but this was not true for seedlings protected with feeding barriers. Seedlings planted in an untreated humus layer showed a weak correlation between debarked area and seedling height. Many other stress factors may weaken this correlation, like insufficient root development and competition for water and nutrients (Örlander *et al.*, 1991; Nilsson & Örlander, 1999). However, a previous study showed that on fresh and one-year-old clear-cuttings, insecticide-treated seedlings grew considerably better than untreated ones (Örlander & Nilsson, 1999).

Soil treatments (I, III, IV)

The variation in scarification effect often seems to be great and the reason for this variation is not yet fully understood (Örlander & Nilsson, 1999; Petersson, 2000). However, a previous field experiment indicated that the content of humus in scarified plots influences the suppression of damage (Nordlander *et al.*, 2000). Results in Papers III and IV show that colonisation of the scarified patch by vegetation, and the presence of vegetation in the vicinity, both influence the effect of scarification.

In the studies reported in Paper I an operational scarification with a disc-trencher was performed before planting. The area close to the seedling was classified according to humus and mineral soil features. On clear-cuttings, mortality was significantly higher for seedlings planted in a mixture of humus/mineral soil or in cultivated pure humus than for seedlings planted in pure mineral soil. These findings were also confirmed in a large-scale study of pine weevil damage and scarification (Petersson, 2000).

To investigate the influence of humus and mineral soil on pine weevil feeding in a more systematic way an experiment was established, which showed that features of both the soil treatment and the soil type significantly affected the amount of damage to seedlings planted on a clear-cutting (Paper III). Again, damage was lowest in pure mineral soil. Planting in cultivated humus did not reduce damage significantly compared to planting in untreated humus. Two treatments resulted in an intermediate mortality between untreated humus and pure mineral soil; a mixture of humus and mineral soil, and potential hiding places consisting of humus on top of the mineral soil. This finding was not fully in accordance with the results obtained in the practical scarification experiment described in Paper I, where the mixture and the cultivated humus gave the same mortality after three years. The difference in results may be due to the fact that the Paper III mixture was made very precisely and the humus was fine grained, which was not the case for the Paper I mixture. Placing stones on top of the soil did not affect the damage to seedlings planted in pure mineral soil. Therefore, it seems that pieces of humus provide hiding places for the pine weevil but stones do not. Björklund *et al.* (2003) suggested that mineral soil provides little shelter and therefore fewer weevils will stay in the vicinity of seedlings planted in it. Humus, on the other hand, provides many hiding places and the pine weevil can then repeatedly return to and feed upon the same seedling.

The decrease in area debarked by pine weevil amongst seedlings planted in mineral soil seems to last only one, or sometimes two, years. In the practical scarification (Paper I) there was a significant effect for the first two years with respect to debarked area, but in the soil feature experiment (Paper III) the debarked area was only affected in the first year. This difference between the experiments may be due to the fact that half of the practical experimental material was in shelterwood, where ingrowth of vegetation is slower. The most important factor for the loss of the damage-reducing effect is probably the ingrowth of vegetation (Örlander & Nordlander, 2004).

Scarification is done for several reasons besides reducing pine weevil damage. Soil treatment often creates a more favourable environment for the planted seedling, and therefore stimulates its growth. Fast growth of the stem base diameter will make the seedling more resistant to pine weevil attacks (Örlander & Nilsson, 1999; Thorsén *et al.*, 2001). It has also been suggested that water stress will decrease the resistance of the seedling to pine weevil attacks (Selander & Immonen, 1991; Örlander & Nilsson, 1999). It is possible that the reduction in mortality caused by pine weevil amongst seedlings planted in mineral soil can be partly explained by the conditions being more favourable for the seedlings (Örlander *et al.*, 1991; Nilsson & Örlander, 1999; Nordborg *et al.*, 2003).

Vegetation influencing pine weevil damage (I, II, III, IV)

The influence of vegetation close to the seedlings on pine weevil damage is not unimportant according to previous studies, but the reported effect varies between studies. Two studies have found a decrease in damage when vegetation increased (Jutinen, 1962; Långström, 1982), whereas others have found an increase (Christiansen & Bakke 1971, Wilson & Day 1996). In addition, Örlander & Nilsson (1999) found no effect at all for herbicide treatments when seedlings were planted in an undisturbed humus layer. In a recently published study the ingrowth of vegetation in pure mineral soil was correlated to increased damage, and damage remained low if the mineral soil was kept free from vegetation with herbicides (Örlander & Nordlander, 2004).

Vegetation influenced damage in different ways depending on the soil treatment and seedling treatment. Papers I and II report a significant correlation between vegetation in contact with the seedling and the frequency of feeding by pine weevils. This correlation was most pronounced for seedlings protected with feeding barriers, especially those with shields. The exact position of the vegetation was not examined, so vegetation could have caused the increase in damage in several different ways. A possible explanation was that pine weevils use vegetation as a “bridge” to walk across, and thus avoid the feeding barrier and the mineral soil. In the study described in Paper IV, seedlings were planted in mineral soil and surrounded by vegetation from the area just outside the scarification. The presence of wavy hair-grass (*Deschampsia flexuosa* (L.)), significantly increased damage to seedlings, but the hypothesis that vegetation was used as a bridge could not be confirmed. Vegetation influences the microclimate close to the seedling, so its impact on air temperature, global radiation and air humidity was investigated. However, these micro-climatic factors and pine weevil damage were not significantly correlated, so the micro-climatic changes caused by vegetation cannot solely explain the increase in damage. There may be a low threshold value for the effects of vegetation density on pine weevil damage, but damage could also be linearly correlated to global radiation; neither explanation could be excluded based on this study.

Is vegetation cover also important for pine weevil damage when seedlings are planted in undisturbed humus? In the studies presented in Papers I and II, damage

increased with increasing vegetation cover, but when the artificial vegetation system described in Paper IV was tested, it did not affect damage significantly for seedlings planted in undisturbed humus. Humus will provide abundant possible hiding places for pine weevils, and the additional shelter that vegetation provides may therefore not have much effect.

Björklund (2004) found that increases in wind speed increased the likelihood for pine weevils to use artificial shelters. The cited author suggests that wind is an underestimated factor, and that open areas such as scarified patches might be avoided. Therefore, reductions in wind speed due to high vegetation surrounding the scarified patches may be one explanation for the observed difference in damage frequency.

The most likely explanation for the increase in damage observed when seedlings are planted in mineral patches and surrounded by vegetation seems to be that pine weevils perceive vegetation as a shelter that helps them avoid potential threats such as predators or extreme temperatures. However, the possibility cannot be excluded that other changes in microclimate also interact in some way.

Combinations of methods (I, II, III)

Three methods that are already known to reduce pine weevil damage (shelterwood, soil scarification and seedling treatment) were combined to test if the effects were additive or not, and if there were any interactions between some of the damage-reducing methods. The results showed that the reduction of pine weevil damage (mortality and debarked area) for a single method could be added when combined with the other factors included in the study (although this did not apply to insecticide-treated seedlings, since mortality was <5% regardless of treatment). When all three methods were used (shelterwood, scarification and feeding barrier), the mortality due to pine weevil damage was reduced to 7%, whereas there was 88% mortality in the control (clear-cuttings with no scarification and unprotected seedlings).

The effect of scarification was significant irrespective of the cutting regime. However, the effect tended to be more long-lasting in the shelterwood compared to the clear-cutting. On a clear-cutting the soil type in the vicinity of the seedling after scarification affected damage, and pure mineral soil was most effective while cultivated humus was less effective. Seedling height three years after planting was significantly higher for seedlings planted in scarified soil or protected with either feeding barriers or insecticides. The use of different cutting regimes (clear-cutting/shelterwood), however, did not affect seedling height significantly.

Predicting the effects of different combinations of regeneration methods that could reduce mortality is not straightforward. Apart from the methods mentioned here (shelterwood, scarification and treatment of seedling) different seedling sizes and seedling types could be used. A model intended to predict the effects of all of

these factors is currently being developed, partly based on knowledge obtained in studies I-II (Nilsson *et al.* unpublished).

Conclusions

Regeneration methods known to reduce pine weevil damage (shelterwood, scarification and feeding barriers) are additive with respect to their reduction of pine weevil feeding (Paper I). When three of these methods were used in combination, mortality was reduced to less than 10% even on sites with high pine weevil pressure. Scarification reduced pine weevil damage equally effectively under a shelterwood as on a clear-cut. However, the scarification effect seems to last longer under a shelterwood than on a clear-cut, due to the slower ingrowth of vegetation.

An efficient feeding barrier must prevent pine weevils from feeding on a seedling for at least two years. The most effective type of feeding barrier (shield with a collar), reduces pine weevil damage as effectively as treatment with permethrin. For coatings and shields without a collar, mortality is significantly higher than for permethrin. Vegetation in contact with the feeding barrier increases pine weevil damage. There is a risk that coatings may sometimes damage seedlings, because several studies have found mortality that is not related to pine weevil damage to be more frequent for treatments with coatings than for other treatments.

Planting seedlings in cultivated humus does not significantly reduce their mortality three years after planting compared to planting in undisturbed humus. However, mixing fine grained humus with mineral soil reduces damage significantly, although not to the same extent as planting in pure mineral soil. The presence of hiding places on top of the pure mineral soil can increase pine weevil damage, at least if they consist of humus.

Damage caused by pine weevil is higher in mineral patches where planted seedlings are surrounded by vegetation than in patches without vegetation. When seedlings are planted in humus, vegetation has no significant effect on pine weevil damage. Pine weevils do not reach the seedlings by using vegetation as a “bridge” to cross over the mineral soil. The increased feeding may be due to the pine weevils perceiving vegetation as a shelter providing protection from predators and extreme temperatures. Changes in other micro-climate factors associated with the vegetation cover seem to be of less importance.

Management implications

When generalizing the results, the geographic distribution of the experiments may be important. All study sites were located in the interior of southern Sweden. However, several studies have indicated that pine weevil damage parameters are

fairly constant throughout regions of the Nordic countries with a two-year generation time, i.e. in the latitudinal range 56-60 °N (Beijer-Petersen, 1962; von Sydow, 1997; Petersson, 2000).

All insecticide treatments described in Papers I and II involved the use of permethrin. Other insecticides will have to be used instead from now on, across the European Union, because permethrin is no longer registered. Preliminary results from unpublished studies indicate that the substitutes have approximately the same effect on pine weevil damage as permethrin, implying that the results in Papers I and II concerning permethrin can most likely be applied to the insecticides that will be in use from 2004.

Feeding barriers have not yet been used on a large commercial scale, except for a coating made of mineral wax called Bugstop (Hellqvist *et al.*, 2001). Its protective effect is likely to be less efficient if used on a large scale rather than experimental scale. In experiments, the treatment and planting of the seedling with coatings or shields will probably be more carefully done than in commercial practice. This could be highly significant since, for instance, shields with a collar at the top must be placed accurately in the soil preventing humus coming into contact with the collar to maintain its protective effect.

The economic aspects of using feeding barriers instead of insecticides have not yet been resolved. A feeding barrier retaining its protective effect for two years or more should be compared financially with insecticide-treatments applied twice: once before planting and once in the field in the second year. The cost of the two applications indicates the approximately maximal cost for a cost-effective feeding barrier. Clearly, therefore, the production and application of any such system must be highly mechanised, and it must be robust.

Scarification is widely used in modern regeneration practices in Sweden, Finland and the UK. To improve its results with respect to reducing pine weevil damage, the method can be further developed and new techniques may be needed. Advice that should perhaps be followed, where possible, is that the scarification spot should consist of pure mineral soil and be large enough to avoid shelter effects of surrounding vegetation. Scarification should prevent the ingrowth of new vegetation and the planting point should be above the ground line. Planting immediately after harvest, when field vegetation is often relatively scarce, should help avoid the damage-increasing effect of vegetation. On the other hand, the feeding pressure of the newly arrived immigrant weevils is often very high on fresh clear-cuttings.

There is always a risk that windfalls may occur if shelterwood trees of Scot pine are left after harvesting (Karlsson & Örlander, 2004). Indeed, a study in southern Sweden showed that on average approximately 30% of shelter trees are felled by wind (Örlander, 1995). However, a shelterwood density of approximately 110 to 140 stems/ha will reduce pine weevil damage significantly and still allow the new generation of Norway spruce seedlings to survive (Paper I).

A useful finding for practical forestry is that several methods (feeding barriers, scarification and shelterwoods) that reduce pine weevil damage can be combined to obtain an additive effect (Paper I). If a high risk of heavy pine weevil attack is expected when regenerating a stand, several counter-measures should be applied in the best possible way (Papers I-IV). Site conditions are important considerations because they limit the possible efficiency of the various methods. A sound strategy for any given site may be to focus on methods that are likely to be effective under its specific conditions. For example, if the soil is stony and the stand is dominated by Scots pine, the damage-reducing effect of scarification will be weaker than that of a dense shelterwood. In such cases feeding barriers may also be a more efficient way to reduce damage than scarification. Management strategies should be carefully analysed to obtain an acceptable level of mortality in a cost-efficient way.

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