Reforestation by Direct Seeding of Beech and Oak: Influence of Granivorous Rodents and Site Preparation

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Abstract

In southern Scandinavia there is a general desire to increase the amount of broadleaved forest using, for example, beech and oak, in order to preserve biodiversity and spread risk in the face of climate change. In order to realise this goal cheaper regeneration methods are needed. Although there are a number of uncertainties at present, direct seeding has the potential to fulfill this role. Two of the greatest obstacles to successful regeneration of beech and oak using direct seeding are seed removal by granivorous rodents and competition from ground vegetation. These issues need to be addressed before direct seeding can become a reliable regeneration method.

The work described in papers **I**, **II** and **IV** in this thesis investigated the influence of site, sowing dates, rodent population densities, site preparation and repellents on rodent damage to sown beech nuts and acorns. Paper **III** describes a study which examined the effect of different mechanical site preparation methods, and different sowing dates, on the growth of young oak seedlings.

Seedling establishment was more successful at large sites surrounded by mixed forests, compared to smaller areas surrounded by broadleaved forest (**I, II**). Oak seedling establishment was more successful than that of beech. Fewer acorns were lost and seedling establishment was better following spring sowing compared with summer sowing. In all years, more rodents were captured in the summer/autumn period than the spring. However, no clear correlation between rodent numbers and the success of direct seeding could be established. More rodents were captured in traps close to features providing cover, for example slash piles and the remains of stone walls. There were no clear relationships between the various mechanical site preparation treatments and rodent distribution and seed removal. In a laboratory study, mink excrement was found to have potential as a bank vole repellent, since it reduced consumption of beech nuts to half that of water soaked seeds, and reduced consumption of acorns was also indicated. No decrease in the germination of acorns treated with mink excrement was found, and there was only a minor negative effect on beech nuts (**IV**). The growth of young oak seedlings was better following sowing in spring than in summer, and mounding was the mechanical site preparation treatment most beneficial for oak seedling growth (**III**).

The results indicate that successful direct seeding of oak on clear-cuts is most likely when acorns are sown at large sites situated in areas surrounded by coniferous forest, in spring rather than summer. In addition, more successful regeneration could be achieved through preparing sites by mounding, removing slash and sowing seeds treated with mink excrement. The data collected in this study indicate it is more difficult to achieve successful direct seeding of beech, than of oak.

Keywords: Fagus sylvatica L., forest restoration, granivorous rodents, pest control, *Quercus petraea* (Matt.) Liebl., *Quercus robur* L., regeneration, repellents, seed removal, site preparation

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Gabriel och Jakob

Sanningen är en svår vän att leva med för han öppnar dina ögon för sånt du inte vill se.

Drömmar, Ratata, 1987

Contents

List of Papers

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

I Birkedal, M., Fischer, A., Karlsson, M., Löf, M. & Madsen, P. (2009) Rodent impact on establishment of direct-seeded *Fagus sylvatica*, *Quercus robur* and *Quercus petraea* on forest land. *Scandinavian Journal of Forest Research* 24, 298-307.

II Birkedal, M., Löf, M., Olsson, G.E. & Bergsten, U. (2010) Effects of granivorous rodents on direct seeding of beech and oak in relation to site preparation and sowing date. Manuscript resubmitted to *Forest Ecology and Management*.

III Löf, M. & Birkedal, M. (2009) Direct seeding of *Quercus robur* L. for reforestation: The influence of mechanical site preparation and sowing date on early growth of seedlings. *Forest Ecology and Management* 258, 704-711.

IV Birkedal, M. & Olsson, G.E. (2010) Mink excrement – a potential repellent to prevent bank vole consumption of direct seeded beech nuts and acorns. Manuscript resubmitted to *European Journal of Forest Research*.

Papers I and III are reproduced with the permission of the publishers.

1 Introduction

1.1 Background

Over the last two thousand years the composition of the landscape in southern Scandinavia has changed drastically, from being dominated by diverse broadleaved forest (Björse and Bradshaw 1998, Lindbladh and Bradshaw 1998), to the present situation where 12% of the land area of Denmark and 63% of southern Sweden (Götaland) is covered by forests. Of this only 43% of the forested area in Denmark and 21% of the standing volume in southern Sweden (of which approximately 50% consists of *Betula* spp.) are broadleaved forests (Anon. 2009a, 2009b). Furthermore, the broadleaved forests are often scattered across the landscape in small stands, and between these stands are coniferous forests, agricultural land and/or urban areas. Many rare species of cryptogams, vascular plants, invertebrates and vertebrates are dependent on habitats represented by these remnants of broadleaved forest (Berg et al. 1994), and in order to preserve them it is probably essential not only to keep, but to extend, the area covered by this type of forest in southern Scandinavia (Angelstam and Mikusinski 2001).

Changed precipitation regimes and higher air temperatures are predicted for this region in the next hundred years (Christensen et al. 2007, IPCC 2007). At present, the most common silvicultural system in the area is clear-cutting with subsequent planting of fast growing coniferous monocultures; the aim is to keep rotation periods short. However, to be ready to meet the effects of climate change, new strategies for forest management need to be considered and when environment conditions are unstable, it may be appropriate to spread risk by introducing greater variation in tree species composition and management systems. Therefore, it may be appropriate to restore broadleaved forests that include beech (*Fagus sylvatica* L.) and oak

(*Quercus robur* L., *Q. petraea* Matt. Liebl.) for example, which may be better adapted to the future climate than are many coniferous trees (Koca et al. 2006).

The current artificial reforestation techniques used for beech and oak, i.e. planting large bare-rooted seedlings surrounded by fences to prevent browsing are expensive (Madsen and Löf 2005). Thus, where natural broadleaved regeneration is not an option, less expensive methods need to be developed to appeal to land owners. Direct seeding of beech or oak on reforestation sites has the potential to fulfill this role.

1.2 Direct seeding

Direct seeding is a regeneration technique in which tree seeds are used directly on the regeneration site instead of seedlings being transplanted from nurseries. The method is quite well developed for conifers, for example Scots pine (*Pinus sylvestris* L.) (e.g. Bergsten 1988, Wennström et al. 1999, Winsa and Sahlén 2001, de Chantal et al. 2003), and also for oak on former agricultural land. On farm land herbicides can be used to reduce the amount of ground vegetation (Willoughby et al. 2004), which in turn decrease the suitability of the habitats to rodents. For environmental reasons, the use of herbicides in forestry is heavily restricted in southern Scandinavia (Willoughby et al. 2009).

There are several potential advantages of direct seeding compared to conventional planting. First, the technique may reduce the cost of regeneration by 50% or more (Wennström et al. 1999, Madsen and Löf 2005). Seeds are not as expensive as seedlings, and they are less bulky, thus reducing handling time and transportation costs. In addition, the sowing operation is likely to be easier to mechanise than planting (Wennström et al. 1999), since seeds are smaller and slightly less prone to mechanical damage than the seedlings. Furthermore, larger numbers of seed than seedlings can be used due to the lower costs; therefore regeneration without fences may be possible even for broadleaves since dense regeneration is less sensitive to losses caused by browsing animals (Madsen 2005).

Secondly, seedlings produced after direct seeding develop a natural root system, and may therefore be better prepared to withstand the conditions prevailing at the regeneration site. For example, in containerised holm oak (*Quercus ilex* L.) seedlings, tap root development has been found to be restricted to the length of the container (Tsakaldimi et al. 2009), which may lead to increased sensitivity to drought (Canadell et al. 1996). The root systems of bare rooted seedlings, on the other hand, are usually trimmed before transplantation to the forest; in some tree species, such as beech, such loss of root biomass increases mortality and decreases growth under field conditions (Andersen 2001).

Finally, it may be possible to produce higher quality timber when using direct seeding compared to planting, since sowing usually results in denser regeneration and consequently more seedlings from which to select the final crop trees. Furthermore, better self-pruning of beech and Norway spruce (*Picea abies* L. Karst.), for example, occurs in dense stands (Ekö et al. 1995, Pfister et al. 2007) and consequently better wood properties can be expected after direct seeding. On the other hand, a large number of stems per hectare might result in higher pre-commercial thinning costs.

In spite of the advantages mentioned above, direct seeding is currently associated with a number of problems. For example, sown seeds are under severe threat of animal consumption, for example by wild boar, insects, birds and rodents (Watt 1919, Ashby 1959, Tanton, 1965, Jedrzejewska et al. 1994, Nystrand 1998, Bellocq et al. 2005) which readily feed on nutritious seeds. Methods to prevent this are equally underdeveloped for both broadleaves and conifers. Wild boars feed on large seeds, and do not constitute a major problem to conifer sowings. However, in areas where wild boars are abundant, fencing sites where beech nuts and acorns, for example, have been sown is highly recommended. Insects are primarily pre-dispersal acorn consumers (Bellocq et al. 2005), but may be responsible for considerable post-dispersal losses in pine sowings (Nystrand and Granström 2000). Birds find seeds primarily by visual cues (Nystrand 1998) and therefore protection can be achieved by covering the seeds with a thin layer of soil. Granivorous rodents, on the other hand, are often abundant in forest habitats (Hansson 1978), they are post-dispersal seed consumers (Hulme and Borelli 1999, Heroldova et al. 2008) and locate food by smell (Vander Wall 1998). Consequently, granivorous rodents are a severe problem for forest regeneration based on direct seeding of either broadleaved or conifer species (Buckley and Sharik 2002, Nilson and Hjältén 2003, Madsen and Löf 2005); this subject is discussed further in subsequent sections of this thesis.

Furthermore, acorns are particularly susceptible to drought (Gosling 2002), and germination is delayed in desiccated Scots pine seeds (Zhu et al. 2006). Therefore, successful direct seeding is somewhat weather dependent. In addition, the seedlings produced after sowing are small in the beginning and consequently more sensitive to competition from ground vegetation than are larger transplanted seedlings (Löf et al. 2004). Mechanical site preparation reduces competition from ground vegetation (Knapp et al. 2008), and thus the risk of drought may be lessened (Nilsson and Örlander 1999), as well as other negative effects on seedling growth caused by excessive ground vegetation. At fertile sites it is essential to keep the growth of ground vegetation under control for a couple of years following sowing, to promote the survival and growth of seedlings derived from direst seeding (Willoughby et al. 2004). Information on appropriate methods of preparing a site is available for direct seeding of, for example, Scots pine (e.g. Pohtila and Pohjola 1985, Béland et al. 2000, Bergsten et al. 2003, de Chantal et al. 2003), but is still lacking for many broadleaved species.

Moreover, a couple of years' growth may be lost compared to transplanted seedlings that have often been grown on for a number of seasons in a nursery before transfer to the forest. However, results presented by Ammer and Mosandl (2007) indicate that the growth loss in beech seedlings produced after direct seeding compared to transplanted ones may not be of great importance. One probable reason for this may be that beech has large seeds that are able to produce rather large seedlings even during the first growing season; it can, therefore, rapidly achieve positive net carbon uptake. In addition, sown seedlings avoid transplantation shock that nursery grown seedlings may suffer from after transfer into the forest (Ammer and Mosandl 2007). On the other hand, Valkonen (2008) reported poor height growth in oak seedlings following direct seeding compared to planted individuals, although acorns are even larger than beech nuts. Ammer and Mosandl (2007) conducted their study under a shelter of Norway spruce, while Valkonen's (2008) study was performed on afforestation sites, hence differences in the amount of competing vegetation may be the reason for the different results.

1.3 Methods for studying seed predation

Predation refers to the destructive consumption of an organism (Anon. 1994), and consequently, when a seed has been subjected to complete predation it is no longer able to produce a seedling.

As mentioned above, predation of seeds is a major concern when attempting reforestation by direct seeding. To improve our understanding of how to prevent the consumption of seeds it is essential to gain information on which species of granivores are involved, and when and how seed predation occurs. There are several ways to study seed predation, and the appropriateness of each method in a particular situation depends on the kind of information that is sought. Data pertaining to dispersal distances and the location of caches can, for example, be obtained by inserting magnets into seeds (Takahashi et al. 2006) or preparing them with a radioactive substance

(Jensen 1985), while the use of exclosures with different mesh sizes can provide information on the size of the predator, which may in turn suggest which group of animals is responsible for seed removal (Shaw 1968, Bellocq et al. 2005). Fixing seeds in place so that seed coats cannot be taken away can be used to determine the proportion of seeds that has been damaged (Nilson and Hjältén 2003). This approach can also provide information on what kind of animal ate the seed, since marks left on the coats of seeds are species-specific (Nystrand and Granström 2000). Presenting seeds of different species in a seed tray is one way of studying species preferences in the field (Hulme and Hunt 1999). It may also provide information on which species remove seeds and how fast the removal occurs since small plots or trays with seeds are relatively easy to monitor with cameras (Jansen and den Ouden 2005).

To study the impact of seed predation after direct seeding, the experimental conditions need to be as similar as possible to conditions after an actual seeding operation; therefore, in the studies described in this thesis the number of established seedlings, excavation of seeding points, inventories of predation signs and, in some cases, camera-surveillance were used to examine predation pressure.

1.4 Granivorous rodents

According to optimal foraging theory, as described by Wilson in 1976, animals strive to optimise their energy budgets when searching for food, which means that the amount of energy in a food item is weighed against the amount of time it takes to locate, retrieve, eat and digest it. In deciding where to forage, consideration must also be given to the risk of being taken by a predator while foraging. Defensive mechanisms employed by the intended prey (in this case the seed), for example the amount of indigestible secondary compounds, also affect the decision about whether to consume a located item or not.

The diet of a granivore consists entirely or partly of seeds (Anon. 1992). The granivorous rodent species examined in the studies comprising this thesis were the bank vole (*Myodes glareolus* Schreber), the yellow-necked mouse (*Apodemus flavicollis* Melchior), and the wood mouse (*Apodemus sylvaticus* L.). Squirrels (*Sciurus* sp., *Tamiasciurus* sp.) also feed on seeds (Bellocq et al. 2005), but are not considered a major problem in the geographical area considered herein (see paper **I**).

Bank voles are habitat generalists, but within the study region, which is in the nemoral zone, they prefer forests with deciduous elements (Pucek

1983). Yellow-necked mice are more strictly associated with broadleaved forest, and wood mice occur in farm fields as well as forested areas (Angelstam et al. 1987). Apart from seeds, bank voles also eat green plant parts, lichens, fungi, and insects (Watts 1968, Gebczynska 1983). The mice are more dependent on concentrated food and their diet, to a large extent, consists of seeds and insects, but also some green parts of plants (Watts 1968, Hansson 1971). Small rodents are popular prey for many mammalian carnivores and raptors (Goszczynski 1983), hence they generally prefer habitats with plenty of places to hide, for example ground vegetation, stones and fallen trees (Hansson 1978, 1994, Olsson et al. 2005, Takahashi et al. 2006).

Rodent populations in the study area (i.e. southern Scandinavia) typically fluctuate during the year, with few animals in the spring and peak densities in late summer and early autumn (Pucek et al. 1993, Hansson et al. 2000). Variations in rodent populations between years also occur, often in relation to years with abundant seed production by large-seeded tree species such as beech or oak (Hansson et al. 2000). In these years, breeding may also take place during the winter months (Jensen 1982), and a major decline in numbers may not occur until the next winter (Pucek et al. 1993).

Naturally occurring food sources, for example green plant parts and seeds other than those spread on regeneration areas by humans, are more abundant in the summer than in the spring, a fact that could ease the effect of the increased number of granivorous rodents likely to be present on regeneration areas during summer. However, the quality of green plant parts as a food source may decrease over the season since secondary metabolites, which often make plants less palatable, tend to increase at least until after flowering (Covelo and Gallardo 2001, Cirak et al. 2007, Elger et al. 2009), and both protein and energy content decrease from spring until summer for several plant species (Seccombe-Hett and Turkington 2008).

With the aforementioned behavioural traits in mind and the optimal foraging theory as a framework, it may be important to consider the surrounding forest type when choosing areas for regeneration by direct seeding. It may also be well worthwhile modifying the regeneration areas in order to make them less appealing to granivorous rodents, for example by removing ground vegetation, stones and fallen trees. In addition, there is a possibility that seeds sown in early to mid summer suffer less from rodent predation, since populations have not yet reached maximum densities, and food other than sown seeds is readily available. The fact that the olfactory senses of rodents are important when they are searching for food (Vander Wall 1998) may also have a bearing on ways to reduce their impact on forest regeneration by direct seeding. One possibility could be to mask the smell of the seeds with strong odours and thereby make the rodents less likely to find them. Another option could be to introduce smells that frighten the rodents, for example predator odours.

1.5 Objectives

The overall aim of these studies was to investigate possible ways to improve the efficiency of direct seeding of beech and oak on forest land as a practical reforestation operation, to be used for restoration or commercial forestry purposes. The specific questions addressed were:

- Does the choice of site affect establishment results after direct seeding of beech nuts and acorns, and is any such effect connected to the number of granivorous rodents captured? (**I**,**II**)

- Does the sowing date of beech nuts and acorns affect establishment? (**I**,**II**)

- Do different methods of site preparation affect establishment and subsequent survival after direct seeding of beech nuts and acorns, and is any such effect connected to rodent behaviour? (**II**)

- Does the sowing date, or different methods of mechanical site preparation, affect the growth of young oak seedlings? (**III**)

- Do methods manipulating the taste and/or smell of seeds, a method for inducing fear in rodents, or a method creating a mechanical barrier around the seed that makes breaking of the seed coat more difficult, have any potential to discourage granivorous rodents from consuming beech nuts and acorns after direct seeding? (**IV**)

2 Materials and Methods

2.1 Study area and sites

All sixteen field study sites were located in southern Scandinavia; eleven (1-11) in Denmark and five (12-16) in southern Sweden (Fig. 1). In this region, mean annual air temperatures range from 6ºC to 8ºC, and mean annual precipitation from 700 mm to 900 mm (Anon. 2010a, 2010b).

Land use in Denmark and the province of Scania, in southern Sweden, is dominated by agriculture, with small and scattered forests between the fields; in contrast, the land around the Asa experimental forest (sites 15 and 16), in south-eastern Sweden, is dominated by coniferous forests (Anon. 2009a and 2009b).

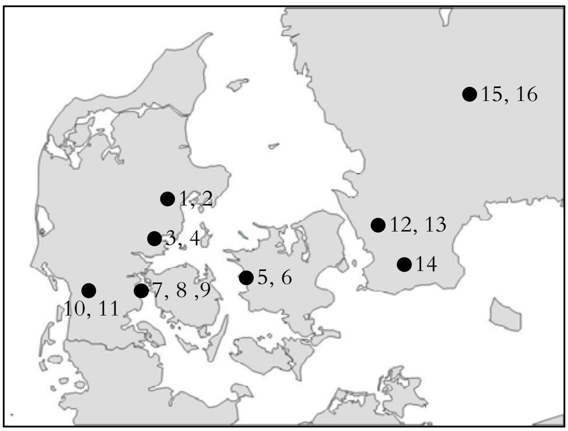

Figure 1. Map of southern Scandinavia, showing the location of the sixteen field study sites.

Four of the sites in Denmark (sites 3-6) were located in areas surrounded by broadleaved forests dominated by beech and oak (**I**). At these sites, acorns were sown in small gaps or under a shelter of mature beech trees. The remaining sites in Denmark (sites 1, 2, 7-11) were surrounded by mixed forests (**I**). Two of them (sites 1, 2) were situated in outgrown Christmas tree (*Abies nordmanniana* Spach.) plantations, while the remaining five (sites 7-11) were clear-cuts where the previous stands had been various coniferous species such as Norway spruce or black pine (*Pinus nigra* J. F. Arnold). Sites 12 and 13 were situated in the Söderåsen national park in the province of Scania (**I**). The Söderåsen sites are part of a rather large broadleaved forest dominated by beech containing scattered patches of Norway spruce. The study sites were located in clear-cuts where two such coniferous patches had been felled. Site 14 was situated in a large clear-cut following Norway spruce forest in Krageholm, in the southern part of Scania. The stands around this experimental site consisted of broadleaved trees such as beech, sycamore (*Acer pseudoplatanus* L.) and common alder (*Alnus glutinosa* L. Gaertner). The two remaining field study sites (15, 16) were located in the Asa experimental forest (**II, III**). These sites were situated on clear-cuts following Norway spruce and surrounded by Norway spruce forest.

2.2 Experimental design and measurements

2.2.1 Field studies (I, II, III)

The sites used for the field studies presented in this thesis represented a variety of forest types, and were selected so that a variation in rodent population densities could be expected. At sites 12-16 randomised block designs were used to cover any small scale differences in soil properties or rodent abundance across the sites. See papers **I, II** and **III** for details of the number of blocks at each site. Most of the field study sites were manually sown following different methods of mechanical site preparation, reflecting the differences in availability of suitable machinery in different parts of Denmark, and the experimental treatments and increased need for precision of the location of seeding spots at the Swedish sites, where the fate of single seeds was to be studied. Direct seeding was completely mechanised only at site 7 in Denmark. All seeds were covered with soil after sowing (**I, II, III**). With the exeption of sites 12 and 13 in the Söderåsen national park, where seeds of local origin were required and such acorns were not available, acorns were sown at all sites. In addition, beech nuts were sown at all the sites in Sweden (12-16). At sites 12-14 all seeds were sown together with a piece of white paper to facilitate their relocation (**I**).

At all eleven sites in Denmark a treatment for snap-trapping of rodents was installed over approximately one third of the sown experimental areas, and at sites 1-9 a treatment with perches for raptors and a control was installed in addition to the snap-trapping (**I**). The intention was to test non-chemical rodent reduction measures that could be used on a large scale. In addition, a possible relationship between oak establishment and the number of captured rodents could provide input into a decision support tool to assess the suitability of a site for direct seeding. For such a tool to be practically applicable it is necessary that it is not too labour intensive, which is why snap-traps were used rather than live-traps. Most of these sites were rather large so that they resembled commercial forestry operations. The study in Denmark led to the conclusion that rodent impact on regeneration by direct seeding needed to be studied in more detail; this is why the experimental sites set up in Scania in 2005 were small enough to allow a study of the fate of each sown seed. This study in turn, provided the insight that if experimental sites are too small the impact of predation can be very high. Based on these experiences the experimental sites set up in the Asa experimental forest in 2006 were large, and samples of seeds were chosen for a detailed study of seed fate.

At sites 15 and 16 in the Asa experimental forest, acorns were sown in May and July 2006 (**II, III**), as well as in May 2007 (**II**). Beech nuts were sown in May 2007 (**II**). At sites 12-14 seeds were sown in May and June in 2005. Furthermore, beech nuts were sown at two soil depths (1 cm and 3 cm) on each date (**I**). Sowing on different dates was a way to investigate whether fluctuations in rodent populations or differences in the availability of rodent food sources other than sown seeds could affect establishment success after direct seeding of beech and oak. Previous studies (Johnson 1981, Nilsson et al. 1996) have shown that sowing acorns at soil depths between 5 and 10 cm can reduce predation on seeds, but no corresponding information was available for direct seeding of beech. At sites 12-14 two different sowing depths for beech, a little less deep than recommended for oak, were examined. Beech cannot be seeded as deep as oak since the young seedlings need to be able to push the cotyledons through the soil in order for them to develop aboveground (Watt 1923). In addition to the different sowing dates at sites 15 and 16, direct seeding following four different mechanical site preparation treatments - disc trenching (DT), patch scarification (PS), topsoil removal (TSR) and mounding (M) - was tested against an untreated control (C) (**II, III**). The mechanical site preparation methods exposed 0%, 36%, 11%, 100%, and 25% of the mineral soil in the C, DT, PS, TSR and M treatments, respectively; these differences were expected to influence rodent behaviour. The fact that the seeding spots in the mounding treatment were higher than the surroundings was expected to have the result that rodents feel more exposed and thus avoid the mounds.

Trapping of rodents was performed at all sixteen field study sites, with two snap-traps at each trapping-point at the sites in Denmark (**I**), and one live-trap at each trapping-point at all sites in Sweden (**I, II**). Traps were placed in grids with 10 m (**II**) or 15 m (**I**) between each trapping point. Snap-traps were emptied approximately once a week, and live-traps twice in each 24h period. Live-traps were used instead of snap-traps in Sweden in order to affect the rodent populations as little as possible, to allow the study of their predation of sown seeds in more detail.

To measure the losses of beech nuts and acorns after direct seeding and to establish the cause of any losses, several methods were applied. At sites 12-14 in Scania (**I**) signs of predation (visible pieces of paper, holes after animal digging in the ground, seed coat remains) were recorded one and three weeks after sowing. In addition, all or a sample of seeding points were excavated at sites 12-16 in southern Sweden at the end of the first growing season (**I, II**). To monitor when seed predation occurred a surveillance-camera was installed at two of the sites in Scania (**I**). The camera was operated at each of the two sites on different occasions during the first growing season. Establishment of seedlings was recorded at the end of the first growing season at all experimental sites, and establishment and survival was recorded at some sites after the second (sites 1-4, 15 and 16) and third growing seasons (1, 2, 7, 9, 15 and 16) as well (**I, II, III**). The sites in Denmark (1-11) were inventoried again after the first growing season if there were sufficient resources, and sites 12-14 were not inventoried again after the first growing season due to the destructive sampling method used.

Oak seedling growth (height, biomass and rooting depth) was measured at the two sites in the Asa experimental forest (**III**).

2.2.2 Laboratory study (IV)

In order to investigate the potential of a number of candidate repellents that might discourage bank vole consumption of beech nuts and acorns, a no-choice feeding trial with twenty laboratory-bred voles per seed species was conducted over a ten day period (**IV**). A laboratory study was chosen in order to remove factors other than the intended repellent substances that may affect rodent food choices, for example availability of cover or other food sources. No-choice tests are conservative in their measure of repellency (Clark 1997), since the test animal either must eat the substance on trial or go hungry. Therefore this kind of trial was considered appropriate as an initial test of the potency of substances for deterring rodents. Laboratory-bred voles have almost identical previous food experiences, which is beneficial since former diet influences present food preferences (Hansson 1993). Furthermore, voles bred in the laboratory are accustomed to the experimental environment and are consequently less stressed during the tests.

On ech day of the no-choice feeding trial, each vole was presented with ten beech nuts, or five acorns, treated with water or one of four repellent substances: chilli/coconut fat, citronella/rape oils, mink excrement or a sand coating. The water treatment was included in the experiment as a control. Capsaicin in chilli peppers creates a burning sensation in the mouths of mammals feeding on them (Szolcsanyi 1990), and both Nolte and Barnett (2000) and Jensen et al. (2003) found capsaicin to have a repellent effect on certain species of rodents (*Mus musculus* L., *Rattus norvegicus* Berk.). Citronella has a strong smell, which may conceal the scent of the seeds, and thereby make them more difficult for rodents to find. Predator odours have previously been shown to affect the behaviour of prey animals (Jedrzejewski et al. 1993). In the study described in paper **IV** the odour tested came from mink excrement. Coating living tissue with sand is a strategy that works well to protect conifer seedlings from pine weevil (*Hylobius abietis* L.) damage (Nordlander et al. 2009). In study **IV** each vole was subjected to each of these treatments twice; each substance was presented during the first session, and then once again during a second session to document any habituation effect that might have occurred after the first encounter. Furthermore, the five potential repellent substances were each applied to batches of 200 beech nuts and 200 acorns, so that possible effects on germination could be tested.

2.3 Calculations and statistics (I-IV)

Since several different seed batches were used in the field studies in this thesis, establishment results were presented as the percentage of seedlings established from viable seeds (determined before direct seeding) (**I, II**). Thus, the results were comparable even if germination percentages differed between the seed lots. Similarly, the rodent captures were standardised to rodent individuals caught per one hundred trap-inventories or trap-nights, to make the results from different sites possible to compare even though the trapping methods were different (**I, II**).

The distribution of rodents in relation to a number of micro-site features was studied by comparing trapping-patterns to the presence of certain features, for example slash and stones, that occur frequently on a clear-cut (**II**). To determine the effect of the different features on the number of rodent captures in a trap, a model based on logistic regression with binomial distribution and logit link, and with block as a factor was constructed.

Most of the statistical analyses referred to in papers **I-IV**, as well as the analysis of data relating to different sowing dates presented herein, were performed using the general linear model procedure for the analysis of variance in the software SAS or Minitab (SAS Institute Inc., Cary, NC, USA; Minitab Inc., Pennsylvania, USA). Tukey's tests were used to separate the levels ($P < 0.05$). In order to meet assumptions of normality, equal variances and independent residuals in the data, appropriate transformations were applied. If assumptions could not be achieved by transformation, data were ranked before analysis (Conover and Iman 1981).

3 Results and Discussion

3.1 Site

The characteristics of the site appeared to have a great influence on establishment success following direct seeding of beech and oak on forest land (Fig. 2). For sites 1-9 only establishment data from the snap-trapping treatment are presented in the figure, but no significant differences in establishment success were found between the three treatments applied at these sites. The mechanical site preparation at sites 15 and 16 was conducted one year before the 2007 sowing; thus, the establishment results from this year may not be comparable to the other sites. Therefore, only data from the direct seeding in 2006 are presented from sites 15 and 16. In the experiments the proportion of establishment from viable seeds varied from 0 to 62% (**I, II**). However, the studies did not definitively identify the decisive site features, since they were not designed for a thorough study of such factors. For example, surrounding forest type co-varied with the size of the regeneration area, and these are two factors which previous studies have suggested affect establishment success after direct seeding (Johnson 1981, Madsen and Löf 2005). There was a strong indication that the forest type surrounding the reforestation area influenced the results of direct seeding (Fig. 2). However, in the studies presented in this thesis none of the sown areas surrounded by broadleaved forests were larger than 0.32 hectares, while several of the ones with mixed forest around them were around 1 hectare or larger, a fact that complicated the interpretation of the results. Although the influences of these factors were difficult to separate, they were probably related to rodent abundance and distribution. Two plausible explanations for this are that broadleaved forests generally support high populations of granivorous species (Hansson 1967), and that rodents are important prey to several mammal and avian predators (Goszczinsky 1983) and therefore prefer areas in or near suitable cover, such as canopy cover, fallen trees, shrubs or lush ground vegetation (Hansson 1978, Olsson et al. 2005, Takahashi et al. 2006, Moro and Gadal 2007).

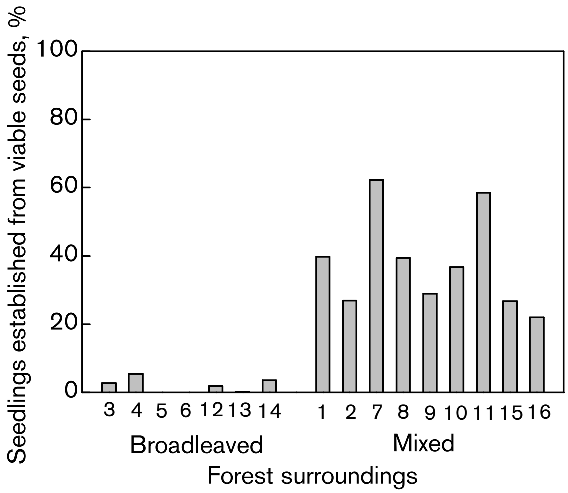

Figure 2. Proportion of seedlings established from viable seeds after the first growing season at sixteen experimental sites, surrounded by broadleaved or mixed forests, in southern Scandinavia. Beech nuts were sown at sites 12-14, while acorns were sown at all sites except 12 and 13. Mean values over all treatments and tree species at each site are shown, except at sites 1-9 where only the rodent snap-trapping treatment is included, and sites 15 and 16 for which only data from the sowing in 2006 were used.

3.2 Sowing date

The sowing date influenced the establishment success after direct seeding of oak (**I, II**; Fig. 3), and both the sowing month and year had an effect on the results. For both years (2005 and 2006), oak seedling establishment after one growing season was better following spring than summer sowing, but only significantly so ($P < 0.01$) in 2006. For beech sown in May and June 2005, there were no differences in establishment between the dates (see paper **I**). At the end of the 2006 growing season, 44% of viable acorns sown in spring the same year had become established as seedlings. This was significantly more ($P < 0.05$) than the 19% of viable acorns sown in spring 2007, which had formed seedlings by the end of the same year.

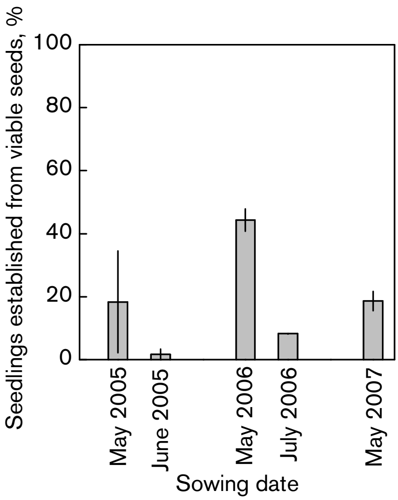

Figure 3. Oak seedlings established from viable acorns, at the end of the first growing season, after sowing on different dates (Mean ± SE). Establishment results from May and June 2005 are from site 14, and results from May 2006, July 2006 and May 2007 are from sites 15 and 16. The bars represent means over all treatments at each site.

Rodent density was one factor that probably contributed to the variation in oak seedling establishment between sowing dates and years. In the experiments described in papers **I** and **II**, there were more rodent captures during the summer than in the spring at all sites and during all years. In addition, more rodents were caught at sites 15 and 16 during 2007 than 2006. It can also be seen from data presented in paper **I** that the disappearance rate of seeds was higher in the summer than in the spring, and from data presented in paper **II** that there was a general trend (all treatments except TSR) for a greater proportion of seeds being lost from the summer than the spring sowing (Table 1).

Table 1. *Proportion of seeds not found at the end of the first growing season (Mean ± SE) for oak sown in May and July 2006, and calculated dry biomass per seedling in 2008 for seedlings sown in May and July 2006. Treatments followed by different letters are statistically different (P < 0.05), within sowing date. For descriptions of the different site preparation treatments see Materials and Methods section, and papers **II** and **III**.*

	Oak May 2006		Oak July 2006	
Site prep.	Lost seeds, %	Calculated dry biomass, g seedling^{-1}	Lost seeds, %	Calculated dry biomass, g seedling^{-1}
C	18 ± 5 a	4.8 ± 0.8 b	43 ± 20 a	2.8 ± 0.2 ab
DT	20 ± 11 a	5.7 ± 0.7 ab	50 ± 24 a	2.2 ± 0.2 b
PS	27 ± 12 a	6.4 ± 1.3 ab	48 ± 8 a	3.0 ± 0.4 ab
TSR	25 ± 10 a	5.6 ± 0.2 ab	13 ± 5 a	2.9 ± 0.3 ab
M	13 ± 3 a	9.2 ± 0.9 a	43 ± 5 a	3.6 ± 0.3 a

Therefore, it appears that the increased availability in summer of food sources other than sown seeds, does not compensate for the increased number of rodents present on the regeneration areas, and consequently this may cause the observed higher proportion of lost seeds from the summer sowing. Another reason for the better establishment after spring sowing may have been differences in soil water availability, since acorns are sensitive to desiccation (Gosling 2002), and soil water deficiency can have a great negative impact on germination success. Thus, an additional plausible explanation for the better establishment after spring sowing compared to summer sowing, as found in the studies described herein, is that soil water conditions were more favourable early in the season.

Results described in paper **III** indicate that the time of sowing also affects oak seedling growth. After three growing seasons, seedlings originating from the sowing in May 2006 achieved approximately twice the mean dry biomass compared to seedlings sown in July the same year (Table 1). Many of the seedlings sown in July did not emerge above ground until the second growing season after sowing, which means that they lost almost a whole year's growth compared to the seedlings sown in May. Drier soil conditions during the summer sowing may also have contributed to the decreased growth recorded for these seedlings compared to the ones sown in spring. Similar findings have previously been reported for direct seeding of Scots pine and Norway spruce (de Chantal et al. 2004)

3.3 Rodent population density

Fedriani (2005) found it difficult to establish a clear relationship between wood mouse abundance and consumption of fruits from *Helleborus foetidus* L.; he attributed this to the influence of factors other than the presence of a

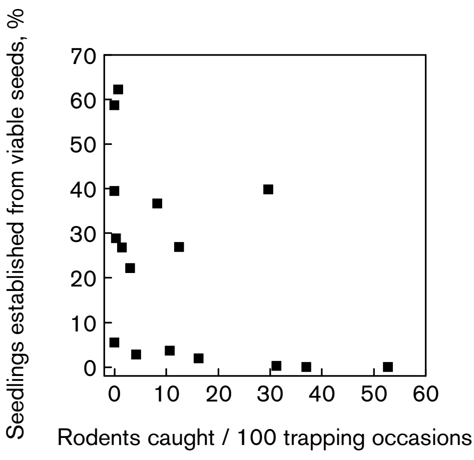

Figure 4. The correlation between number of granivorous rodents caught per 100 trapping occasions and seedling establishment from viable seeds at the sixteen sites in southern Scandinavia. All rodent trappings performed at each site are included, and seedling establishment after the first growing season for both tree species and in all treatments at all sites, except site 1-9 where only establishment in the rodent snap-trapping treatment is included. For sites 15 and 16 only results from 2006 are included.

suitable prey on a predator's foraging decisions (compare this with the earlier description of optimal foraging theory). Data from papers **I** and **II** suggest that there is a negative correlation between the number of granivorous rodents captured and the number of established beech and oak seedlings, but the linear regression was rather weak (Fig. 4; adjusted $r^2 = 0.19$; $P = 0.05$). Interpreting the relationship between rodents and seedling establishment was complicated by the fact that the trapping methods used at the different sites were different. When separating the two methods of rodent trapping, the linear regression for the sites where snap-trapping was used (1-11) resulted in an adjusted $r^2 = 0.17$ and $P = 0.12$. The regression for the sites with live-traps (12-16) resulted in an adjusted $r^2 = 0.59$ and $P = 0.08$. For sites 1-9 establishment data from the snap-trapping treatment only were included since no rodent density estimates were available for the other treatments. For sites 15 and 16 only data from the first year of the experiment were included. Data obtained during the second year may not be completely independent of that obtained during the first year, since the same sites were used. Rodent density estimates were not available separately for each treatment for sites 12-14, and the rodent trapping at sites 15 and 16 did not take place in immediate connection to the different sowing occasions; this is why mean values of rodent numbers and seedling establishment per season and site were used for sites 12-16. In addition to actual rodent abundance and seedling establishment, the outcome of the correlation analysis was affected by the fact that at sites 3-6 there were beech nuts from natural seed fall available to the rodents during the period of trapping. This may have made the rodents less inclined to enter the traps. Furthermore, the manner of seed removal at sites 12-14 (all seeds in one seeding row removed, and seed coats found in a heap at the end of the row) indicated that just a few, perhaps only one, specialised granivorous rodent have the potential to completely ruin small sown regeneration sites. Although the linear relationships were weak, the lower establishment rates in habitats generally preferred by rodents, i.e. small regeneration areas surrounded by broadleaved forest, compared to larger areas without cover and surrounded by coniferous forest, suggest, indirectly, that rodents have an effect. Higher numbers of lost seeds after sowing in summer, when more rodents were captured, than in the spring, also indicates that rodent densities were important for the success or failure of regeneration of beech and oak following direct seeding.

A relationship between the number of captured mice and voles and disappearance rates of acorns is supported by the findings of Kikuzawa (1988), who studied the interactions between several species of Japanese granivorous rodents and acorns of *Quercus mongolica* var. *grosseserrata* (Fisch ex. Turcz). Inconsistencies when trying to determine whether relationships between rodent captures and disappearance rates of their prey actually exist may be partly explained by the fact that proper determination of population densities of rodents is difficult to achieve (Slade and Blair 2000); this has to be taken into account when analysing the relationship between rodent numbers and regeneration success after direct seeding.

3.4 Site preparation

The effect of different mechanical site preparation techniques on rodent predation of seeds, as described in paper **II,** was difficult to interpret. For acorns sown in 2006 there were no statistically significant differences in the proportion of lost seeds between the different mechanical site preparation treatments for the same sowing date (Table 1).

From the acorns sown in May losses tended to be slightly lower in the M and C treatments, compared to the other treatments, while for acorns sown in June losses seemed to be lower from the TSR treatment. Hansson (1978) found more rodents with greater vegetation cover. In study **II** the amount of field vegetation at the end of the 2006 growing season was lowest in the PS and M treatments and highest in the control. However, the differences between treatments were rather small, which is normal in recent clear-cuts in the study region. One possible explanation for the absence of treatment effects here could be the relatively low number of granivorous rodents captured, i.e. 1.9 rodents/100 trap-nights (0.6 bank voles/100 trap-nights), on the experimental clear-cuts during the 2006 growing season, 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 produced capture rates varying from 0.1 to 7.1 bank voles/100 trap-nights (Hörnfeldt 2010 and pers. comm.). Furthermore, the vegetation surveys were conducted in the site preparation rows or spots, while vegetation cover over the whole treatment plot affects rodents. It is also possible that the mechanical site preparation treatment plots were too small to have the desired discouraging effect on rodents (see paper **II**). Although the influence of mechanical site preparation was difficult to interpret, there were indications that other methods of preparing the site may be important for rodent management. For example, micro-site features present within the regeneration area seemed to affect the distribution of rodents, since captures increased in traps located close to slash piles left after the felling operation (**II**). More captures were also recorded near remains of stone walls, as discussed in paper **I**. Removal of such features, where feasible, before direct seeding of beech nuts and acorns may improve the chances of successful regeneration.

Mechanical site preparation has an effect not only on environmental factors important for granivorous rodents, but also on factors affecting seedling growth, e.g. soil temperature (Landhäusser 2009) and soil water potential (Knapp et al. 2008). Löf et al. (2006) found that preparing a site by mounding improved the growth of transplanted oak seedlings. Mattsson and Bergsten (2003) found an increase in the growth of young lodgepole pine trees (*Pinus contorta* Dougl. var. *latifolia* Engelm.) grown in ploughed plots. In the study described in paper **III** an increased seedling biomass was recorded in the M treatment compared to the control when sown in May, and compared to the DT treatment when sown in July (Table 1). This indicates that mounding may be a favourable site preparation method for improving the growth of oak seedlings produced by direct seeding. Bergsten et al. (2003) suggests that direct seeding of conifers on mineral soil upturned over humus is not to be recommended since such a treatment damages the capillarity of the soil. The soil water potential was lower in the M treatment compared to all other treatments during a dry period in June, while in July and August, when there was considerable precipitation, the lowest values of soil water potential were found in the control treatment (**III**). This indicates that there is a risk of drought in the mounds. However, young oak seedlings may be less sensitive to reduced soil capillarity than many other tree species since they develop a deep taproot during their first growing season (Löf and Welander 2004).

3.5 Repellents

In paper **IV**, three different approaches to deterring bank voles from feeding on beech nuts and acorns are described. These were examined in a no-choice laboratory trial. The approaches were: taste and smell repellents, inducing fear (predator odour), and mechanical protection. The first approach included seeds treated with chilli/coconut fat and citronella/rape oils, while the second approach involved soaking seeds in water and mink excrement, the final approach was to encase the seeds in a coating of sand. During the second no-choice feeding trial session, the bank vole consumption of beech nuts treated with mink excrement was reduced by half compared to that of the water treated seeds (Table 2). A reduction of consumption of a similar magnitude for beech nuts was achieved with the chilli/coconut fat treatment. Although less pronounced, a tendency towards decreased consumption was also recorded for acorns treated with chilli/coconut fat and mink excrement. Germination of seeds of both tree species was negatively affected by the chilli/coconut fat and citronella/rape oils treatments, and beech nut germination was also slightly reduced by the mink excrement treatment (Table 2).

Table 2. *Percentage of bank vole consumption of repellent treated seeds (Mean ± SD) in the second session of the no-choice feeding trial, and percentage germination of treated seeds after 14 weeks. Sample size in the germination test was 200 seeds per tree species and treatment. Treatments followed by different letters are significantly different (P < 0.05), within tree species.*

Tree species	Treatment	Seed consumption (wt %)	Germinated (%)
Beech	Water	62 ± 12 ab	79 ± 7 a
	Chilli/coconut fat	34 ± 19 cd	18 ± 9 c
	Citronella/rape oils	49 ± 18 bc	6 ± 2 c
	Mink excrement	30 ± 25 d	61 ± 11 b
	Sand coating	69 ± 15 a	71 ± 8 ab
Oak	Water	7 ± 4 a	74 ± 3 a
	Chilli/coconut fat	4 ± 2 a	52 ± 11 b
	Citronella/rape oils	6 ± 5 a	52 ± 12 b
	Mink excrement	5 ± 3 a	71 ± 7 ab
	Sand coating	18 ± 9 b	63 ± 8 ab

Previous research on the behavioural response of rodents to the presence of predator odour has produced highly variable results (Apfelbach et al. 2005), although the majority of studies have demonstrated some kind of response in the prey animal when exposed to the odour of different predators. Furthermore, Epple et al. (1993) found no sign of habituation by mountain beaver (*Aplodontia rufa* Rafinesque) to coyote (*Canis latrans* Say) urine when exposed to it for five days, which further indicates the potential of predator odours as repellents. Paper **IV** describes results indicating a reduction in consumption of beech nuts when soaked in predator faeces, although an increase in consumption, compared to the first encounter, was detected the second time the voles encountered this treatment. Compared to the other substances tested in study **IV,** mink excrement seemed to have the best potential as a repellent to be applied on beech nuts and acorns since the chilli/coconut fat treatment, which also reduced vole consumption of beech nuts, adversely affected seed germination. Mink excrement only decreased the germination of beech nuts slightly and had no effect on the germination of acorns.

3.6 Management implications and suggestions for the future

There are limits, set by the study designs, to how general the interpretation of the results presented in this thesis can be. For example, the field study sites were spread over a rather large area and included several different site types; therefore, the results relating to sowing dates and the combination of the surrounding forest type and the size of the regeneration area should be useful at least for forest managers operating in southern Scandinavia. Recommendations concerning site preparation treatments are best interpreted with more caution since these factors were studied at a limited number of sites, and little can therefore be said, for example, about the effect of different mechanical site preparation treatments in combination with different soil types or different levels of soil moisture. Moreover, the results regarding repellents should be interpreted with caution since they are just a first step towards the development of a repellent to be used in reforestations based on direct seeding.

With these limitations in mind, there are several forest management implications that can be drawn from the present research. First, rodents are a major concern if regeneration of beech and oak by direct seeding is intended. It is likely that the chances of successful regeneration decrease when there are more granivorous rodents. However, a clear relationship between rodent numbers and predation on seeds can be difficult to establish. Furthermore, since determination of the true local rodent densities through trapping is difficult and labour intensive it cannot be recommended as a method for obtaining input for a decision support tool to assess site suitability for direct seeding. High labour requirements and/or lack of improvement of seedling establishment also eliminate snap-trapping of rodents and installation of raptor perches as means to keep rodent populations down. Secondly, any measures undertaken to reduce rodent damage need to be applied directly at the time of sowing since the disappearance of seeds often seems to occur shortly after sowing. Thirdly, when selecting which regeneration method to use it is important to consider the surrounding forest type and the size of the regeneration area. Small sites surrounded mostly by broadleaved forest are probably better regenerated with transplanted seedlings than by direct seeding. Based on results from the present studyies, it is difficult to provide recommendations concerning the relative impact of these two factors separately. Fourthly, removal of micro-habitats suitable for rodents, such as piles of slash, is likely to be beneficial for seedling establishment after direct seeding. The aforementioned precautions are recommended since granivorous rodents thrive in habitats that have good cover where they can easily hide from predators. Collection of slash would support the current need for wood fibre for bio-energy, but may contribute to creating soil nutrient deficiency if sustained. Fifthly, in southern Scandinavia sowing in spring is preferable to summer sowing, both because rodent population densities in this region usually increase from early spring until late summer/autumn and because of better conditions for seed germination and seedling growth. Furthermore, mounding seems to be an appropriate mechanical site preparation method in combination with direct seeding of oak under the site conditions tested in this research, since it improved the growth of young seedlings, as well as slightly improving establishment. Successful regeneration of beech on clear-cuts by direct seeding seems to be more difficult to achieve. More information on rodent behaviour in response to different methods of mechanical site preparation is needed to clarify the effect of the various methods. In addition, both mounding and top soil removal are methods of mechanical site preparation that cause rather severe disturbance to the soil and may for reasons other than seedling establishment and growth, i.e. aesthetic and nutrient management, be undesirable. Finally, mink excrement is a potential repellent to prevent granivorous rodents from consuming and handling beech nuts after direct seeding. The effect when applied to acorns requires further study. However, its considerable effect on the consumption of beech nuts, together with the reduction in handling of acorns, indicates its potential for both tree species. Further studies are also needed to determine the effect of mink excrement on rodents and seeds under field conditions, as well as optimisation of application to the seeds, before recommendations can be made to forest managers. One possible way to reduce rodent predation of seeds after direct seeding to acceptable levels and to improve seedling establishment and growth could be through using a combination of careful site selection, seeds treated with mink excrement and preparing the site by mounding.

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