Effects of granivorous rodents on direct seeding of oak and beech in relation to site preparation and sowing date

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Abstract

Planting bare-rooted seedlings is a rather expensive method to regenerate oak (*Quercus robur*) and beech (*Fagus sylvatica*). Direct seeding could reduce artificial regeneration costs substantially, but the method currently suffers from a number of problems, one of which is seed consumption by rodents. In the present study clear-cut areas in southern Sweden were prepared using one of four different mechanical site preparation methods - disc trenching, patch scarification, topsoil removal and mounding - then manually sown with acorns and beech nuts. Acorns were sown in May and July 2006, and both acorns and beech nuts were sown in May 2007. Three years following sowing, best seedling establishment from viable acorns, 60-70%, was achieved after sowing in mounds in May, and the subsequent survival reached 90-100%. After the first growing season for beech, both seedling establishment and subsequent survival was lower than for oak, which coincides with a higher number of lost beech nuts at the excavation to investigate the fate of seeds. Granivorous rodents (*Apodemus flavicollis*, *A. sylvaticus*, *Mus musculus*, and *Myodes glareolus*) were live-trapped more frequently in the vicinity of slash piles compared to other micro-site features, such as uprooted stumps, snags and stones. In 2006, no connection was found between number of rodents captured and proportion of lost seeds, while in 2007 the two were in good accordance. No clear relationship was found between number of captured rodents, vegetation cover class and mechanical site preparation method. More rodents were captured in 2007 than in 2006, and there was an increase in captures from spring until late summer/autumn for both years, which was mirrored in the seedling establishment result from the three different times of sowing. Based on experiences from the present study the recommendation for successful direct seeding of oak on clear-cuts is a combination of mounding site preparation, removal of slash and sowing in May rather than July. However, the results indicate that successful direct seeding of beech is more difficult to achieve.

Keywords: granivorous rodents, reforestation, regeneration, seed removal, site preparation

1 Introduction

The changes to climate projected to occur in southern Sweden this century (Christensen et al., 2007) require the development of new approaches to forest management. Such approaches could include increasing the prevalence of some broadleaved tree species, e.g. oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.), that are likely to be better adapted to the new climate conditions (Koca et al., 2006) than Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.). Because planting broadleaves is associated with high costs from expensive seedling purchases and protective measures to avoid browsing damage, many forest owners continue to plant Norway spruce in those cases where natural regeneration of broadleaves is not feasible. However, reforestation costs for broadleaved plant material could be markedly reduced if seeds could be used for regeneration instead of the large bare-rooted seedlings that are often used today. Unfortunately, the likely success of direct seeding of oak and beech on forest lands is far from certain when using the methods currently available (Madsen and Löf, 2005; Ammer and Mosandl, 2007).

Granivorous rodents are particularly responsible for contributing to this uncertainty, due to their capacity to rapidly consume and remove seeds from regeneration areas (Birkedal et al., 2009). There are a variety of suitable rodent habitats that often occur within or adjacent to forest clear-cuts, including shelter trees, forest edges, patches of vegetation, and logs and stumps abandoned after clear-felling (Buckley and Sharik, 2002; Takahashi et al., 2006; Dey et al., 2008). These habitats increase the likelihood of seed mortality due to their associated contribution to the viability of local rodent populations (Hansson, 1978; Mazurkiewicz, 1994). Moreover, Hansson (1978) showed that vegetation and boulders are preferred micro-site features, and that rodent numbers generally increase after pre-commercial thinning of stands before cutting operations. Hansson (1978) hypothesised that rodents generally preferred recently cleared forests due to the subsequent flush of ground vegetation. A finding that is consistent with Larsson (1977), who found that bank voles were more abundant with increased cover of tall herbs and dwarf shrubs. High moisture levels have also been linked to a greater abundance of rodents (Hansson, 1978; Torre and Arrizabalaga, 2008), possibly as a result of the dense vegetation often associated with wetter areas. Slash, often retained in large quantities after forestry operations, may also be a suitable habitat for rodents (Jensen, 1984). In order to increase the success of direct seeding strategies, more information is needed regarding possible measures for reducing the availability of suitable rodent habitats in and adjacent to regeneration sites. One way to affect micro-site characteristics is through site preparation, and in this way creating environments where rodents might be less efficient seed consumers. However, any measures taken to reduce rodent consumption of seeds must not compromise the establishment and growth of the seedlings.

In Sweden, about 150 000 ha annually are treated with mechanical site preparation during reforestation (Anonymous, 2007). Mechanical site preparation generally improves the growth of both transplanted seedlings and seedlings produced by direct seeding (Dey et al., 2008; Löf and Birkedal, 2009), but any effect on rodent feeding behaviour is little studied. For example, different methods create different sized vegetation-free areas around the seeding spots - something that may influence rodent distribution and seed consumption. In addition to providing vegetation free zones, mounding creates elevated seeding spots, a feature that also might reduce rodent activity. In Sweden, disc trenching (DT) is a common method, as are patch scarification (PS) and mounding (M). Complete topsoil removal (TSR) is a more extreme form of mechanical site preparation, and is rarely used in commercial forestry. For experimental purposes it remains of interest, due to its relatively large influence on habitat features that are likely to affect the behaviour of foraging rodents.

Rodents are affected by access to hiding places, but also by food supply (Olsson et al., 2005; Fedriani and Boulay, 2006). Acorns and beech nuts are considered a high quality food item by granivorous rodents (Jensen, 1985) and are therefore worth taking risks for, but if other food is more readily available the attractiveness of these seeds may be reduced. In the summer, the supply of herbs and other seeds is greater than in the spring, thus providing rodents with a wider range of alternative food sources that may distract them from consuming sown seeds. Little is known about the effect of rodents on acorns and beech nuts sown in spring contra summer during the same year.

Our overall goal was to increase knowledge on how to develop new low-cost reforestation techniques where direct seeding of oak and beech may be one option if the problem of seed consumption by rodents is minimised. The objectives of the study were to examine: 1) the effect of four different mechanical site preparation methods on oak and beech seedling establishment and survival, and on rodent consumption of acorns and beech nuts, in comparison with a control (no site preparation); 2) the effect of two different sowing dates on oak seedling establishment and survival, and on rodent acorn consumption; and 3) the influence of soil moisture, vegetation cover and a number of micro-site features on rodent distribution.

2 Materials and methods

2.1 Site and climate description

The experiment was located at two sites in the Asa experimental forest, southern Sweden: Oxafällan (19 ha, 14°45´57´´E, 57°08´26´´N, 250 m a.s.l.); and Nybygget (27 ha, 14°44´26´´E, 57°08´55´´N, 255 m a.s.l.). Norway spruce previously occupied both sites, but were felled by a storm in January 2005 at the ages of 44 and 38 years, respectively. The experiment was initiated in spring 2006 and continued until autumn 2008. When the experiment started both sites were free from logs and fallen trees and almost free from herbaceous vegetation. However, large amounts of slash and uprooted stumps were still present. During the study period, the herbaceous vegetation was mainly dominated by *Rubus idaeus* L., *Deschampsia flexuosa* L. and *Juncus* sp., as well as some naturally regenerated birch (*Betula* sp.). The soil type at both sites was sandy till (Löf and Birkedal, 2009)

Weather data were collected by the Asa weather station (approximately 3 km from the two experimental sites) and measurements were recorded using a Campbell CR10 data logger (Campbell Scientific Inc., Utah, USA) equipped with a ventilated and radiation-shielded thermistor (Campbell type 107) 1.7 m above the ground and a tipping bucket rain gauge (Campbell ARG100). In 2006 there was high rainfall during April and May, while June and July were dry and warm (Table 1). Spring months 2007 and 2008 were dry, but during the summer months there was high rainfall.

2.2 Experimental design

Of the four experimental blocks, three were located at Oxafällan and one at Nybygget. The distance between the blocks at Oxafällan was approximately 25 m, and the size of each block was 42 × 83 m (0.35 ha).

Table 1. *Monthly precipitation (mm) and average air temperature (°C) during spring 2006 through to autumn 2008 at the Asa experimental forest in southern Sweden.*

Year	Month	Precipitation	Air temp.
2006	April	80	4
	May	98	10
	June	22	16
	July	24	19
	Aug.	107	16
	Sept.	74	13
2007	April	28	7
	May	41	11
	June	114	16
	July	150	15
	Aug.	125	15
	Sept.	99	11
2008	April	34	6
	May	28	11
	June	22	14
	July	129	16
	Aug.	150	15
	Sept.	50	11

The design comprised randomised blocks with split-plots; each plot measured 20 × 15 m, and there was 2 m between them. In each block there were five different site preparation treatments (main plots): Untreated control (C); Disc trenching (DT); Patch scarification (PS); Top soil removal (TSR) and Mounding (M). Site preparation was carried out using an excavator in April to early May 2006. The scarified rows in the DT-treatment were approximately 60 cm × 20 m, and the PS and M treatments consisted of twelve patches (ca 60 × 50 cm) or mounds (ca 80 × 50 cm and 20 cm in height) per row. In the DT and PS treatments the mineral soil was exposed in the rows/patches, while in the TSR treatment mineral soil was exposed across the whole plot. In the M treatment the mineral soil was placed on top of the humus layer in the mounds. There were eight or ten rows available for direct seeding in each treatment plot, and the distance between them was around 1.5 m. The scarification resulted in approximately 0%, 36%, 11%, 100%, and 25% exposed mineral soil in C, DT, PS, TSR and M treatments, respectively. All slash was removed from the treatment plots and collected into large piles around the experimental blocks. In the control plots only sufficient slash was removed as to facilitate the direct seeding.

In 2006, direct seeding was carried out on two occasions (in sub-plots): at the end of May and in mid-July resulting in ten treatment plots per block. Half of the seeding rows in each plot were randomly selected to be sown with acorns, and the remaining rows were sown with beech nuts. Due to poor seed material, the beech nuts sown in 2006 were excluded from further studies. One PS plot at Oxafällan was not seeded in the spring due to water logging. In 2007, the seeding took place at the end of May and on this occasion four rows (originally sown with beech nuts in 2006) in the C, TSR and M treatments were sown: two with acorns and two with beech nuts. All direct seeding was manual and conducted using a planting tube designed for containerised seedlings. The tube point, 3 cm in diameter and 10 cm long, was pressed into the ground and the seed was put into the hole and covered with soil. In the C, DT and TSR treatments, one seed was planted every 25 cm, resulting in 80 seeding spots and seeds per row. In the PS and M treatments, there were four seeding spots per patch or mound, resulting in 48 seeds per row. Here seeds were planted towards the four corners of each patch or mound, approximately 20 cm from the centre. All acorns were sown at a depth of 5-10 cm, which is recommended by Nilsson et al. (1996) to avoid extensive rodent predation. Beech nuts were sown at approximately 3 cm, since beech cotyledons, in contrast to oak, need to be able to penetrate the soil and develop above ground, which is difficult if seeds are sown too deeply (Watt, 1923). In total, 14 320 acorns and 1 664 beech nuts were included in the present study. To minimise any residual smell of humans, gloves were worn while handling the seeds. From August 2006 onwards, all blocks were fenced to exclude larger herbivores.

Each of the four blocks was covered by a 90 m × 50 m rodent trapping grid, with one "Ugglan" multi-capture live trap (GRAHNAB, Hillestorp, Sweden) placed every 10 m, thus comprising 60 traps per block. The traps were baited with oats and pieces of fresh apple, and contained hay as a bedding material. In addition, to perceive local rodent abundance, two 50 m × 40 m (30 traps) trapping grids were placed in the forests adjacent to the clear-cuts at Oxafällan and Nybygget. Where possible, traps were placed adjacent to micro-site features (see below and Table 2) preferred by rodents.

2.3 Seed material

All seeds were handled according to international guidelines (Anonymous, 1993). From the time of delivery until the seeds were sown they were stored at + 4 °C. Before the spring sowing in 2006, acorns were soaked for two days in running water in a small stream; prior to the summer sowing no such treatment was possible because the stream had run dry due to drought. Before the sowing in 2007 acorns and beech nuts were soaked in water for two days. The viability of all seed batches was determined by cut-tests prior to sowing.

Two batches of acorns (*Quercus robur* L.), collected in 2005, were used for the 2006 seeding. They were mixed together for equal distribution in the experiment; the provenances were Renswoude 01, the Netherlands and

Kolleberga L130, Sweden. Dutch acorns dominated and approximately 93% of all seeds were of this provenance. The Dutch acorns had been stored at Levinsen Treeseed Ltd, Lynge, Denmark, and the Swedish ones at Ramlösa Plantskola, Helsingborg, Sweden. The viability of the two batches before sowing in May was 60% and 65%, respectively. In July the viability of the Swedish acorns had decreased to 35%, while the Dutch acorns had retained their viability. The acorns used in 2007 were collected in 2006, their provenance was RD 0346, Poland, and they were stored at Ramlösa Plantskola. The beech nuts used in 2007 were collected in 2006 from Haderslev F.692, Denmark, and were stored and pre-treated at Statsskovenes Planteavlsstation, Humlebæk, Denmark. The viability of both the acorns and beech nuts, used in 2007, was 80%.

2.4 Measurements

At the end of September 2006, 2007 and 2008 a complete inventory of seedling establishment was compiled. However, treatments C, PS, TSR and M from the July sowing in one block at Oxafällan were not inventoried in 2006 due to technical problems. During these surveys all established seedlings were checked for rodent damage. At the end of September 2006, ten acorn seeding spots per treatment plot, in all blocks, were thoroughly excavated to determine the fate of the acorns. Previously planted and now collected seeds were recorded as: seedlings (visible epicotyl or hypocotyl above ground); germinated (visible radicle outside seed coat); germinable (healthy endosperm/cotyledon); ungerminable (empty or unhealthy endosperm/cotyledon) or lost if the seed was not retrieved at all. At the end of September 2007, ten acorn and beech nut seeding spots per treatment from that year's sowing were excavated, and recorded as in 2006.

Surveys of rodent numbers were conducted on three occasions during 2006 (June 12-15, July 24-26 and September 18-20), and on two occasions in 2007 (June 13-15 and September 17-19). During these trapping sessions, traps were visited twice each day and all rodents of the species *Apodemus flavicollis* Melchior, *A. sylvaticus* L., *Mus musculus* L. and *Myodes glareolus* Schreber that were caught were individually marked before release. Some specimens of *Microtus agrestis* L. and *Sorex* sp. were caught in the traps but they were not included in the analysis, since they are generally considered to consume very few seeds (*M. agrestis* – Hansson, 1971; *S.* sp – Shvarts et al., 1997).

Inventories of ground vegetation were compiled for all treatment plots, in all four blocks, in the middle of August 2006, and at the beginning of September 2007. The vertical projection of vegetation cover, within the treated area, was estimated in twelve quadrats (60 cm × 60 cm) in one row per treatment plot. Vegetation cover in each quadrat was classified as follows: 1) 0-5; 2) 5-10; 3) 10-25; 4) 25-50; 5) 50-75 and 6) 75-100 percent vegetation cover.

In April 2009, the distance to, and the number of different micro-site features was recorded in a circular area of 5 m radius around each rodent trap-point across the four trapping grids in the clear-cuts. The features, which were the ones occurring in any considerable amount, taken into account are listed in Table 2. In addition, the distance from each trap-point to the nearest forest edge was recorded, and the moisture of the area around the trap-point was classified as follows: 1) dry; 2) fresh to swampy; 3) wet to open water. The number of traps in each moisture class was 101, 127 and 12, respectively.

Table 2. *Characteristics of the micro-site features measured around the trap-points in the clear-cuts at Oxafällan and Nybygget.*

Micro-site feature	**Size/amount**
Tree-stump	Ø ≥ 20 cm
Stone	Ø ≥ 75 cm
Cairn	≥ 5 stones, Ø ≥ 20 cm/stone
Snag	Ø ≥ 10 cm
Uprooted stump	Ø ≥ 20 cm
Slash pile	Ø ≥ 1 m

2.5 Statistical analysis and calculations

The general linear model (GLM) procedure for the analysis of variance was used to examine the effect of site preparation treatment and sowing date on seedling establishment from viable seeds, lost seeds and seedling survival (Minitab Inc., Pennsylvania, USA). Tukey's test was used to separate the effects of the different site preparation treatments ($P < 0.05$). The values for seedling survival were ranked before analysis, since they were not normally distributed (Conover and Iman, 1981). Seedling survival was calculated as the proportion of seedlings recorded in 2006 that were still present in 2007.

Rates of establishment of viable seeds were calculated as the percentage of viable seeds (determined before direct seeding) from which seedlings had developed at the time of the inventories. Rodent capture rates were calculated as the number of rodents caught per 100 trapnights according to Nelson and Clark (1973). When calculating the total capture of granivorous rodents in the whole experiment, recaptured animals were excluded. However, when calculating the number of rodents caught per site preparation treatment, recaptured animals were included in the analysis, since one individual sometimes visited several different treatments. In the latter analysis only traps placed strictly inside the treatment plots were taken into account, and the number of traps per treatment in total was 20, 16, 18, 19 and 20 for C-, DT-, PS-, TSR- and M treatment, respectively. Each site preparation treatment plot was divided into two zones in order to determine whether the plots were large enough to discourage rodents from removing seeds. The outer zone represented all seeding spots within two and a half metres of the edge of the plot. The rest of the seeding spots were in the inner zone. GLM was used to analyse the difference in establishment between the two zones at the treatment level. The analysis was based on seedling establishment data from September 2008. Each trap-point in the clear-cuts was allocated a micro-site index based on the number of features within the designated circle (Table 2), and the distance from the trap-point to these features. A shorter distance between the trap-point and the feature, and a greater number of features within the circle, resulted in a higher

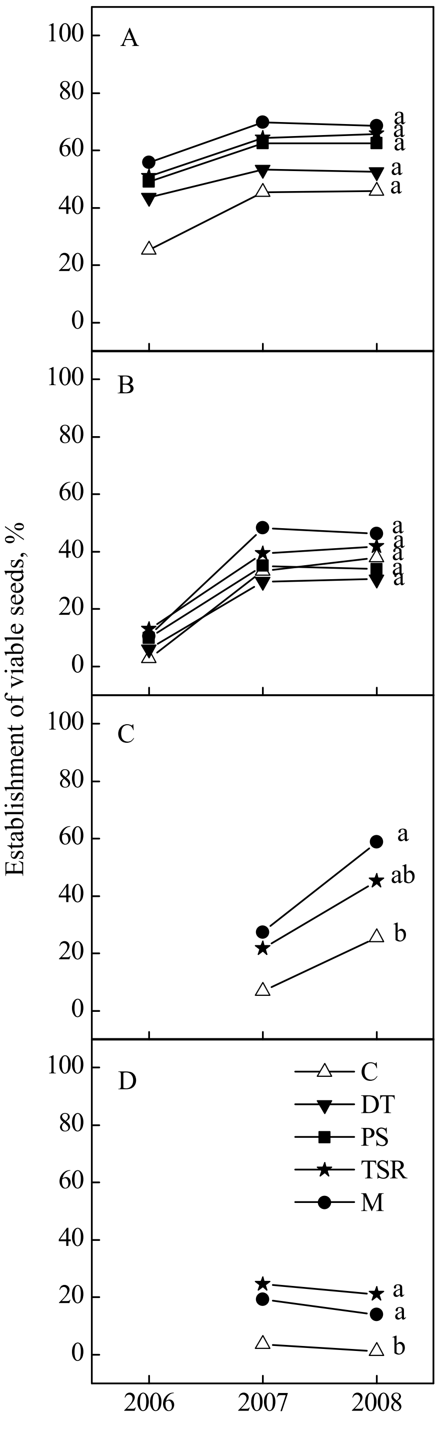


Figure 1. Seedling establishment from viable seeds in five site preparation treatments; C – control, DT – disc trenching, PS – patch scarification, TSR – topsoil removal and M – mounding (legends in box D), for; A) oak sown in May 2006; B) oak sown in July 2006; C) oak sown in May 2007; and D) beech sown in May 2007. Treatments with different letters are significantly different ($P < 0.05$) in 2008.

index value. For example, features at a distance of five metres from the trap-point were assigned the value one, and features at zero metres from the trap-point were assigned the value eleven, and then the values of all features in the circle were added together to give one index-value per trap-point. To determine the effect of different features on the number of captures, a logistic regression with binomial distribution and logit link, with block as a factor in the model, was used.

3 Results

In general, oak seedling establishment tended to increase from the end of the first growing season until the end of the second, while beech seedling establishment tended to decrease during the same time period (Fig. 1A-D). At the end of 2008 and compared to the other site preparation treatments, the M treatment produced the best oak seedling establishment from viable seeds for both sowing dates and both years, although the difference was only significant ($P < 0.05$) from the control in the 2007 seeding (Fig. 1A-C). In the same year, the oak seedling establishment varied from 26-46% and 46-69%, in the C and M treatments respectively. The beech seedling establishment was only 1% in the C treatment and 14% in the M treatment ($P < 0.05$; Fig. 1D). In 2008, oak seedling establishment was better ($P < 0.05$) than beech seedling establishment in the C and M treatments. After three growing seasons, sowing of oak in May 2006 resulted in more ($P < 0.01$) seedlings than sowing in July the same year (Fig. 1 A and B).

Table 3. *Seedling survival ± SE two growing seasons after direct seeding of acorns and beech nuts. Treatments followed by different letters are statistically different at P < 0.05 within year, sowing date and species.*

	Sowing date			
Site prep.	**Oak May 2006**	**Oak July 2006**	**Oak May 2007**	**Beech May 2007**
C	92.8 ± 0.7 a	80.0 ± 7.3 a	97.1 ± 5.0 a	33.3 ± 10.9 a
DT	97.0 ± 0.7 a	79.6 ± 11.0 a	-	-
PS	97.7 ± 0.7 a	81.6 ± 8.1 a	-	-
TSR	95.4 ± 0.9 a	85.4 ± 1.0 a	100 ± 0.0 a	83.3 ± 2.7 b
M	93.5 ± 2.5 a	68.4 ± 5.9 a	100 ± 0.0 a	72.9 ± 3.4 b

Seedling survival was generally high two growing seasons after direct seeding, and higher ($P < 0.01$) for oak, ranging from 80-100%, than for beech, ranging from 33-83% (Table 3). There were no statistically significant differences in oak survival between site preparation treatments. The survival of beech seedlings was considerably lower ($P < 0.01$) in the control than in the other site preparation treatments. In 2007, oak seedling survival was higher ($P < 0.05$) for the May sowing than the one in July. Oak seedling survival, from the seeds sown in 2006, was consistently high after three growing seasons (data not shown).

Table 4. *Proportion of seeds not found at the end of the first growing season for oak in 2006, and oak and beech in 2007. Treatments followed by different letters are statistically different (P < 0.05), within year, sowing date and species.*

	Sowing date			
Site prep.	**Oak May 2006**	**Oak July 2006**	**Oak May 2007**	**Beech May 2007**
C	17.5 ± 4.8 a	42.5 ± 20.2 a	42.5 ± 8.5 a	70.0 ± 9.1 a
DT	20.0 ± 10.8 a	50.0 ± 23.5 a	-	-
PS	26.7 ± 12.0 a	47.5 ± 7.5 a	-	-
TSR	25.0 ± 10.4 a	12.5 ± 4.8 a	22.5 ± 4.8 a	42.5 ± 13.1 a
M	12.5 ± 2.5 a	42.5 ± 4.8 a	27.5 ± 8.5 a	47.5 ± 8.5 a

Except for the M treatment in 2006, from which more ($P < 0.01$) acorns were lost from the July sowing than the one in May, the differences in lost seeds were not statistically significant either for treatment, sowing date, year of sowing, or species when analysed at the end of the first growing season (Table 4). However, except for the TSR treatment in 2006, there was a trend of greater losses of acorns from the July sowing than the May sowing; in addition, more beech nuts than acorns tended to disappear after the direct seeding in 2007. Acorn losses ranged from 13-50%, and losses of beech nuts from 43-70%.

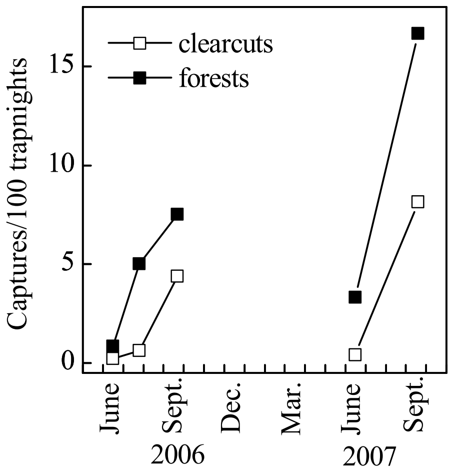
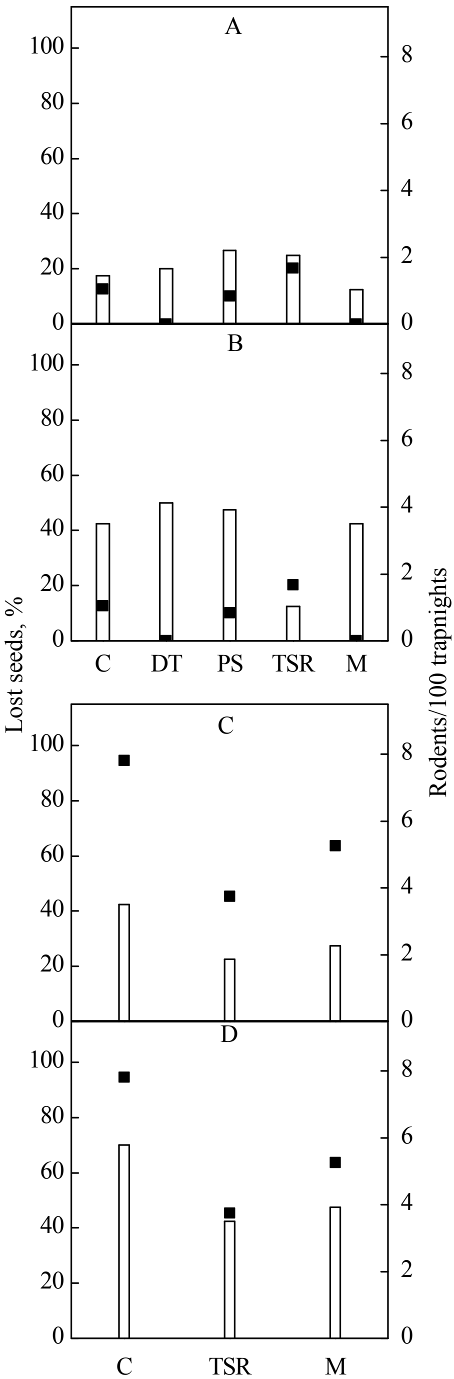


Figure 2. Rodent captures per 100 trapnights on five occasions during two years, in two clear-cuts and two forested areas.

More granivorous rodents, i.e. *A. flavicollis*, *A. sylvaticus*, *M. musculus*, and *M. glareolus*, were captured in the adjacent forests than the clear-cuts during the whole study (Fig. 2). The number of captures generally increased from spring through to autumn, and more rodents were captured in 2007 than in 2006.

In 2006 there was little connection between the treatments in which rodents were captured and the treatments in which most seeds were lost (Fig. 3A and B). In 2007, however, there was a good accordance between rodent captures and seed disappearances (Fig. 3C and D). The control

Figure 3. Proportion of seeds that were not found at the end of the first growing season (bars) in five site preparation treatments: C – control, DT – disc trenching, PS – patch scarification, TSR – topsoil removal and M – mounding, for: A) oak sown in May 2006; B) oak sown in July 2006; C) oak sown in May 2007; and D) beech sown in May 2007, in relation to rodent captures in the treatment plots (■).



treatment sown in 2007 had both the highest level of rodent capture and the greatest number of seeds lost. In the same year, in the TSR treatment, there were fewer rodents and fewer seeds had been lost by the end of the growing season. Rodent damage to seedlings was a minor problem during all three seasons considered in this study.

Over both years, sowing dates and seed species, there was no statistically significant difference between seedling establishment in the outer and inner zones of the plots in 2008, except in the M treatment where establishment was higher ($P < 0.05$) in the inner zone (Fig. 4).

More rodents tended to be captured in traps placed in wetter areas (Fig. 5A). Mean vegetation cover class in the different site preparation treatments in the two years

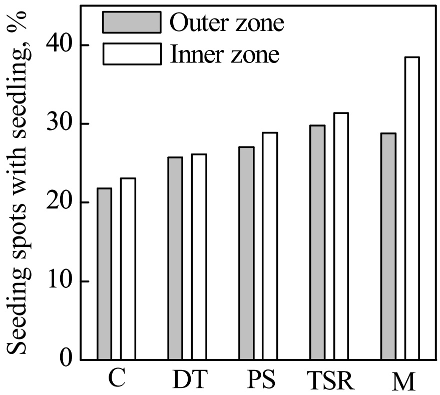


Figure 4. Proportion of seeding spots with established seedlings in 2008 in the inner and outer zones of the site preparation plots. Data from two sowing dates, five site preparation treatments, two years, and two species.

had no apparent effect on rodent captures in the plots (Fig. 5B and C). In addition, the distance to the forest edge had no effect on the number of rodents caught in the traps (data not shown).

Increased amount and proximity of slash piles near a trap was associated with an increased ($P < 0.01$) number of captured rodents (Fig. 6). Differences in amount of rodents captured in the different blocks led to four different curves, showing the probability of capture depending on the slash pile index for a particular trap. Taking other micro-site features (Table 2) into account did

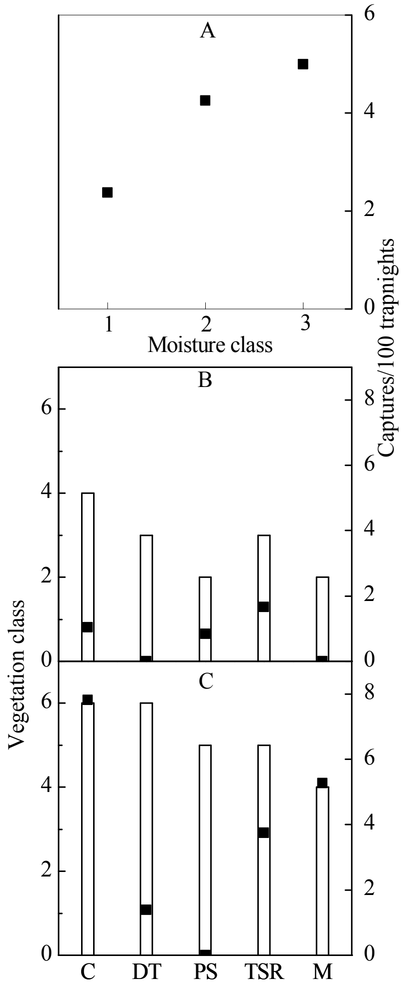


Figure 5. A) Rodent captures (all trapping occasions in both years) per 100 trapnights (■) in relation to moisture class around trap-points. Rodent captures (all trapping occasions in each year) per 100 trapnights (■) in the plots in relation to vegetation class (bars) in five site preparation treatments: C – control, DT – disc trenching, PS – patch scarification, TSR – topsoil removal and M – mounding, in: B) 2006; and C) 2007.

not add to explaining the trapping-pattern, and was therefore not used in the analysis presented here.

4 Discussion

This study, conducted in large clear-cut areas surrounded by coniferous forest, demonstrated that the best establishment from viable acorns sown in the spring reached 60-70%, in the mounding treatment. Furthermore, the survival of established oak seedlings reached 90-100%. This indicates that direct seeding of oak on clear-cuts, in combination with intensive mechanical site preparation, has the potential to be developed into a robust regeneration method. In comparison with previous research (Birkedal et al. 2009) these results should be seen as rather successful. This could be an effect of that the number of rodents caught per hundred trapnights on the clear-cuts was rather low. Much lower establishment percentage can be expected when more rodents are present at sites with for example broadleaved surroundings.

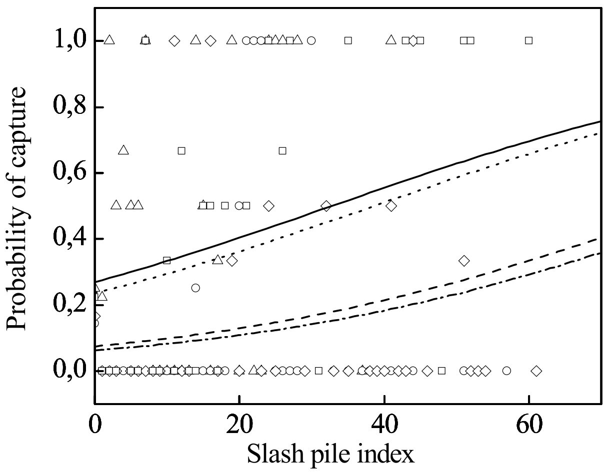


Figure 6. Probability of rodent capture in a trap with a specified index value for slash piles, within a radius of 5 m, in the four blocks. (Δ; continuous line) Block 1; (○; broken line) Block 2; (◇ ; broken line with dots) Block 3; (□; dotted line) Block 4.

For beech, both seedling establishment and subsequent survival was lower than for oak which has also been found by Löf et al. (2004). In the present study more beech nuts than acorns tended to disappear during the first growing season. Jensen (1985) found a higher bank vole preference for beech nuts than for acorns and related this to the fact that the energy content per weight unit of seed was higher for beech than for oak. Furthermore, rodents are usually less successful in finding seeds as the sowing depth increases (Nilsson et al., 1996). Hence, probably either the deeper sowing of acorns compared to beech nuts or the lower energy content per weight unit of acorns, or the two in combination, caused the losses of beech nuts to be greater than that of acorns. We observed little rodent damage to young seedlings in this study. However, small beech seedlings may be less tolerant to the harsh climate, i.e. high irradiance levels and temperature fluctuations including frost events, often prevailing on clear-cuts (Childs and Flint, 1987), which may be one contributing factor to the lower beech survival compared to oak. The oak seedling establishment in the mounds was better than that of beech and, as mentioned above; one reason for this may be rodent preferences. Another contributing factor could be that optimal conditions for acorn germination occur at higher temperatures (20°C; night/25°C; day), than for beech nuts (5°C; night/15°C; day) (Anonymous, 1993), and mounding increases the soil temperature (Knapp et al., 2008), which was also found in this experiment (Löf and Birkedal, 2009). Beech nuts just prior to germination are sensitive to temperature increase, and at temperatures around 20°C many will die (Suszka, 1966).

An interesting finding from the present study was that granivorous rodents were captured more frequently in the vicinity of slash piles, indicating that it is important to remove slash after felling if a site is to be regenerated by direct seeding of tree species with seeds desirable to rodents. A similar finding was reported by Jensen (1984), although his study was conducted in a mature forest. The present study also showed that, for example uprooted stumps, snags and stones, had less impact on rodent distribution than slash piles. Previous studies (Hansson, 1978) have concluded that, in general, cover is beneficial for rodents, but the present results imply that certain types of cover are better than others. It is possible that, in a recent clear-cut, mosses and lichens growing on the twigs and branches in the slash piles provide food (Hansson, 1999) as well as shelter, and therefore such piles are preferable to other types of hiding place. However, the effect of different features is most likely related to their relative abundance, for example Birkedal et al. (2009) found that rodent captures increased in the vicinity of large stone wall remains. In general, as well as in the present study, more rodents tend to be captured in moister areas (Hansson, 1978; Torre and Arrizabalaga, 2008), although there are exceptions (Larsson, 1977). Most likely, the difference in rodent abundance in relation to site moisture class is an indirect effect, where the amount of vegetation which is usually favoured by increased soil moisture, is the actual decisive factor.

In the present study the mean vegetation cover was higher in the control treatment compared to the various mechanical site preparation treatments. Best vegetation control during the first two years was achieved with mounding. However, the effect of the different site preparation methods on the rodents is hard to interpret in this experiment. There were no differences in the proportions of seedling establishment between the two zones in any of the site preparation plots except for the M treatment, where establishment was higher in the centre of the plot. This indicates that the plots might not have been large enough to discourage rodents from foraging inside them. Johnson (1981) concluded that oak sowings in forest openings larger than approximately 1 hectare, and almost completely free of vegetation, suffer less rodent damage than smaller areas. However, Johnson states that it is not known whether that size is the minimum. The clear-cuts in this study were larger than 1 hectare, but each site preparation plot was smaller. Although the areas were essentially free from vegetation at the start of the present experiment, there was a lot of slash surrounding the blocks and, as the investigation into the importance of micro-site features indicates, this may provide the rodents with hiding places.

In general, it is difficult to find a clear correlation between sizes of predator populations and the disappearance rate of their prey (Fedriani, 2005). Additionally, it is difficult to determine densities of rodent populations (Slade and Blair 2000). Also in this study a correlation between number of captured rodents and amount of lost seeds was hard to establish, although there was a general trend of better seedling establishment in the TSR and M treatments. Mounding was the site preparation treatment that tended to produce the best oak seedling establishment in both years and for both sowing dates. One reason for the improved establishment may be that rodents dislike entering the mounds, where they are doubly exposed, both because there is less vegetation and because the mounds are higher than the surroundings. TSR was the site preparation treatment associated with the second highest oak seedling establishment; this treatment resulted in there being less ground vegetation than in the control. However, the pattern of captures in 2006 did not indicate any particular preferences with respect to site preparation treatments, but the interpretation of the data is complicated by the overall low number of captures during that year. In 2006 1.9 rodents/100 trap-nights (0.6 bank voles/100 trap-nights), were captured on the experimental clear-cuts, compared to for example 4.3 rodents/100 trap-nights (1.3 bank voles/100 trap-nights) during 2007. Results from bank vole snap-trapping in Norra Kvill (approximately 100 km northeast from Asa) conducted between 1981 and 2003 show capture rates varying from 0.1 to 7.1 bank voles/100 trap-nights (Hörnfeldt 2010 and pers. comm.). In 2007 in this study, more granivorous rodents were found in the control than in the TSR and M treatments, which mirrors the seed losses from the different treatments. No such relationship was found for 2006, which is probably also a result of the low number of rodents caught. Although the amount of rodents generally increase with increased ground vegetation cover (Larsson, 1977), we found little connection between mean vegetation cover class and amount of rodents captured in the various mechanical site preparation treatments during the first two years. However, the vegetation cover measurements were conducted in the mechanical site preparation treatment rows or spots, whereas the rodents are dependent also on vegetation cover between the scarified rows or spots. More studies are needed to understand rodent behaviour in relation to different mechanical site preparation treatments.

The patterns of rodent trapping in this study were similar to those previously reported for granivorous species in the temperate zone, with increasing numbers of captures from spring through to autumn (Pucek et al., 1993; Hansson et al., 2000). This trapping pattern mirrors the greater losses of acorns sown in July 2006 than in May the same year. The greater number of other food sources available for granivorous/herbivorous rodents later in the summer than in the spring is apparently not enough to keep them from preying upon high quality food such as acorns. Similar observations were reported by Birkedal et al. (2009) when comparing sowing in May and June. Furthermore, the greater rodent abundance in forests than in more open areas is also in line with results from previous studies (Jensen, 1984; Torre and Arrizabalaga, 2008). The differences in seedling establishment between the two sowing dates are greater than the difference in lost seeds. This is probably related to the poorer conditions for germination, for example drought in the summer (Löf and Birkedal, 2009), compounding the effect of rodents. It appears that more seeds disappeared in 2007 than in 2006, which correlates well with an increased time since scarification resulting in more vegetation cover; it also corresponds to the larger number of rodents captured in the study sites in 2007. The increase in the number of captures in the forests and on the clear-cuts follows the same pattern, which makes it likely that the general increase in rodent numbers in 2007 is the primary factor causing the greater losses of seeds, rather than the increase in vegetation cover on the clear-cuts.

5 Practical implications

Several management implications can be drawn from this research, although they should be interpreted somewhat carefully since the study was conducted at a limited number of sites only sown during two years. First, it can be concluded that mounding and topsoil removal are mechanical site preparation methods that seem to work satisfactorily for successful establishment of oak following direct seeding, while it appears that successful direct seeding of beech is more difficult to achieve. One effect of mounding and topsoil removal site preparations could be that granivorous rodents are less inclined to enter scarified areas. However, top soil removal may for other reasons, i.e. nutrient management and aesthetic considerations, not be a preferable mechanical site preparation method in forest management. Secondly, to improve the chances of successful regeneration through direct seeding of oak and beech, slash should be removed from the entire regeneration area since it is likely to provide suitable and often well utilised shelter for rodents. This operation coincides with today's trend in forestry to collect slash for bio-energy reasons, but also may contribute to a risk for reduction of some soil nutrients on certain soils in the future. Finally, postponing the sowing of acorns from May until July is not recommended, since this tends to reduce the number of subsequent seedlings, probably both because of increased consumption from rodents and because at this time conditions are worse for germination and establishment. The most successful result following direct seeding is probably achieved through using a combination of different measures to reduce rodent predation on seeds. For example the above mentioned precautions together with sowing acorns at a soil depth of 5-10 cm (Nilsson et al., 1996) in large open areas (Johnson, 1981) surrounded by coniferous forests (Birkedal et al., 2009). Finally, the number of rodents present at a particular site in a particular year is also likely to affect the regeneration outcome.

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