

Regeneration of pine on the aeolian sand dunes in Starmoen nature reserve, south-east Norway



Jon Morten Risberg



Master thesis in Environment and Landscape Geography

Department of Geography

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Abstract

This study aims to elucidate ecological processes and human interaction concerning regeneration of pines (*Pinus sylvestris* and *Pinus mugo* ssp *uncinata*) 36 years after a fire in Starmoen nature reserve (1976). The reserve has an underlying substrate of aeolian sand dunes, which create a unique landscape with a varying topographic relief. This results in a difference in exposure to solar radiation among the different topographic units, which again affects growth conditions of the different types of vegetation through for example moisture.

Sampling of data was done under a stratified approach with 8 transects of 8 plots each. Within these plots, measurements were made of relative radiation index, number of recruits, DBH structure, degree of canopy cover and cover of ground vegetation. Soil samples were taken to estimate moisture and loss-on-ignition. Several analyses were done with the compiled data, including correlation, t-tests, regression, multiple regression and analysis of spatial autocorrelation.

The size of adult trees varied greatly, depending on which topographic unit they were located on, and its specific growth conditions. Regeneration was mostly successful for the native *Pinus sylvestris*, whereas the introduced pine, *Pinus mugo* ssp. *uncinata* had little to no on-going reproduction. The inferential statistics indicated that difference in exposure to solar radiation (expressed as radiation index) across the sand dunes had an effect on the %-moisture in the soil, which also affects distribution of lichens and ericaceous dwarf shrubs.

Regeneration of Scots pine was interpreted to be strongly inhibited by lichens as well as ericaceous dwarf shrubs (mainly heather) when one life-form dominated the ground vegetation. However, a mosaic of both life forms gave the optimal conditions for *Pinus sylvestris* seedlings. The study questioned the decision to introduce an alien pine species for reforestation, and shows that future sustainability would be better with the native Scots pine.

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Introduction

Pine, specifically Scots pine (*Pinus sylvestris*, hereafter referred to as *P. sylvestris*) is, together with European spruce (*Picea abies*) the most dominant evergreen tree species in Norway. It is one of the oldest species in Norway (9000 B.P. (Øyen 2006)) and can be found in many habitats due to its wide ecological amplitude (Ellenberg et al. 1988). It dominates in large parts of northern Europe (Richardson 1998) (Fig. 1). *Pinus sylvestris* is generally drought tolerant, and can therefore be found on dry substrates such as sand or moraines, unlike other conifer in Norway, which need more moisture to thrive. One such type of forest is lichen-pine forest (Fremstad 1997, Moen 2010). This is the driest forest type in Norway and is normally found in the mountainous regions of eastern Norway and on well-drained moraine substrates. It is dominated by *P. sylvestris* a ground vegetation of various lichens (e.g. *Cladonia*) and dwarf shrubs (Fremstad 1997, Moen 2010, Gjærevoll 1984). Another habitat where this forest type thrives is on aeolian sand-dunes, where wind has deposited fine sand. These are often found on the coast of Norway and sporadically in places in eastern Norway (Hafsten 1971). One of these places is Starmoen nature reserve near Elverum, Hedmark in south-east Norway.

This study aims to investigate the regeneration of a forest in Starmoen nature reserve which has recently undergone secondary succession due to a severe forest fire in 1976. Scots Pine and Mountain Pine (*Pinus mugo* ssp. *uncinata*, hereafter referred to as *P. uncinata*) are canopy dominants in a relative young forest in this nature reserve, with its underlying substrate of aeolian sand-dunes. The sand dunes create a landscape with ridges, slopes and flat slacks in-between (Klemsdal 2010). Such a landscape, with its different topographical units, will have a wide variation in incoming radiation and distance to the underlying water-table that affect moisture availability, temperature and ground-layer vegetation (Holland and Steyne 1975, Gallardo-Cruz et al. 2009). Bakkestuen et al. (2008) identifies topographic relief on a crude scale as one of the main gradients for environmental variation in Norway, but in this study area there was a unique possibility to study the effects of variation in incoming radiation on a relatively small spatial scale, which may resemble the zonation found in alpine zones with lichen-dominated ridges and dwarf shrub-dominated slopes towards the snow-beds (Gjærevoll 1984).

The forest contains mainly the native *P. sylvestris*, but an alien species, Mountain Pine has also been planted in various places. The ground vegetation is a mix of different life-forms. One life-form is ericaceous dwarf-shrub, mainly dominated by heather (*Calluna vulgaris*), but with some scattered individuals of blueberries (*Vaccinium myrtillus*), cowberry (*Vaccinium vitis-idaea*) and

crowberry (*Empetrum nigrum*). Another life-form is lichen; *Cladonia rangiferina*, *Cladonia arbuscula* and *Cladonia stellaris*. And thirdly, different feather and hepatic mosses. These life-forms might affect the regeneration of the present trees in a negative (inhibition) or positive (facilitation) way (Mallik 2003, Brooker 2006, Porter 1929). The spread of these life forms might also be affected by the different ecological factors induced by the unique sand-dune landscape.

I will investigate the present biological and abiotic environmental factors that might influence regeneration in the nature reserve and try to understand the general ecological pattern that has resulted in the forest we can observe today. Hopefully, this study will be able to give insight into the complex process that involves succession, planting, regeneration, disturbances and various environmental factors that are present in the study area at hand, and tie this up to a perspective of forest management concerning reforestation, thinning and introduction of alien species. These issues are further elaborated into research questions and according hypotheses in the conceptual framework.



Figure 1 Range of *P. sylvestris*; 1) Main range of the species. 2) Isolated occurrences. 3) Natural populations extinct due to human intervention (reintroduced populations established in some areas). 4) Arctic Circle.

Conceptual framework

As this study wants to assess the varying ecological factors in a specific forest, there are a number of existing theories and concepts that are important to include.

Vegetation change

The thesis aims to elucidate factors that may influence regeneration of pine trees after a major fire more than thirty years ago. It is therefore important to define what is meant by regeneration and succession. Miles (1979, p. 36.) explains regeneration as follows: “When vegetation keeps the same overall composition in terms of the combinations and proportions of the species present, the replacement processes may be thought of as *regeneration*”. Succession, on the other hand, is defined by Miles (1979) as vegetational change that occurs away from an initial state. In this study, I am in a sense studying both succession and regeneration, depending on which scale I am observing in the landscape. If I limit the view to the burned forest, this area is in the process of restoring the forest that burned, through secondary succession, which may create a forest which is similar, but not equal to the forest that has been burned. However, if I look at the whole area with burned and non-burned forest, I may say that it is in the process of regenerating itself. The non-burned forest may have had a role as a seed pool to the opened area, so the newly grown forest inside the nature reserve can therefore be looked on as an expansion of the mature forest that originally inhabited the area before the disturbance, which was a fire in this case. As described, the conceptual definition might change when one changes the spatial scale, however, the question might also be different depending on the scale of time. Secondary succession is taking place in the nature reserve. However, the seed pool for regeneration may come from the reserve itself or from the surrounding mature pine forest. It is also possible to see how well the young forest is capable of reproducing itself without the surrounding seed pool, or rather, how it is not capable to reproduce itself. The process can be perceived as regeneration viewed at a short timescale. Finally, it also depends on the organisational level: either species or community. The species themselves are trying to regenerate, but the community is going through a successional change in vegetation.

Species interaction

The process of succession and regeneration involves a large degree of interactions and mechanics between different species. These interactions are a key part of understanding the composition of vegetation in an area, and can widely affect the diversity and function of an ecosystem (Brooker 2006). Interactions may manifest as competition between species such that some species may not

be able to co-exist with other species, making it harder for certain species to become established in an ecosystem (inhibition), or as positive interactions which might either be beneficial for each other or beneficial for further/later colonization of other species (facilitation) (Burrows 1990, Vetaas 1992). To understand the regeneration in this area, it is natural, and important, to take a closer look at these dynamics.

Facilitation

Facilitation is a model within succession theory. Its original concept is that certain species are well suited for first-time colonization during primary or secondary succession. Later on, it then makes the site more suitable for colonization by other species (Connel 1977). Facilitation does not necessarily have to be a part of a successional cycle, but can also happen during interaction between coexisting species. This may "... promote species survival and regulate community composition" (Brooker 2006; p. 637, Vetaas 1992).

Brooker (2006) also suggests a specific interaction of facilitation which is relevant for this study. He claims that saplings of *P. sylvestris* growing within heather might be protected from browsing and the general severity of the environment. This might influence both survival and biomass response. As there are moose grazing in this area, this may be an important factor in the landscape. Heather surrounding seedlings or saplings might also facilitate recruits by physically protecting them from wind and cold.

Inhibition

The inhibition model is a conceptual model that explains how some species at a certain site can make the site less suitable for colonization of other, new species (Connel & Slatyer 1977). This is an assumed process in succession, where species that first colonize a new area may be able to prevent or inhibit other species from establishing in the same area. The model implies that the "inhibiting-state" will remain the same until a new disturbance opens the area that allows new species to establish. The inhibiting species can also suppress the growth of vegetation that is already present in the system (Connel & Slatyer 1977).

The operational inhibition process may act in different ways. One way is through the production of organic chemicals, allelopathy. Miles (1979) defined allelopathy as plants which produce toxic chemicals which inhibit the growth of other plants. Mallik (2003) writes that "Allelopathy [... has] been implicated in conifer regeneration failure in the presence of dense ericaceous understory resulting from forest harvesting and fire in boreal forest and sub-alpine spruce

forests”. He also gives ericaceous plants the name “ecosystem engineers”, due to their ability to modify the habitat. By modifying the habitat, and inhibiting the growth of conifers, a retrogressive succession might happen. Mallik (2003) identifies three mechanisms which may help explain the conifer regeneration failure, and shift from forest to an ericaceous understorey. These are: (1) the absence of severe natural fire and the limitation of good enough conifer seedbed in the presence of thick humus, (2) competition resulted by quick vegetative regeneration of ericaceous dwarf shrubs after forest canopy opening by removal of trees or nonsevere fire, and (3) degradation of the habitat, due to phenolic allelochemicals of ericaceous plants causing a nutrient imbalance in the soil. The poisonous substances which may cause inhibition against other species are called phytotoxins. Jalal (1982) documents that acid compounds of high phytotoxicity have been isolated and identified from *Calluna* heathland soil. He continues to explain that heathlands with communities of *Calluna vulgaris* (outside anthropogenic heathlands) often have an absence of trees, and how observations show that “roots of trees or herbs may fail to develop or be markedly inhibited in *Calluna* heathland soil”.

Another type of inhibition that has been observed is the concept of physical inhibition. This means that a species physically covers the soil so that other species do not get a chance to germinate seeds (Porter 1929). An example of this might be a carpet-like cover of lichens.

The study area is dominated by lichens and dwarf shrubs (heather), which are commonly found in dry lichen pine forests (Fremstad 1997). From this, one may suppose that there could be an inhibiting effect by these on the vegetation in the study area. I hypothesize that both the cover of lichens and heather will have an effect on the number of recruits found in the sample plots.

Radiation

Topographic features, such as the sand dunes, may create a habitat with different features from the main vegetation, primarily due to variations in incoming solar radiation (Holland and Steyne 1975, Gallardo-Cruz et al. 2009). Topographic relief is claimed to be one of the main working gradients for variation in vegetation in Norway (Bakkestuen et al. 2008). The primary source of energy for any ecosystem is the degree of incoming solar radiation. A landscape with north- and south facing slopes will have a big variation in the distribution of solar radiation (Fig. 2). A result of this variation is a spatial difference in the micro-climate (temperature) and soil moisture, which are two of the key explanations for the composition and regeneration of the vegetation in the area

(Woodward, 1987; Gallardo-Cruz et al. 2009). However, radiation is a dubious factor: although it is the source of energy, increased radiation also evaporates more moisture. Given a specific species, as well as the general climate of the area, increased incoming radiation might be positive or negative, depending on the initial moisture level. For instance in arid conditions, where access to moisture is the depending factor, the highest biotic production might be found on north-facing slopes with low solar radiation, whereas under moist conditions, more optimal conditions might be found on the sun-exposed south-facing slopes (Sternberg & Shoshany 2001, Hawkins et al., 2003).

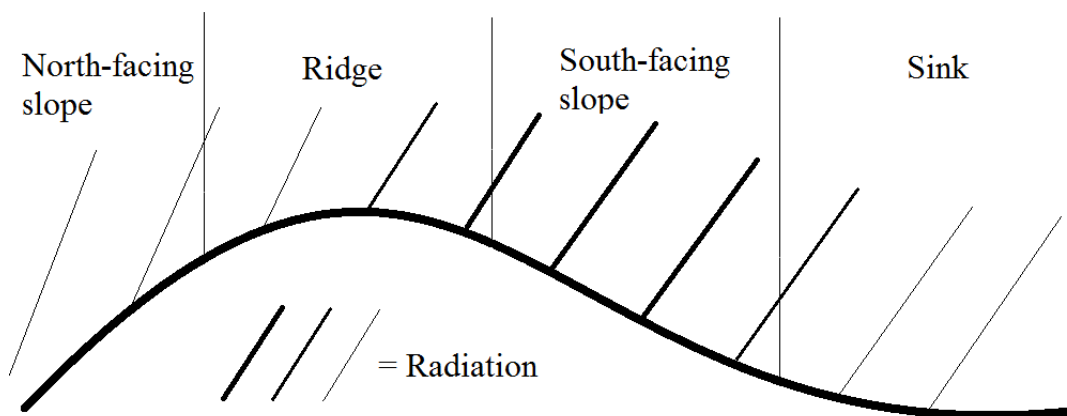


Figure 2 Conceptual cross-section of a dune of sand with incoming radiation. Thicker lines depict more accumulation of radiation.

Moisture

Aeolian sand has a relatively high permeability and does not hold moisture as well as other substrates (Pye 2009). Thus sources of soil moisture will be a crucial factor in shaping vegetation dynamics. Such a substrate will generally be more suitable for drought-tolerant species. Scots pine is known to tolerate drought, but its seeds need a certain amount of water to germinate (Oleskog 2000). One may also expect that the dune-shaped landscape results in micro-topographic differences in soil-water content. This is due to the varying degree of incoming radiation which can result in different rates of evaporation, as well as the dune-slacks being physically closer to the water-table and thus generally having better access to moisture. Precipitation will also drain from the ridges/slopes to the slacks, resulting in better growing conditions for vegetation. As previously mentioned, the ground is widely covered by lichens, and this may also influence moisture level. Porter (1929) writes that lichens will absorb incoming precipitation and can swell up to 4.5 times its own weight when dry, preventing the moisture from

running down into the soil. However, because of the physical barrier it produces, it can also help retain a certain amount of moisture in dry periods which would otherwise normally evaporate.

Shade tolerance

All trees need a certain level of light to be able to grow, but the minimum level varies between species and life stages within the same species, i.e. shade tolerance. This concept identifies the minimum level that some trees may tolerate, while still being able to grow (Valladares 2008). It is closely related to incoming radiation, and estimates of degrees of canopy closure are important because canopy cover will indirectly indicate how much light is likely to penetrate to the ground where the initial establishment and regeneration of recruits take place. There are a number of ways to categorize species into degrees of shade tolerance, but Mason (2004) mentions three categories: shade-tolerant, intermediate, and light-demanding. Shade tolerance does not necessarily affect a species' growth rate, rather that shade-tolerant trees have a better chance of surviving under low light conditions than the light-demanding species (Ameztegui 2011) Mason also claims that *Pinus* species are generally light-demanding. In his research, he estimated the specific shade tolerance of Scots pine (*P. sylvestris*) (Fig. 3). The figure depicts that pine is sensitive to light, which implies that incoming solar radiation and canopy cover are relevant parameters that may indicate if variation in light influences regeneration to include in this study of regeneration.

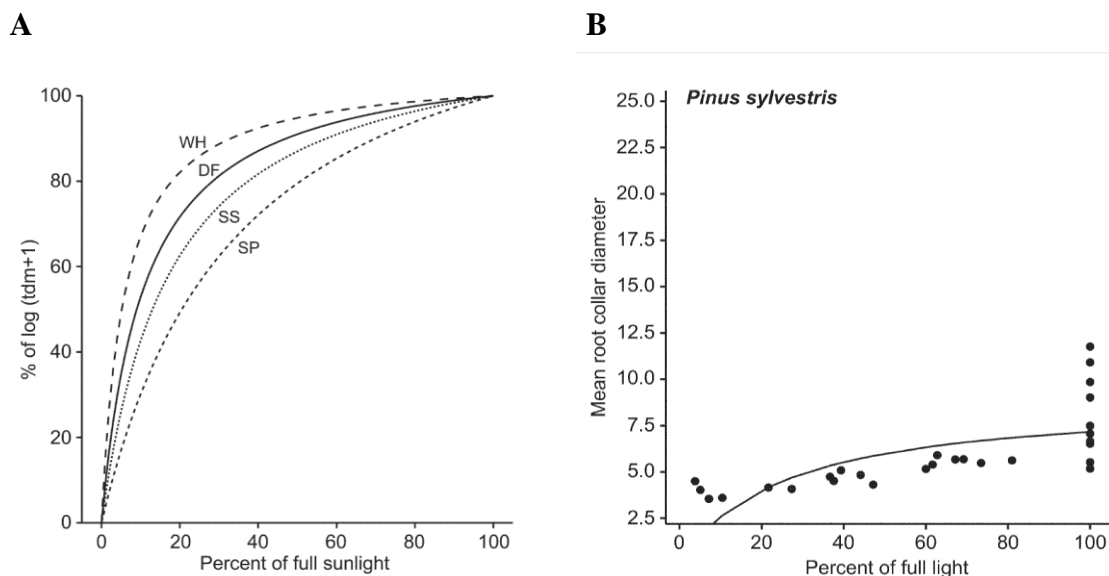


Figure 3 (A) The dry matter of scots pine (SP) in relationship with sunlight compared with other species (western hemlock (WH); Douglas fir (DF); Sitka spruce (SS)). (B) The mean root collar diameter of four year old scots pine, in relationship with degree of sunlight. From Mason (2004).

Alien species

Species might be introduced into new habitats intentionally (often plants) or un-intentionally (often animals). Intentional introduction usually happens due to human interest in nurturing a species that may be positive, for example in forestry (McNeely 2001). Planting of trees far away from their native habitat can be for commercial interest or for control of erosion or drift sand, for example (Richardson 1998). The main reasons for using alien species, as opposed to native species, are that alien trees often grow much quicker than native species, seeds of native species are often more difficult to obtain, aliens might establish more successfully in degraded forest lands, and that knowledge of biology and management of native species are often poor, making it easier for foresters to work with well-studied alien species (Zobel et al. 1987, Mather 1993). Richardson et al. (2000) explains the different stages of alien species establishment: **Introduction** is the action (by humans) of transporting a species across geographical space to establish it outside its native location; **Naturalization** happens when the environmental barriers of survival are overcome, and the introduced species manage to start reproduction; and **Invasion** is a fact when the alien vegetation manages to produce reproductive recruits a certain distance from the original place of introduction. Invasion of certain alien trees has in later decades been shown to cause major problems in the ecosystems to which they have been introduced (Richardson 1999). Richardson continues to explain that pine trees are especially problematic. This is due to the pine's low seed mass, short juvenile period and frequent occurrence of large seed crops. The introduction of an alien species may therefore cause a shift in the dominant life-form, reduce diversity, increase the biomass and density of trees and change nutrient cycling (Richardson 1999).

Thinning

Thinning—the removal of usually young trees at intervals—is an established method to manage forest stands (Oliver and Larson 1990). This type of management can either be done through schematic thinning or selective thinning. Schematic usually means corridor thinning in rows and columns, giving more area for the remaining trees to increase in volume. This practice also makes it easier for machinery to perform future cutting (Bergström 2009). Bucht (1981), however, reported that this type of thinning might not be optimal for future growth. This is due to the unexploited growing area the corridors create, as well as the retention of poorly-growing trees rather than selecting to keep the healthiest and fastest growing trees. This problem is avoided through selective thinning, where the poorly-growing trees are cut away to make growing conditions optimal for the strongest trees in the stand (Karlson et al. 2012).

Questions and hypotheses

Conferring with the introduction and conceptual framework, I have made the following research questions that I will discuss, and according hypotheses that I will try to test.

Q1: Are all individuals of pine (*P. sylvestris* and *P. uncinata*) planted, or does the forest also self-regenerate?

- H1: All trees are planted
- H2: The planted trees are producing recruits
- H3: The forest present today has undergone natural succession with no planting

Q2: Does the sand-dune landscape, and the associated micro-topographic units influence the general vegetation in the area and the regeneration of the two pine species?

- H4: Increased radiation is positive for regeneration of recruits
- H5: Increased radiation is negative for regeneration of recruits
- H6: Radiation affects the ground vegetation

Q3: Do the different environmental factors have an observable effect on the regeneration in the area?

- H7: Increased radiation means decreased moisture
- H8: Moisture has an observable effect on regeneration
- H9: Canopy cover and density of trees has an observable effect on regeneration

Q4: Are there biological inhibiting factors that prevent regeneration?

- H10: Lichens have a negative effect on regeneration
- H11: Dwarf shrubs have a negative effect on regeneration

Q5: How has the interaction between management and the biotic/abiotic environment influenced the demonstrated regeneration dynamics, and which consequence has this for the future management of the protected landscape?

Study area

Location

The area for this study is Starmoen nature reserve. This reserve lies approximately 7.5 km south east of Elverum in Hedmark county, south east Norway. The midpoint of the nature reserve, which has an area of 0.6km², is located at 60°51' 20''N, 11°41'21''E. (See Fig. 4 and 5) The elevation above sea level is 210 – 225m.

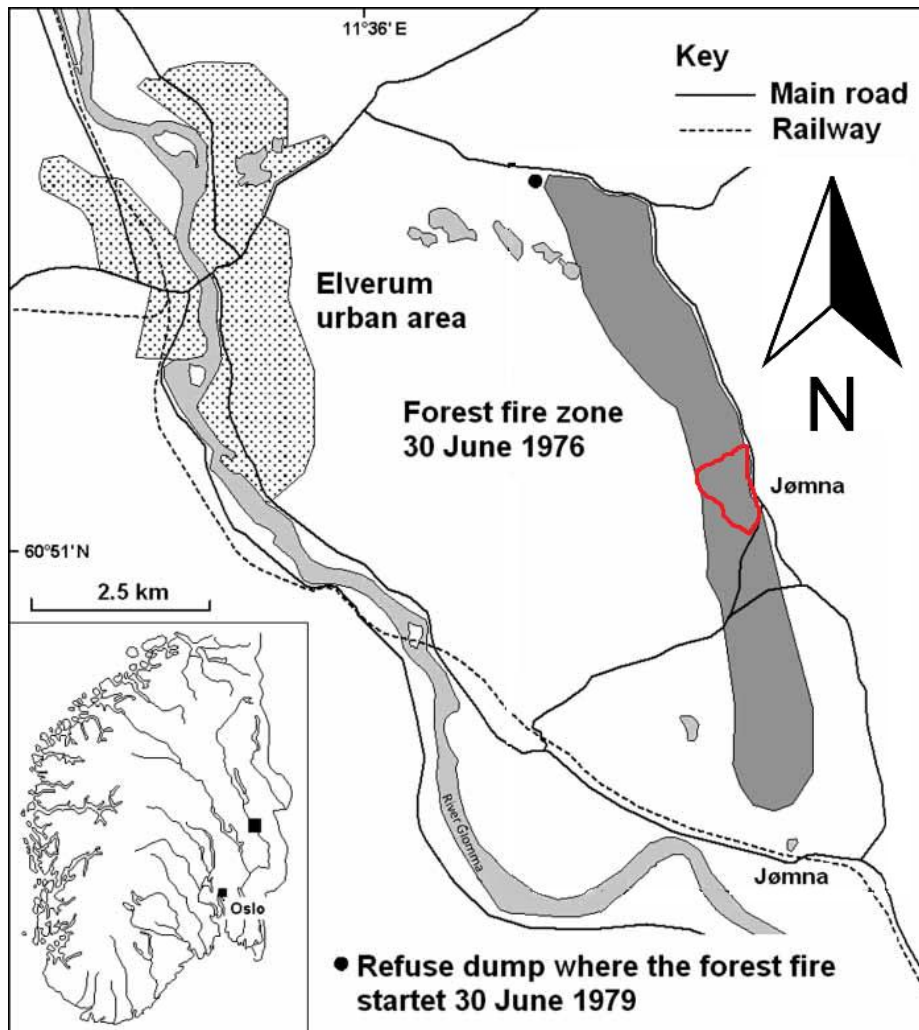


Figure 4 Sketch map showing the location of Starmoen nature reserve, marked in red. Modified from Klemsdal (2010)

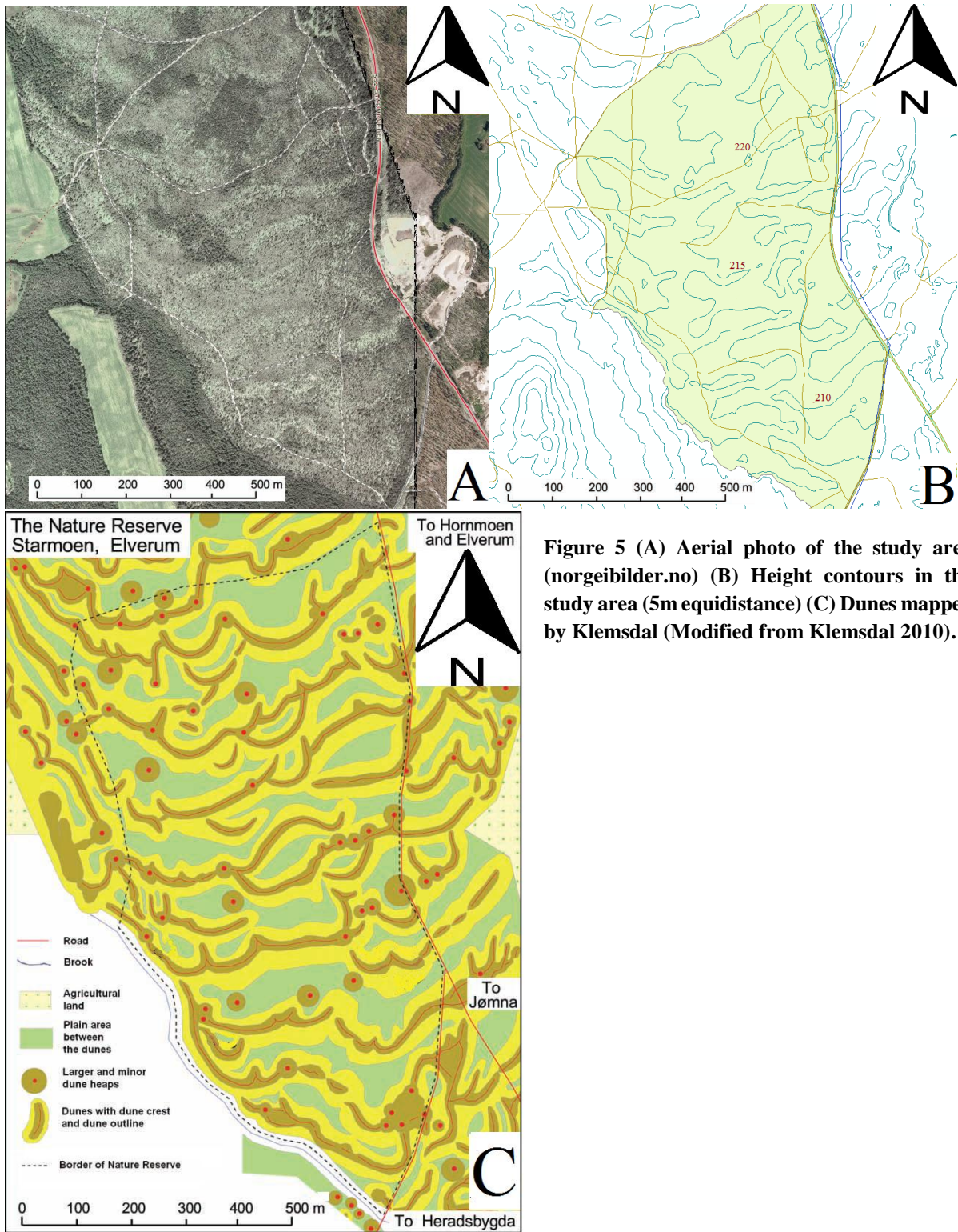


Figure 5 (A) Aerial photo of the study area (norgebilder.no) (B) Height contours in the study area (5m equidistance) (C) Dunes mapped by Klemsdal (Modified from Klemsdal 2010).

Geology

The underlying bedrock in the area is a layer of limestone and clay slate (snl.no). The overlying geomorphological substrate is composed of wind-built (aeolian) sand dunes. These dunes have previously been mapped by Klemsdal (2010) (Fig. 5C). Starmoen nature reserve is located on one of the largest fossil aeolian fields in Norway, created after the last deglaciation (10,000 yr. before present (BP)) when melt-water transported large amounts of fluvio-glacial sediments to the area. After this, strong winds blowing from north-northwest down the slope of the glacier started to build up sand dunes. This was possible because of the lack of vegetation (Klemsdal 2010). The sand dunes create a varying landscape with ridges, south-facing slopes, north-facing slopes and flat areas between these (slacks), and the different ecological factors that follow from this. Due to the sand-substrate, the soil has a relatively high permeability, and will therefore mostly only be able to host draught-tolerant species. However, the slacks in the landscape will generally have better access to moisture because they are physically closer to the underground water-table (Fig. 6). Precipitation will also drain from the ridges to the slacks, resulting in better growing conditions for vegetation. The shape and orientation of the dunes in the landscape result in a different exposure to sunlight and radiation (Fig. 6). This results in a unique opportunity to study the impact of these environmental changes on a relative small scale, instead of comparing the same changes on a crude scale such as mountain slopes.

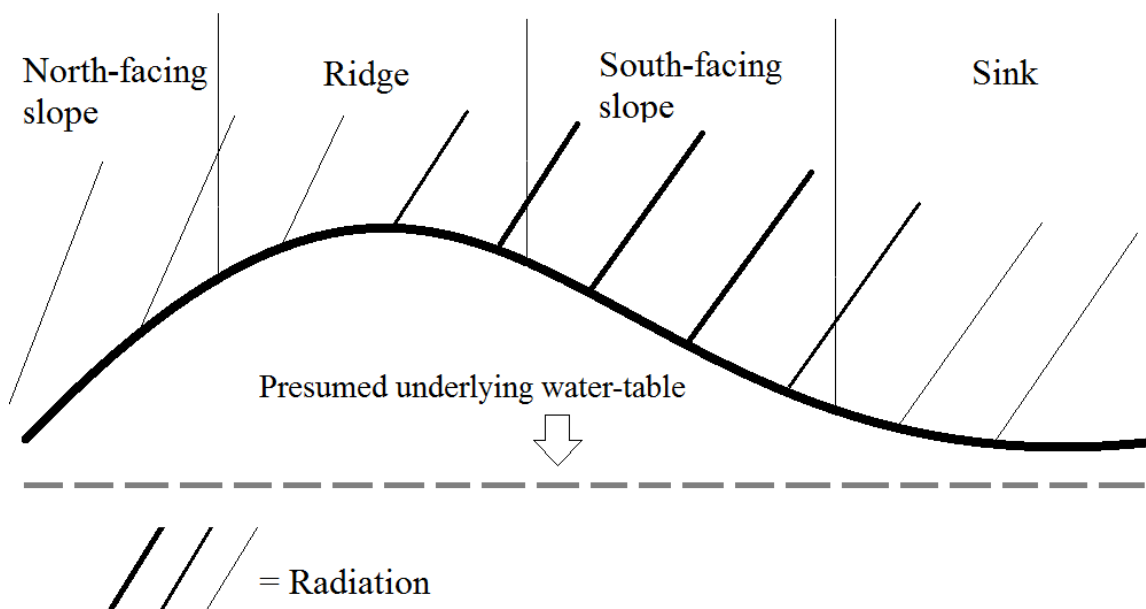


Figure 6 Conceptual cross-section of sand dune with variation in incoming radiation (thicker lines depict larger accumulation of radiation) and a presumed underlying water-table.

Climate

Starmoen is located in south-east Norway, and has a continental climate with relatively low precipitation, cool winters, warm summers and a big difference in day/night temperatures during summer. The mean annual temperature of the closest station (Elverum) is 2.7 °C. Average monthly temperature in January is -10 °C and average monthly temperature in July is 15 °C (met.no). Moen's map of growth season also depicts that the area has 160-170 days per year with temperatures of 5 °C or more. Average, yearly rainfall is 670 mm, and the number of days per year with rainfall >0.1 mm is 150-160 (Moen 2010). See Fig. 7 for monthly temperature and precipitation data.

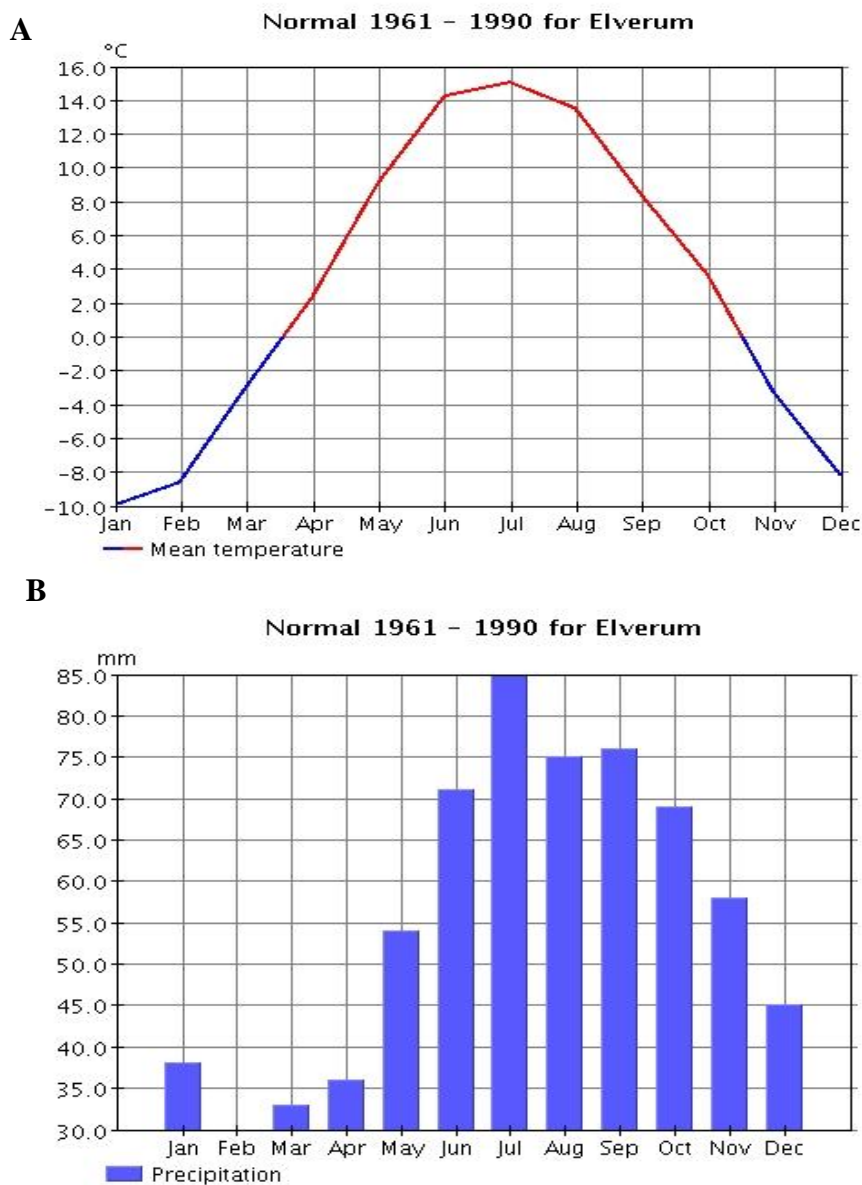


Figure 7 (A) Monthly mean temperature. (B) Monthly mean mm precipitation (from eklima.met.no).

Vegetation

The area is located within the south boreal zone. The vegetation we can observe in the nature reserve today is a dry lichen-pine forest of Scots pine (*P. sylvestris*) containing a number of mountain pine (*P. uncinata*), with varying ground vegetations, possibly as a result of microscale variations in ecological factors. These ground-level vegetation types include different types of lichen: *Cladonia rangiferina*, *Cladonia arbuscula* and *Cladonia stellaris*; dwarf shrubs, mostly dominated by heather (*Calluna vulgaris*); and a scarce cover of different types of moss. The ground cover might also provide different conditions for growth and regeneration of the target pines. Both species of pines, and the two main ground cover life-forms, have a characteristic distribution on the topographic units. *Pinus sylvestris* is generally found everywhere in the area, except for some areas on the ridges and south-facing slopes where *P. uncinata* seemed to dominate. The ridges and south-facing slopes were generally covered by a continuous layer of lichens, but some dwarf shrubs were distributed sporadically. The slacks and north-facing slopes mostly contained a dense spread of ericaceous dwarf shrubs, but lichens also seemed to be randomly distributed (Figs. 8, 9, and 10).

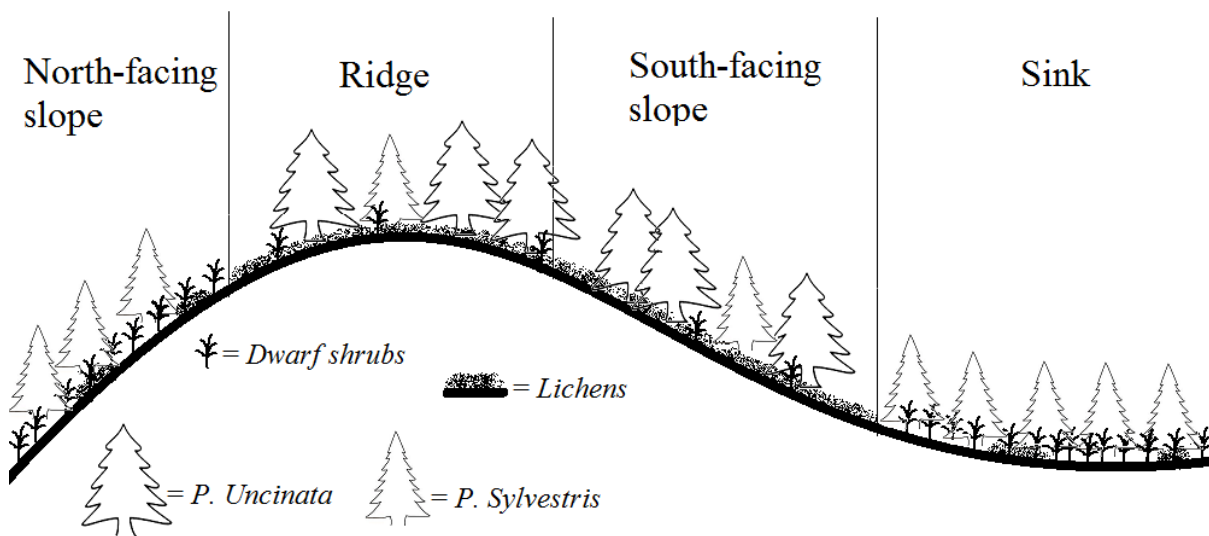


Figure 8 Conceptual cross-section of sand dune with generalized variation in vegetation distribution.



Figure 9 Slack with mainly dwarf shrubs (heather).



Figure 10 South facing slope covered by lichens. Photo: Ole Reidar Vetaas.

Target species

Scots pine (Pinus sylvestris)

Scots pine is a widespread and dominant tree-species in Norway. It is long-lived (250-300 yrs.) and is generally large in size, growing up to 45 m, with an average height of 20-25 m. It thrives in soil that is well-drained, often of mineral composition, and has no problems growing in poor, infertile ground. It is resistant to drought and needs a large amount of light to grow (low shade tolerance) (Mason 2004). Lawesson (2002) explains how pine is adapted to both dry and moist habitats, and thereby has a very wide niche tolerance. Its abundance is high at the dry end of the scale, but also in habitats with excessive amounts of moisture, such as marsh or wetlands. In habitats with intermediate moisture levels, pine may be outcompeted by other trees such as *Fagus* on the continent and *Picea abies* or *Betula pubescens* in Norway. Its extensive root system is good for preventing soil erosion (Richardson 1998). The seed production cycle of Scots pine is complicated and long-lasting. We differentiate between 3 stages in the cycle. The first is the stage of pollination, and it is recorded that high temperatures at this time are beneficial for the next stage (Nygaard 2007). Most of the pollen is spread during the daytime between 08:00 and 20:00. The next stage, flowering, is also strongly affected by the springtime temperature. High temperature results in earlier blossoming. The last stage is seed dispersal. Scots pine mostly releases its seeds over a short time span, which is reported to be around April–June in south-east Norway (Nygaard 2007). This stage is also decided by temperature, and because of this, seed dispersal might be non-existent in April, or even start in March when conditions are favourable. Øyen (2006) verifies this dependence on temperature, and writes that “Scots pine needs a minimum summer air temperature (June to August) of 10.5°C to produce viable seeds”, which corresponds to the climate of the Starmoen area.

The fact that Scots pine disperses its seeds so late is a negative factor. Spruce seeds, which have an earlier dispersal, can be transported further away from their source because they can travel easily across the snow crust aided by the wind. Scots pine seeds are less prone to undergo this due to their late seed dispersal, when the snow has already melted, and will therefore not be able to be transported far away from their source. Seeds usually fall up to 18 m away from the mother tree, and not longer than 30 m (Booth 1984). A free-standing Scots pine can be fertile at 10–15 years, but in a stand forest, not until 30–50 years. Maximum seed production is not reached until an age of 60–80 years. Under mountainous or unfavourable conditions, it may take even longer.



Figure 11 The two pine species side by side. *P. sylvestris* to the left and *P. uncinata* to the right. Photo: Ole Reidar Vetaas.

Mountain pine (Pinus mugo ssp. uncinata)

The geographical distribution of mountain pine covers mountain ranges in south and middle Europe (Øyen 1999). It is widely used in gardens, parks, plantations and in forestry. It was introduced to Norway in the 1870s, with most of the seeds coming from the French Alps and Pyrenees. Until now, it has been used extensively in reforestation of Western Norway, and it is estimated that 60 million mountain pine trees have been planted, covering an area of circa 6000–7000 hectares (Øyen 1999). The mountain pine can grow as tall as 25 m, but the multi-stemmed individuals seldom grow taller than 10 m. Together with the dwarf mountain pine (*Pinus mugo ssp. mugo*), it is known to have extremely low requirements of soil quality and depth. They also

have a strong tolerance against wind, and are therefore excellent for reforestation on especially aeolian sand (Øyen 1999). Another known ability is that the different mountain pines can transform poor heathlands into forested areas, by facilitating the establishment of other trees which may develop into a forest so that future trees can develop normally without inhibition from ericaceous dwarf shrubs. They have therefore been referred to as “nursing-trees”. This is because mountain pine may, even on bare mountain or washed-out sandy soils, gradually build a thick layer of humus.

Both of the mountain pines have a generally shallow root system, and are therefore more subject to wind-throw at an older age and height. It is a known practice to plant other trees under the cover of the so called nursing-trees (Øyen 1999).

Heather (Calluna vulgaris)

The cover of dwarf shrubs in the area is mainly dominated by heather. Heather is a widespread low-growing shrub in the *Ericaceae* family. It is usually 20–50 cm tall but can reach up to 1 m. It needs a considerable amount of moisture to thrive and reproduce. Because of this, it is mostly dominant in the west of Europe (Fægri 1970). It is evergreen and the leaves are covered with a thick layer of wax. Because of this, it can keep moisture well during dry and sunny periods (Haaland 2002). It mostly grows in well-lit openings within reach of sunlight. Ecologically, heather can make the soil unfavourable for other plants. This is due to both leaching of nutrients and the production of allelopathic chemicals. This, combined with its large seed production, explains how the shrub is able to rapidly spread in open landscapes and become the dominant species (Fægri 1970). Haaland (2002) also explains that where the cover of heather is at its thickest, only 2% of sunlight reaches the soil. Due to this, heather creates a local climate change by decreasing the temperature under its branches, as well as decreasing access to moisture. This makes it difficult or even impossible for other species to germinate. A well-known practice is to burn the heather to make the soil more favourable to herbaceous plants and tree growth.

Lichens

The lichens present in the study area are different species of the genus *Cladonia*, mainly *Cladonia rangiferina* and *Cladonia arbuscula* which are moss-like lichens. The species are characteristic of dry pine forests on moraine substrate and, as here, on aeolian sand (Fremstad 1997). They are an important food source for reindeer, which gives them their Norwegian name “Reinlav”. They cover the ground in a carpet-like way, which might result in a barrier against moisture and seed

germination of other species. An important indicator-species is *Cladonia stellaris*, known to be more tolerant of snow cover than other *Cladonia*. This was found sporadically in the area.

Additional info

Management and disturbance events

As previously written, the area was subjected to a severe forest fire that started at a refuse dump on 30 June 1976. During a few hours, the fire burned through an area of 1.2–2.0 x 8 km, just inside the field of the fossil aeolian landforms (Klemsdal 2010). After the fire, the area was evaluated for agricultural use. In 1979 and 1980, Klemsdal studied and mapped the underlying sand dunes. With the knowledge that the area contained a fossil aeolian landscape, the Norwegian department of environmental protection proclaimed the area to be a nature reserve. The purpose was to conserve an interesting natural historic area with windblown aeolian sand dunes. The conservation restricts any activity that might compromise the sand dunes, such as digging or road-construction. It does not restrict cutting of trees or management that corresponds with official guidelines for this (lovdata.no). At the time of conservation designation, the forest was divided into several private properties. The local government then decided to trade patches of land with the private owners to make the reserve and surrounding areas government property (oral source, Olav Kaveldiget). Right after the official designation, the nature reserve was managed by the environmental department of the county, but after a certain time, the management was shifted to the local city government, Elverum. Ecologically, the forest fire opened up the area for secondary succession. The type of management undertaken after this is unavailable, despite several enquiries with the local government and official institutes that had anything to do with the area (fylkesmannens miljøvernavdeling). I therefore decided to evaluate for myself what has happened in the reserve after the forest fire.

Additional biotic info

Moose is known to graze frequently in the area. This was supported by frequent observations of moose-droppings all over the area. In the slacks, I observed a limited distribution of birch, which is a known indicator of greater access to moisture.

Methods

Before I present the sample design for this study, I wish to define the explanatory variables that might affect regeneration in the area and the possible response to these.

Environmental / abiotic variables:

- Micro topography; slope, aspect and inclination.
 - o Ridges, slacks, south-facing slopes (SS) and north-facing slopes (NS), calculated into a radiation index-variable.
- Access to moisture.

Biotic

- Degree of canopy cover and shade induced by this.
- Cover of dwarf shrubs.
- Cover of lichens.
- Human interaction; dead stumps

Response:

- Number of seedlings
- Number of saplings
- Number of adult trees
- Diameter at breast height (DBH) structure, including all DBH values summed into the “biomass” variable

Sample design

The sample design intended to investigate these variables by means of a systematic stratified approach. There are several reasons to choose this instead of another random sample design. For example, Bhatta & Vetaas (2012) write that a systematic approach, instead of a random approach, is generally easier to apply in the field. It can also be better to record the ecological variation in the forest, and thus, be more accurate. They also mention a general drawback of the systematic approach in that it does not keep the possible independency between sampled plots, to “enable an appropriate assessment of error”(Bhatta & Vetaas 2012). Transects were placed across the nature reserve in an east-west direction. Each transect followed one of the topographic units in the landscape such as ridges, slacks, south-slopes and north-slopes. The number of transects was

eight: two in each of the four, different topographic units. Each transect had 8 plots. These plots were mapped by GPS and later extracted to ArcGIS, to create a map of the sampling design (Fig. 12).

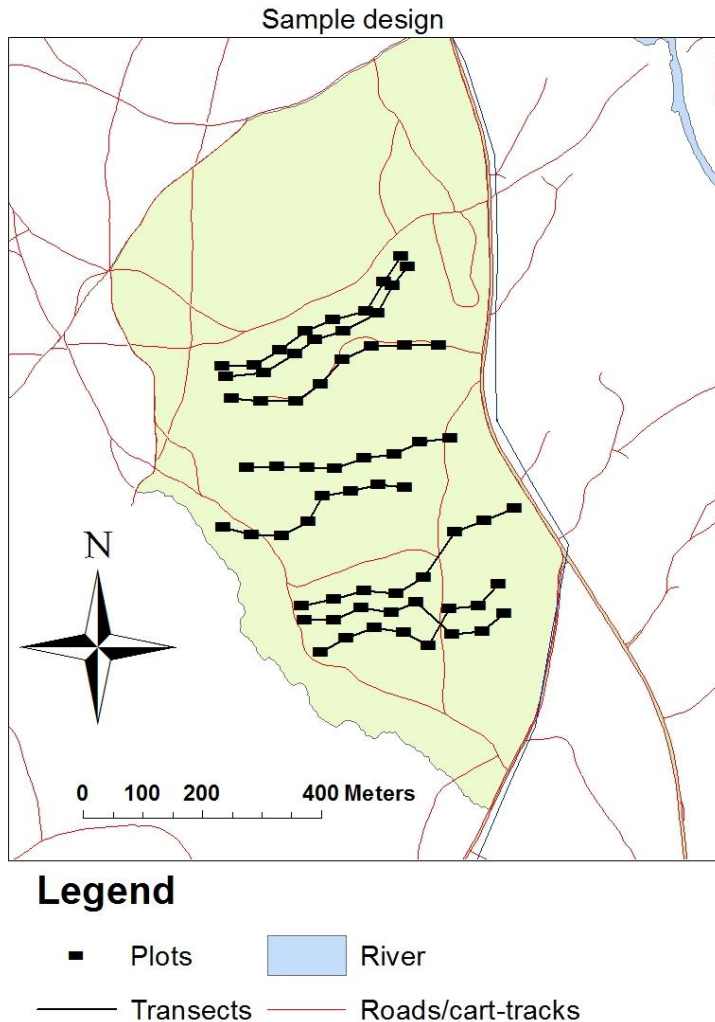


Figure 12 Map of transects and sampling plots in Starmoen nature reserve.

Criteria were used to exclude certain locations of plots, such as crossing foot paths and degree of inclination of slopes. The transects should have ideally followed one topographic unit that was as uniform as possible. I set a minimum inclination of the slopes to be 10° . The ridges had to be a continuous ridge-shaped top, with a noticeable elevation and adjacent slopes with the preferred inclination. The slacks were generally the easiest to find, by following the spaces between dunes. I also tried to lay transects where they could stretch for 400 m or longer, to ensure a certain distance between the plots. The plots were generally placed an equal distance apart within the criterion that the plots should follow a representative type of vegetation for that specific

topographic unit. This would enable me to avoid certain disturbances like cart tracks and places where the vegetation was destroyed by trampling by moose, and other anomalies such as abnormal heaps of sand. In these cases, the plots were located along the transects at a less disturbed site. A north-south running cart track is located in the eastern part of the reserve, disturbing the uniform, geomorphological slope. When crossing this track, I moved the transect to the next similar slope in order to keep the plots in the representative habitats. This is why the two southern-most transects cross (Fig. 12).

Plots

The plots in the sample design, located along the east-west going transects through the nature reserve were rectangular, measuring 20 x 5 m. The rectangular shape of the plot was used to more easily capture the relatively narrow slopes and ridges, than an equally sided square would do.

Biotic factors

Within these plots, I counted all trees, seedlings and saplings, differentiating between *P. sylvestris* and *P. uncinata*. Diameter at breast height was measured on every tree inside the plot. This was later summarized to create a “biomass variable”, reflecting how much biomass there were in the plots. To classify trees, seedlings and saplings, I use the criteria of DBH (breast height being approximately 1.3 m) and height: trees DBH \geq 5 cm, saplings DBH <5 cm, and seedlings with height <1.3 m. One challenge was that the young seedlings of the two species look basically identical. I therefore decided to classify them through the most probable source, i.e. the trees in closest proximity. Seedlings located inside a cluster of *P. uncinata* would most probably be seedlings of this species. However, if there were no seedlings within a cluster, but seedlings appeared close to the border with Scots pine, they would probably be seedlings of *P. sylvestris*. This is, of course, not a solid method to distinguish the two, so several errors might have been recorded. I also measured the DBH of all adult trees within the plot. I dated approximately one adult tree per plot, using dendrochronology from a core taken with a 5 mm drill. An equal number of Scots pine and mountain pine was dated. I also counted the presence of dead stumps in each plot to estimate the extent of human interference through forest management in the specific plot.

From preliminary observations, I realised that the ground vegetation cover in the study area was widely dominated by either lichens or dwarf shrubs. Considering this together with the facts in the conceptual framework, one may hypothesise that a different distribution of these ground vegetation will be found on the different topographic features. As heather known to be moisture-

demanding, and this is the dominant species among the dwarf shrubs, it was thought that this life form would be dominant in the slacks and on north-facing features, while the lichens might be dominant on the south-facing features and ridges, due to the latter two being subjected to more incoming sunlight and radiation and water draining towards the slacks. The third life-form, moss, will probably have an insignificant spread, but will be more normal on the moist features. To measure this, I estimated the percentage cover of these three types of ground cover in each of the plots

Whether or not the forest in the nature reserve had been planted was something I tried to get information about before conducting my fieldwork. This was, however, inconclusive. It was not until I was actually in the field that I observed that the trees were aligned in more or less perfect rows and columns. This was very obvious on the wind-exposed south-facing slopes, but with a more thorough survey, I realised that this was the case for the entire forest. Due to this I made the variable Symmetry (“Sym”) that could indicate derivation from a perfect planting. This was a qualitative value based on how optimal the number and location of trees were compared to a block of three rows with nine trees in each. I observed that in the most symmetrical areas of the reserve, the trees were sited in perfect rows 2.5 m apart. A plot of 20 x 5 m would then contain 3 x 9 adult trees. Values of 1 to 5 were assigned with 1 being the least observable symmetry and low number of adult trees, and 5 being as close as possible to symmetry and with 27 trees. The symmetry variable is, however, not a real continuous variable, which affected the statistical methods that followed. Closely related to symmetry, I estimated per cent canopy cover within the plot, which will relate to the shade tolerance of pine, by making a visual evaluation of how much a perpendicular projection of the canopy will cover the ground.

Abiotic factors

Aspect and slope was measured in each of the plots using a clinometer compass, and assigning a value of degree on the direction of the ridge/slope and the inclination of the slopes (north-facing and south-facing). From these measurements, I could calculate a relative radiation index (RRI) using Oke’s (1987) formula and differentiate this value between the different topographical units in the reserve. RRI is an expression of the annual relative difference in midday radiation intensity between slopes (Vetaas 1992). I also measured soil moisture. To do this, I used a shovel to make an incision at 5 random spots inside the plot. I then sampled a spoonful of the soil immediately under the top-layer humus in each of these spots and mixed these into one sample. This sample was then stored in an airtight plastic bag. Each of these samples were later weighed, then dried in

105 °C for >12 hours, to see the weight difference caused by loss of moisture. After this, I measured loss-of-ignition, to determine the soil's organic content, which is a key factor to how well the soil can keep moisture (Fekete 2012). The dried soil samples were burned at 550 °C for four hours and weighed again to estimate the lost carbon content. Both drying and burning followed the procedures of Heiri et al. (2001).

Statistical methods

It is possible to conduct several tests on the data compiled by the sampling procedures described above, and this will provide knowledge on how the different ecological factors and pine recruits are linked together. The geographical coordinates of all sampling plots were recorded by GPS, which enables me to explain the relationship between biotic and abiotic factors that may affect the regeneration of pine trees, and to check whether the residuals from the multiple regression models with respect to autocorrelation follow the potential spatial patterns in the residuals.

Data for each variable in every plot were entered into a MS Excel sheet, a format accessible by the SAM (Spatial Analysis in Macroecology) program. In SAM, I first derived basic, descriptive statistics. I calculated the minimum value, maximum value, mean, standard deviation, standard error of the mean and kurtosis for each of the variables. For the count variables such as dead stumps, trees, seedlings and saplings, I also summarized all the counted individuals. These calculations were first done on the entire forest, and then for each of the four different topographic units (ridge, slack, north-slopes and south-slopes), divided into explanatory and response variable categories. In this study, there is a certain progressive dependency between the explanatory variables. Some of the variables classified as explanatory at one analyses, may therefore later be used as response variables. The recorded dendrochronological data was imported into SAM and made into a scatterplot showing both age and DBH.

There were a number of anomalies in the dataset, i.e. statistical outliers. These are depicted in box plots as dots outside the whiskers. The frequency histograms of response variables showed that they were not normally distributed. I therefore decided to transform the data of the response variables by square rooting the data (Fig. 13). This was then later used in the correlation and regression analysis.

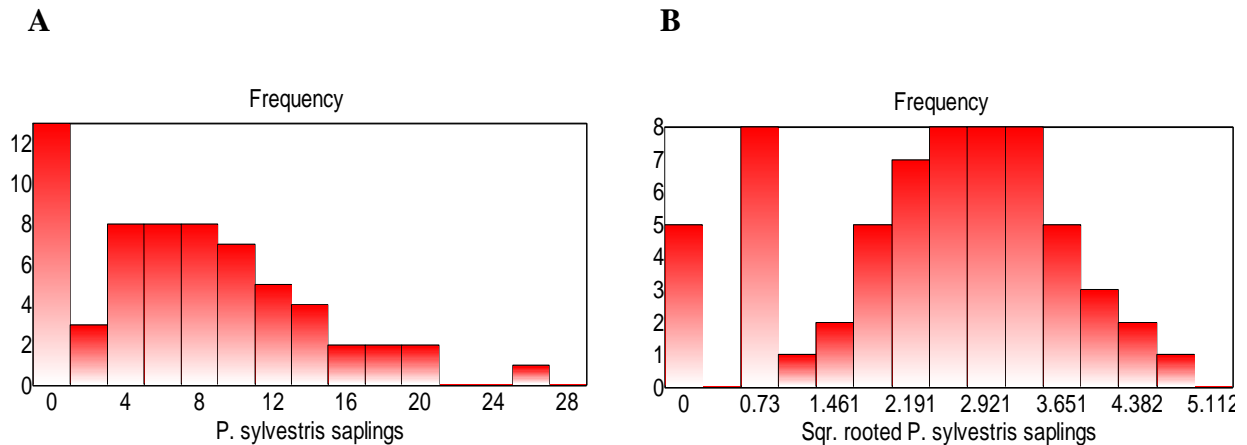


Figure 13 (A) Example of skewed distribution by *P. sylvestris* saplings. (B) Close to normal distribution of *P. sylvestris* saplings after square rooting.

I then proceeded to compile a correlation matrix of all the explanatory variables against each other. Correlation, not to be confused with regressions, only look at how variables vary together (covary), indicating if they are interdependent (Sokal 1987). By doing this, I could see which ones had an immediate, linear correlation. I did the same for the four response variables. I chose to use the Pearson's r matrix instead of Spearman's, because most of the variables were continuous. My data had 64 samples and 62 degrees of freedom, and by looking at a table of p -values of Pearson's correlation coefficients (r), the following limits appeared: $r > 0.250$ to be within the 0.05 p -value (5% chance that the null-hypothesis is still valid) threshold, and $r > 0.325$ to be within the 0.01 p -value threshold (Snedecor 1980).

This was followed by extensive regression analyses in SAM. Regressions deal with the cause-and-effect relationships based on theoretical reason, and is less explorative compared with correlations. A regression tries to "... predict what values of a variable Y corresponds to given values of a variable X" (Sokal 1987, p. 231). In other words, we try to see how a dependent variable (Y) is affected by another explanatory (independent variable) (X). By conducting a regression analysis, one can highlight hypotheses concerning causal relationships (Sokal 1987). In my analysis, a certain explorative approach was used, using the scatterplot function within the SAM software to see how the Y-variable was affected by the X-variable. I decided to include calculations up to the second order, to see if Y could be "explained" by X in a non-linear way. However, I only recorded the significant calculations in the spreadsheet: linear or curved. The curved lines are either X^2 (quadratic) or $X+X^2$ (quadratic, unimodal), the direction of the line is shown with the value being either positive or negative. The numbers recorded for each explanatory variable were coefficient, degrees of freedom, t-value, and p -value (of the single

variable, different p -values if the calculation was of second order), and R^2 -value, F-value and p -value of the full model. The last p -value of the full model is the crucial value of what is significant, and I chose to use the standard value of “0.05” significance as an upper limit. Firstly, four responsive variables (*P. sylvestris* seedlings and saplings, *P. uncinata* seedlings and saplings) were analysed separately against all the mentioned explanatory variables. After this, I also made a regression analysis on a selection of the variables classified as explanatory. These were compared to the other explanatory variables that logically could have an effect on the variable at hand, seeing as there is a certain casual, linear system of effect in the ecology I am studying.

The value I created for symmetry is not a real continuous variable. Thus, the results from the statistical analysis made on the symmetry-variable may not follow the strict assumptions of descriptive statistics, correlations and regressions. The associated mean values, F-values and p -values have primarily a descriptive value to aid the interpretation of casual links.

After doing the single regressions, I decided to combine two explanatory variables that each explained the response variables best into a multiple regression to create a small two-predictor model. This follows a forward selection procedure. It was done by firstly using the variable that explained the most in the single regression (primary variable), and then using an explorative approach to see which other variable could explain the most in addition to the primary variable.

To add a specific, geographical approach to the study, I decided to look at how the recruits, as well as the residuals from the multiple regressions, were spatially autocorrelated. Spatial autocorrelation assesses random pairs of a certain variable that are separated by a spatial distance. These variables are either more or less similar than one would expect from random observations (Legendre 1993). In a sense, this is the essence of Tobler’s first law of geography; “everything is related to everything else, but near things are more related than distant things” (Tobler 1970). By doing this, I can see whether or not the multiple regression managed to explain the occurrence of recruits, or if there might be another significant variable which had been left out of the model.

Results

In this chapter, I shall present the numerical analyses described in the previous chapter, as well as first-hand observations.

Firstly I wish to statistically describe the entire forest, and then each of the topographical units individually, such as slacks and ridges.

Spatial distribution of target pines

Demography

The pines in the area belong to two populations, a population of *P. sylvestris* and a population of *P. uncinata*. These two populations have different size and spatial distributions. The counted *P. sylvestris* in all plots totalled 630 adults, 529 saplings and 2423 seedlings, while *P. uncinata* only totalled 125 adults, 71 saplings and 90 seedlings. The mean numbers of *P. sylvestris* per plot were 9.8 adults, 8.2 saplings and 37.9 seedlings, for *P. uncinata* 1.9 adults, 1.1 saplings and 1.4 seedlings (Table 1). *Pinus sylvestris* was generally distributed across the entire study area, while *P. uncinata* was only found on south-facing slopes and ridges, mainly in the western part of the reserve. In the eastern part, *P. sylvestris* was the dominant tree species. By dividing the number of seedlings by number of adult trees per species, we see that *P. sylvestris* has 3.84 seedlings per adult, while *P. uncinata* has 0.72 seedlings per adult.

Dendrochronology showed that adult trees of both species were approximately 25 to 27 years old, but there were a few outliers of 30 to 35 and 55 years old (*P. sylvestris*). One adult *P. uncinata* was calculated to be 19 years old. The diameter at breast height varied more than age, for instance the 25-year-old individuals of *P. sylvestris* had a minimum DBH of 4 cm and maximum of 19 cm. The recorded DBH of *P. sylvestris* ranged from 4 cm to 55 cm, while *P. uncinata* had a range from 5 cm to 19 cm (Fig. 14).

Pinus sylvestris was present in nearly all plots, but five plots had no seedlings or saplings, whereas recruits of *P. uncinata* were absent in many plots: 47 plots had no seedlings and 45 plots had no saplings.

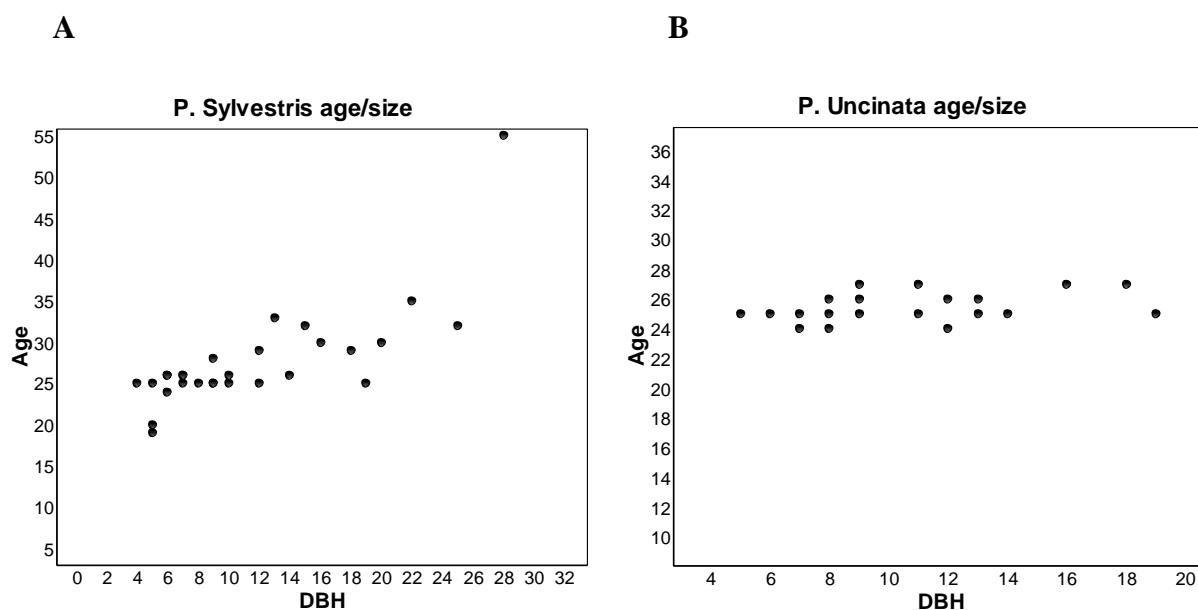


Figure 14 (A) Age/size diagram of adult *P. sylvestris*. (B) Age/size diagram of adult *P. uncinata*

Table 1 Descriptive statistics of explanatory and response variables within each plot in entire forest. Statistics of each topographic unit is in Appendix I, II, III, and IV.

Forest:	Variable	Mean	Min	Max	Std. Dev.	S. E. Mean	Kurtosis	Sum
Explanatory:	Sym	2.828	1	5	1.017	0.127	-	
	CC	0.442	0.1	0.9	0.205	0.026	-0.819	
	INC	8.953	1	35	8.888	1.111	-0.565	
	DIR	131.047	1	355	113.991	14.249	-0.646	
	Lich	56.719	20	100	21.236	2.654	-0.906	
	Hea	38.281	0	80	20.973	2.622	0.977	
	Moss	5.156	0	70	10.54	1.317	22.666	
	DS	3.156	0	13	3.082	0.385	1.994	202
	Moi	4.343	0.22	9.44	2.41	0.301	-0.815	
	LOI	1.327	0.61	3.17	0.488	0.061	3.008	
	RRI	0.493	-0.08	0.823	0.177	0.022	0.744	
	Sytrees	9.8	1	21	5.034	0.629	-0.235	630
	Unctrees	1.953	0	18	4.42	0.553	4.651	125
	Trees	11.75	3	21	4.684	0.585	-0.975	755
Biomass	112.8	33	262	51.625	6.453	-0.296	7819	
Response:	Syseed	37.859	0	100	24.484	3.06	-0.221	2423
	Sysap	8.166	0	30	6.528	0.816	1.175	529
	Uncseed	1.406	0	25	3.816	0.477	23.813	90
	Unssap	1.109	0	10	2.154	0.269	4.586	71

Table 1 explained abbreviations and variables: Sym; Symmetry, CC; Canopy cover, Inc; Degree of Inclination, Dir; Degree of Direction, Lich; Lichens %, Hea; dwarf shrubs (heather) %, Moss; Moss %, DS;# Dead stumps, Moi; Moisture %, Loi; Loss-on-ignition %,RRI; Relative Radiation Index, Syseed; # Seedlings of *P. sylvestris*, Sysap; # Saplings of *P. sylvestris*, Uncseed;# Seedlings of *P. uncinata*, Unssap;# Saplings of *P. uncinata*, Trees; # of trees combined, biomass; DBH combined

Topographical distribution of pine in the study area

Adult trees of *P. sylvestris* had the largest mean number of individuals on south-facing slopes (11.1 per plot). The other features supported similar mean values: 9.4 on the ridges, 9.5 in the slacks, and 9.75 on north-facing slopes. Trees of the secondary pine had a mean number of 3.9 individuals per plot on the ridges and 3.94 individuals on south-facing slopes.

Highest numbers of *P. sylvestris* seedlings were found on the ridges (49.5 mean per plot), and smallest numbers were found on the south-facing slopes (20.9 mean per plot). *P. sylvestris* saplings were most frequent on north-facing slopes and slacks with means of respectively 14.5 and 10.7 per plot. The south-facing slopes and ridges had much fewer saplings, with means of 4.2 and 3.7. Most seedlings of *P. uncinata* were found on south-facing slopes (3.8 mean per plot), while ridges had a mean of 1.9 seedlings per plot. The distribution of saplings was similar, with a mean of 1.9 on the ridges and 0.95 on south-facing slopes. For further details on the topographic distribution, see Appendix I, II, III, and IV.

The relationship between the four different types of recruits can also be seen in the constructed boxplots and associated t-tests.

Differences between the topographically defined habitats

There were obvious differences between topographical units and the magnitude of these differences are indicated in the boxplots (Figs. 15, 16, 17, and 18) and the associated t-tests.

The boxplots show that *P. sylvestris* seedlings on south-facing slopes were the only ones which were significantly different from the other topographical units, having much fewer individuals than the rest. The test gave a p -value of 0.02 between south-facing slopes and slacks. The number of seedlings on the ridges, slacks and north-facing slopes were not statistically different from each other (Fig 15). The test done on *P. sylvestris* saplings show that the features fall into two groups: the ridges and south-facing slopes being statistically alike with the least amount of individuals, and the slacks and north-facing slopes being alike with most individuals. These two pairs are also significantly different from each other, with a p -value of <0.0001 between each group (fig 16). *P. uncinata* is absent from the slacks and north slopes, and numbers of seedlings on ridges and south-facing slopes were not significantly different from one another ($p=0.3409$) (Fig. 17), whereas the number of saplings on the ridges and south sides were statistically different from each other (Fig. 18).

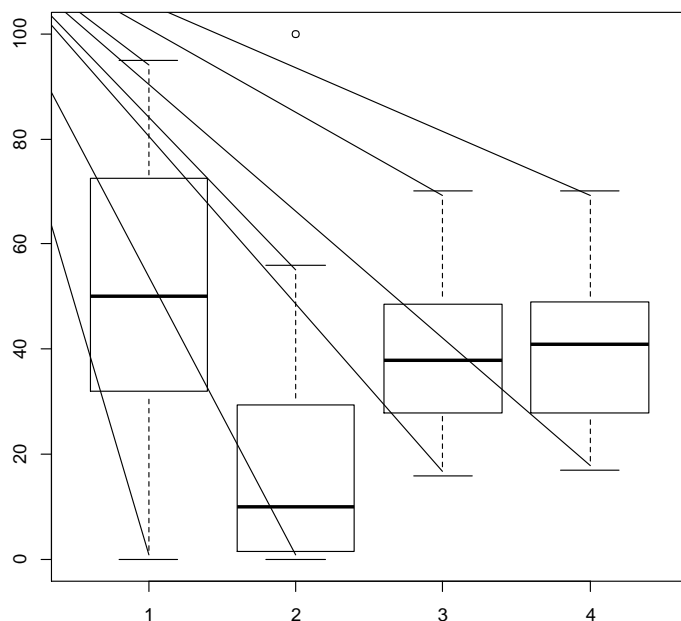


Figure 15 Boxplots of *P. sylvestris* seedlings at the different topographic units and variation around mean. 1= Ridge, 2= South side, 3=Slacks, 4=North side. South facing ridges are different from the other units (2 vs 3 = $p < 0.05$), but the other combinations are similar ($p > 0.05$).

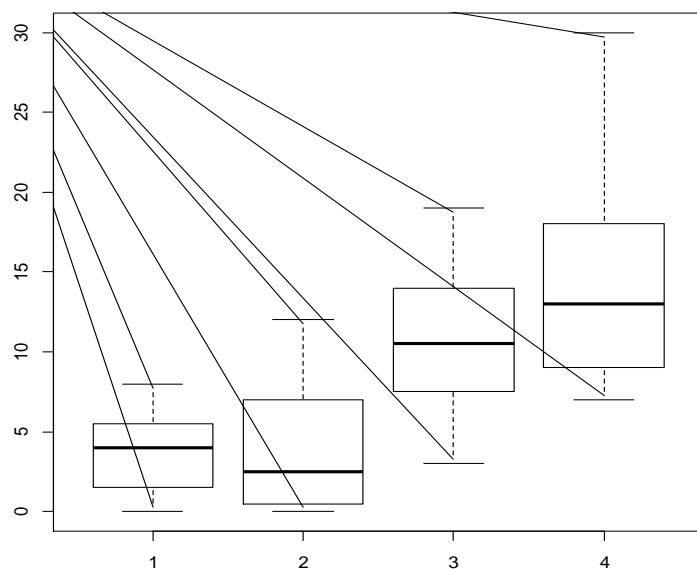


Figure 16 Boxplots of *P. sylvestris* saplings at the different topographic units and variation around mean. 1= Ridge, 2= South side, 3=Slacks, 4=North side. Saplings appear as 2 groups, one of ridges and south facing slopes, the other as sink and north facing. These groups are different from each other ($p = 0.0001$).

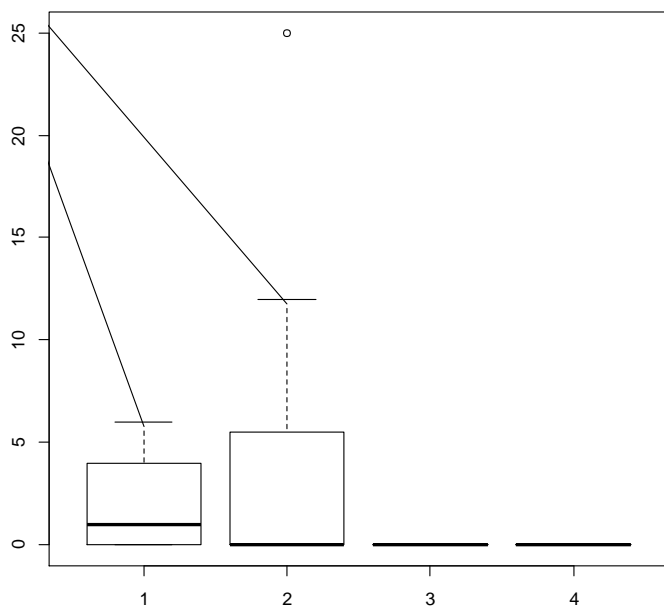


Figure 17 Boxplots of *P. uncinata* seedlings at the different topographic units and variation around mean. 1= Ridge, 2= South side, 3=Slacks, 4=North side. Mean number of seedlings are similar on south facing slopes and ridges ($p>0.05$).

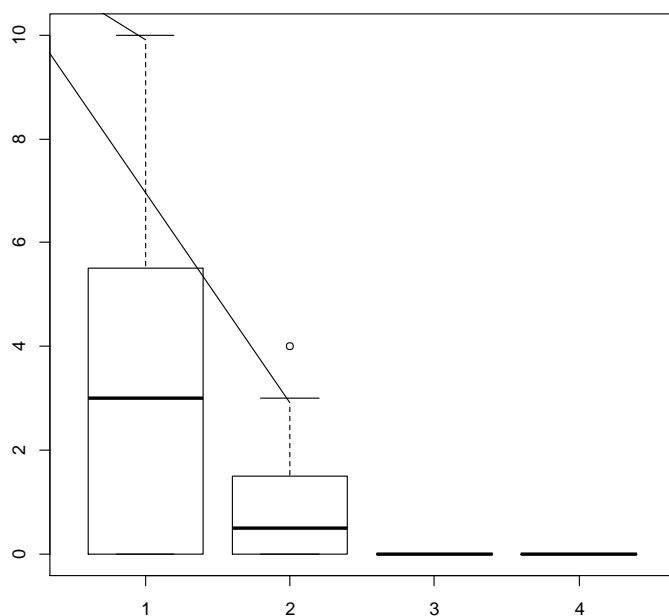


Figure 18 Boxplots of *P. uncinata* saplings at the different topographic units and variation around mean. 1= Ridge, 2= South side, 3=Slacks, 4=North side. Ridges and south facing slopes are different from each other ($p<0.05$).

Explanatory variables and their distribution in the study area

The inclination and aspect of the slopes were used to estimate a radiation index (RRI). The highest mean value of RRI was found, as expected, on the south-facing slopes (0.718), followed by the ridges (0.513), slacks (0.485) and north-facing slopes (0.255) (Appendix I, II, III, and IV).

The overall mean moisture content of the soil was 4.3% (Table 1). The ridges were driest with an average of 2.65%, while the slacks had more than double i.e. 5.7%. The sun-exposed south-facing slopes had a mean of 3.8%, while the shaded north-facing slopes had a mean of 5.2%. The analysis of loss on ignition (LOI) turned out to be less conclusive than initially thought. The overall mean LOI was 1.33% for the entire study area (Table 1). The values for south-slopes and north-slopes were a bit higher (1.45% and 1.42%) than the ridges and slacks which were lower than the overall mean (1.1% and 1.33%) (Appendix I, II, III, and IV).

There was a large variation in the estimated biomass index (sum of DBH in one plot). The south-facing slopes had the highest value (157), while the north-facing slopes only had an average of 75.7 per plot. The ridges and slacks had an average of 121.1 and 97.8, respectively. The “symmetry”-value described how symmetrical the trees appear today, i.e. to what degree the initial planting symmetry had remained. From observation, it looked like the trees on the south-facing slopes were most symmetrical. Appendix III shows that this qualitative variable had a mean of 3.5 on these slopes, while the others had 2.3 (ridge), 2.4 (sink), and 3.1 (north-facing slope) (Appendix I, II, and IV). Most dead stumps were found on the south-facing slopes, with a sum of 81, followed by ridges (71), slacks (32) and north-facing slopes (18). The canopy cover estimates showed that the mean of all the plots was 44%. It was highest in the slacks (59%), closely followed by the south-facing slopes (54%). The ridges and north-facing slopes had a cover of 42% and 44%, respectively (Appendix I, II, III, and IV).

I expected a difference in the distribution of the different life-forms (lichens, dwarf shrubs (mainly heather) and mosses). Looking at the overall mean in the entire study area, lichens were the most dominant life-form (56.7%) followed by dwarf shrubs (38.2%) and lastly, moss (5.1%) (Table 1). Lichens had the largest cover on south-facing slopes (79.4%), while plots on the ridges had a mean cover of 67%. The north-facing slopes and slacks had a mean of 42.5% and 38% lichens, respectively. The mean cover of dwarf shrubs was largest on the north-facing slopes and slacks, both 53%, but there was much lower cover on ridges (29%) and south-facing slopes (17.5%) where lichens dominated. The cover of mosses was always lower than ten percent for all topographic units (Appendix I, II, III, and IV). The distribution of dwarf shrubs and lichens is

very much complementary, or negatively correlated (Fig. 19), which is also shown in photos (Figs. 20 and 21). This distribution of life forms is a generalized description of how the distribution appeared, however, a mosaic of both life forms could also be observed some places, on any of the topographic units, as Figure 22 depicts.

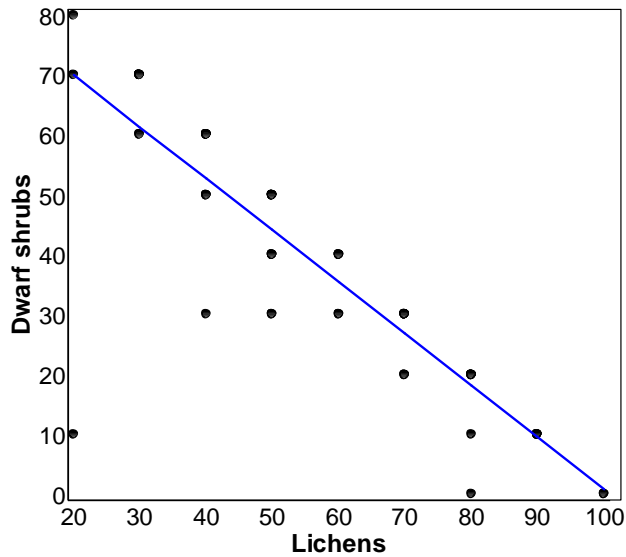


Figure 19 Linear, negative co-variation of mean percentage distribution of dwarf shrubs and lichens.



Figure 20 South facing slope covered with lichens.



Figure 21 Slack mainly covered in dwarf shrubs, but a few scattered patches of lichens, especially towards the north facing slope.



Figure 22 North facing slope covered in a mosaic of lichens and dwarf shrubs.

Correlation between variables

The next step in the analytical procedure was to assess the co-variation of the explanatory and responsive variables. Correlation of explanatory variables is important to know before one uses them in multiple regression analyses, due to the assumption of independence between terms in the regression model. The numerical data were compiled into correlation matrices, one for the explanatory variables (Table 2), and two for response variables, one with transformed and one with raw data (Tables 3 and 4). These correlations showed which variables had linear, statistically significant relationships, and whether it was positive or negative (in this context, significant means from this point on statistically significant). The explanatory variables which were significantly correlated are depicted in Table 2. Here I wish to emphasize those relationships that may be important for the evaluation of plausible causal links further in the regression analyses.

Comparing explanatory variables

Conferring with table 2, the strongest correlation between two variables were, naturally, number of adult trees and the estimated biomass index. Number of trees per plot was also strongly correlated with canopy cover, symmetry, and to a certain degree, dead stumps. All the above-mentioned variables also had significant relationships to one another. The other strong correlation was a negative relationship between percentage of dwarf shrubs and lichens. The radiation index, number of trees and number of adult *P. uncinata* also co-varied strongly with these vegetation variables: positive for lichens and negative for dwarf shrubs. In contrast to this, moisture co-varied positively with dwarf shrubs and negatively with lichens. The radiation index had a strong correlation with the biomass index, and a negative correlation with soil moisture (Table 2). Loss on ignition and mosses did not have any correlation with any of the other explanatory variables.

Comparing responsive variables

Within the non-transformed response variables, there were negative relationships between the spatial distribution of seedlings of *P. sylvestris* and *P. uncinata*. The same negative relationship was also found with saplings for the two species. There was no significant correlation between seedlings and saplings of *P. sylvestris*, but a strong correlation between seedlings and saplings of *P. uncinata* (Table 3). In the table of the transformed responsive variables, it shows that all recruits were significantly correlated with each other, with recruits of *P. sylvestris* and *P. uncinata* being negatively correlated. They were all strongly or very strongly correlated, except for seedlings of *P. sylvestris* which had a negative correlation with saplings of *P. uncinata* (Table 4).

Results

Table 2 Correlation matrix, only explanatory variables (Pearson's r)

	Sym	CC	Lich	Hea	Mo	DS	Sytrees	Unctrees	trees	Moi	LOI	RRI	biomass
Sym	1	0.577	0.201	-0.2	-0.02	-0.093	0.314	0.21	0.524	-0.207	0.022	0.136	0.406
CC	0.577	1	0.31	-0.438	0.251	0.249	0.463	0.25	0.735	-0.249	-0.004	0.137	0.742
Lich	0.201	0.31	1	-0.875	-0.278	0.389	0.025	0.433	0.438	-0.451	-0.155	0.674	0.453
Hea	-0.2	-0.438	-0.875	1	-0.218	-0.408	-0.027	-0.41	-0.417	0.44	0.111	-0.647	-0.534
Moss	-0.02	0.251	-0.278	-0.218	1	0.033	0.021	-0.063	-0.041	0.011	0.074	-0.069	0.158
DS	-0.093	0.249	0.389	-0.408	0.033	1	0.265	0.062	0.344	-0.202	0.146	0.401	0.329
Sytrees	0.314	0.463	0.025	-0.027	0.021	0.265	1	-0.51	0.581	-0.012	-0.147	0.094	0.517
Unctrees	0.21	0.25	0.433	-0.41	-0.063	0.062	-0.51	1	0.4	-0.321	0.137	0.325	0.34
trees	0.524	0.735	0.438	-0.417	-0.041	0.344	0.581	0.4	1	-0.331	-0.023	0.409	0.877
Moi	-0.207	-0.249	-0.451	0.44	0.011	-0.202	-0.012	-0.321	-0.331	1	0.176	-0.291	-0.233
LOI	0.022	-0.004	-0.155	0.111	0.074	0.146	-0.147	0.137	-0.023	0.176	1	-0.109	-0.063
RRI	0.136	0.137	0.674	-0.647	-0.069	0.401	0.094	0.325	0.409	-0.291	-0.109	1	0.514
biomass	0.406	0.742	0.453	-0.534	0.158	0.329	0.517	0.34	0.877	-0.233	-0.063	0.514	1

Abbreviation explanation; refer Table 1. 0.05 p-value = $r > 0.25$ (62 df), 0.01 p-value = $r > 0.325$ (62 df)

Table 3 Correlation matrix, response variables (Pearson's r).

	SySeed	SySap	UncSeed	UncSap
SySeed	1	0.168	-0.33	-0.089
SySap	0.168	1	-0.226	-0.448
UncSeed	-0.33	-0.226	1	0.244
UncSap	-0.089	-0.448	0.244	1

Abbreviation explanation; refer Table 1.

0.05 p-value = $r > 0.25$ (62 df), 0.01 p-value = $r > 0.325$ (62 df)

Table 4 Correlation matrix, square rooted response variables (Pearson's r).

	Syseed	Sysap	Uncseed	Uncsap
Syseed	1	0.436	-0.457	-0.255
Sysap	0.436	1	-0.493	-0.573
Uncseed	-0.457	-0.493	1	0.508
Uncsap	-0.255	-0.573	0.508	1

Abbreviation explanation; refer Table 1

0.05 p-value = $r > 0.25$ (62 df), 0.01 p-value = $r > 0.325$ (62 df)

Analysis

The univariate and multivariate regression analysis that followed showed to what extent the explanatory variables explained the response variables, linear or non-linear, as well as if and how the explanatory variables had a causal relationship in a non-linear way. This provides a more thorough analysis than just the linear correlation (Table 2). Regressions were made on both the non-transformed and transformed data of responsive variables. However, the square rooted values without outliers gave a much more robust result. I will therefore only present the regression results with the transformed data here.

Regression of explanatory variables

The regression analysis showed that radiation index had a significant relationship with degree of moisture found in the soil, with an almost linear response ($R^2 = 0.121$) (Table 5) (Fig. 23), but it had no significant relationship with LOI.

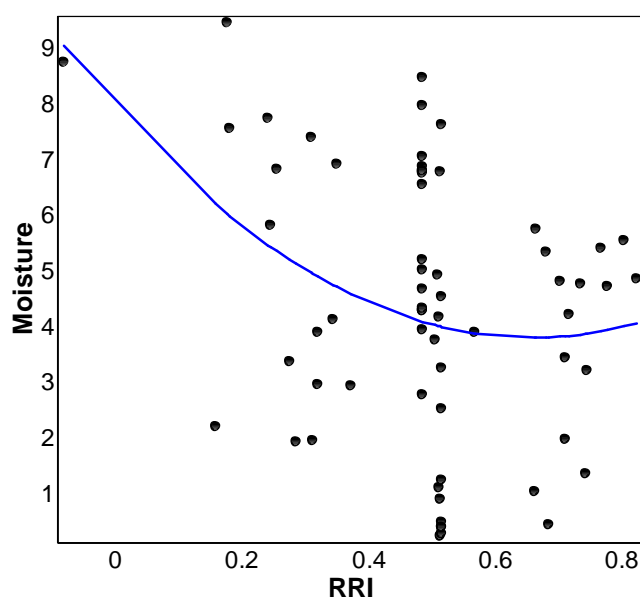


Figure 23 Percentage variation of moisture in soil, as function of Relative Radiation Index (RRI).

Lichens had a very strong (quadratic) relationship with RRI ($R^2 = 0.505$) and a fairly strong (negative quadratic) relation to moisture ($R^2 = 0.219$). Its vegetation cover counterpart, dwarf shrubs, had a similar but opposite response to RRI (negative quadratic) with $R^2 = 0.463$ and to moisture (quadratic) $R^2 = 0.219$ (Table 5, Fig. 24). There were no significant predictors for the cover of mosses.

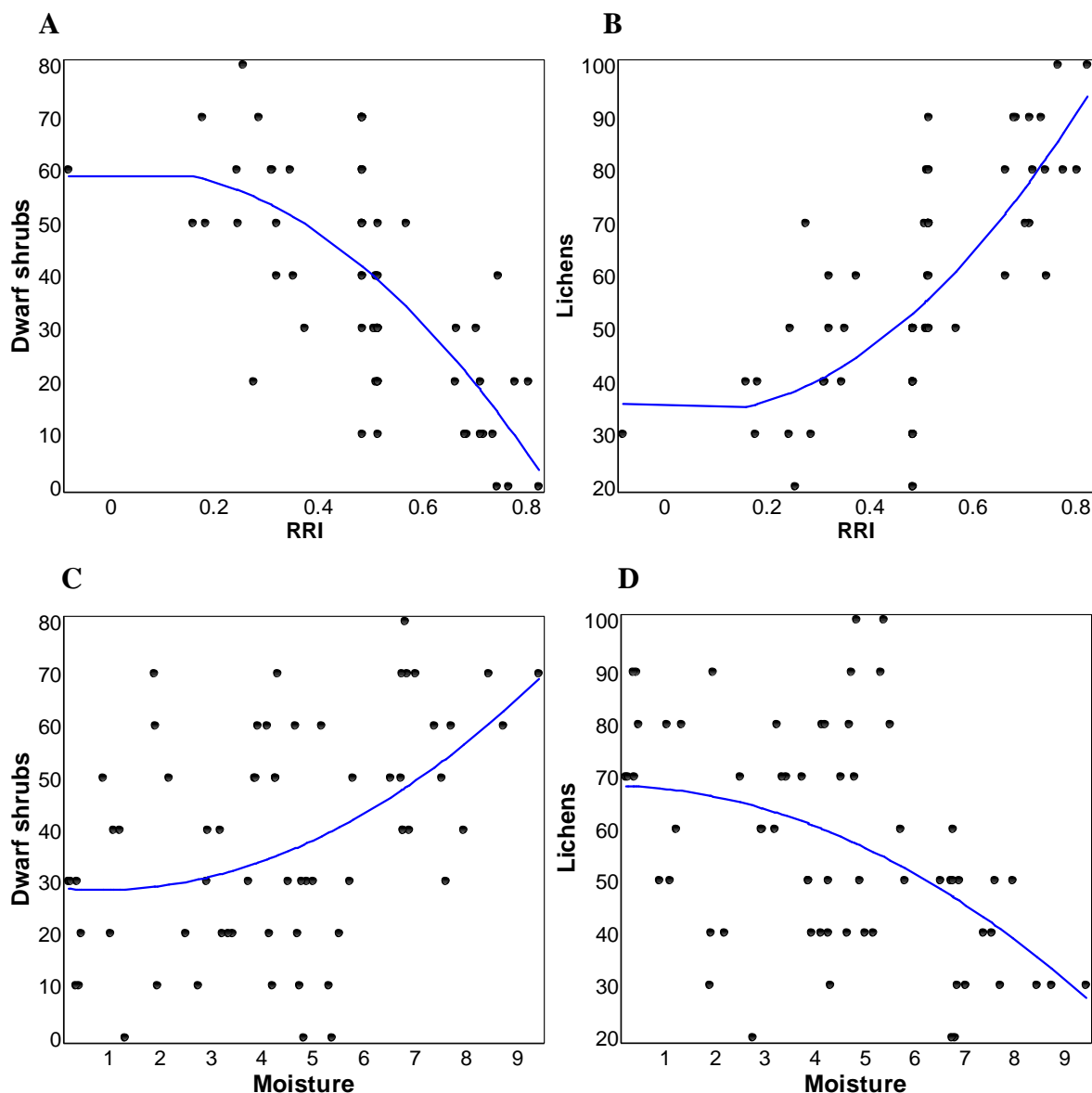


Figure 24 (A) Relationship between the relative radiation index and percentage cover of dwarf shrubs. (B) Relationship between the relative radiation index and percentage cover of lichens. (C) The variation of dwarf shrub cover percentage as a function of percentage soil moisture. (D) Variation of lichen cover percentage as a function of percentage soil moisture. For statistics see Table 5.

The total number of trees per plot had a fair relationship to several of the other predictors. It was especially explained by lichens ($R^2 = 0.192$: linear), dwarf shrubs ($R^2 = 0.173$: negative linear) and RRI ($R^2 = 0.167$: linear). Number of dead tree-stumps (cut stems) was explained by the same variables: lichens ($R^2 = 0.151$: linear), dwarf shrubs ($R^2 = 0.187$: negative quadratic) and RRI ($R^2 = 0.161$: linear). The biomass index was directly related to, and was therefore also significantly explained by number of trees ($R^2 = 0.769$: linear) and canopy cover ($R^2 = 0.55$: linear). It was also strongly explained by the radiation index ($R^2 = 0.307$: quadratic), and had a negative relationship with lichens ($R^2 = 0.218$: quadratic) and dwarf shrubs ($R^2 = 0.286$: linear) (Table 5).

Table 5 Regression results - selection of responsive explanatory variables (Res. Var.) as a possible function of other explanatory variables (Exp. var.).

Res. var.	Exp. var	Coeff.	Res -df	t	p (t)	(full model) R-squared	(full model) F	(full model) p (F)
Lichens	Moi * Moi	0.457	62	-4.174	<0.001	0.219	17.423	<0.001
	LOI	-6.744	62	-1.237	0.221	0.024	1.529	0.221
	RRI * RRI	90.478	62	7.947	<0.001	0.505	63.15	<0.001
D. shrubs	Moi * Moi	0.451	62	4.172	<0.001	0.219	17.409	<0.001
	LOI	4.776	62	0.881	0.382	0.012	0.777	0.382
	RRI * RRI	-85.55	62	-7.304	<0.001	0.463	53.353	<0.001
Moss	Moi	0.046	62	0.083	0.934	<0.001	0.007	0.934
	LOI	1.605	62	0.587	0.559	0.006	0.345	0.559
	RRI	-4.099	62	-0.542	0.59	0.005	0.294	0.59
Dead stumps	Lich	0.056	62	3.322	0.002	0.151	11.036	0.002
	Hea * Hea	<0.001	62	-3.778	<0.001	0.187	14.276	<0.001
	Sytrees^2	0.008	62	2.36	0.021	0.082	5.572	0.021
	Unctrees	0.747	62	2.516	0.015			
	Unctrees^2	-0.05	61	-2.473	0.016	0.095	3.188	0.048
	Trees	0.226	62	2.881	0.005	0.118	8.301	0.005
	Biomass	0.078	62	2.448	0.017			
	Biomass^2	<0.001	61	-1.879	0.065	0.157	5.68	0.005
	RRI	6.997	62	3.445	0.001	0.161	11.868	0.001
Trees	Lich	0.097	62	3.841	<0.001	0.192	14.757	<0.001
	Hea	-0.093	62	-3.607	<0.001	0.173	13.013	<0.001
	Moss	-0.018	62	-0.323	0.748	0.002	0.104	0.748
	DS	0.522	62	2.881	0.005	0.118	8.301	0.005
	Moi	-0.644	62	-2.766	0.007	0.11	7.653	0.007
	LOI	-0.216	62	-0.178	0.86	<.001	0.032	0.86
	RRI	10.849	62	3.529	<0.001	0.167	12.453	<0.001
Biomass	Sym * Sym	3.629	62	3.693	<0.001	0.18	13.636	<0.001
	CC	1.872	62	8.707	<0.001	0.55	75.818	<0.001
	Lich * Lich	0.009	62	4.155	<0.001	0.218	17.265	<0.001
	Hea	-1.315	62	-4.978	<0.001	0.286	24.785	<0.001
	Moss	0.773	62	1.258	0.213	0.025	1.582	0.213
	DS	5.509	62	2.742	0.008	0.108	7.521	0.008
	Trees	9.667	62	14.374	<0.001	0.769	206.615	<0.001
	Moi	-4.993	62	-1.887	0.064	0.054	3.56	0.064
	LOI	-6.641	62	-0.496	0.622	0.004	0.246	0.622
	RRI * RRI	171.432	62	5.235	<0.001	0.307	27.405	<0.001
Moi	RRI	-12.662	62	-2.212	0.031			
	RRI * RRI	9.611	61	1.586	0.118	0.347	4.185	0.02
LOI	RRI	-0.301	62	-0.862	0.392	0.012	0.744	0.392

Abbreviation explanation; refer Table 1

Regression of response variables

The variables which best explained the occurrence of *P. sylvestris* seedlings were radiation index ($R^2 = 0.335$), dwarf shrubs ($R^2 = 0.313$) and lichens ($R^2 = 0.309$) (Table 6). They all showed a unimodal curve of explanation (Fig. 25). This indicates that a moderate occurrence each of these three variables was optimal for seedlings. The seedlings were also fairly well explained by the symmetry-variable ($R^2 = 0.108$) with a negative quadratic curve. This means that number of seedlings decreases as the symmetry-variable goes up. Seedlings had a unimodal relationship with occurrence of adult *P. sylvestris* trees ($R^2 = 0.135$). A barely significant relation was found with canopy cover (unimodal). There was no significant relationship between seedlings and the biomass index (Table 6).

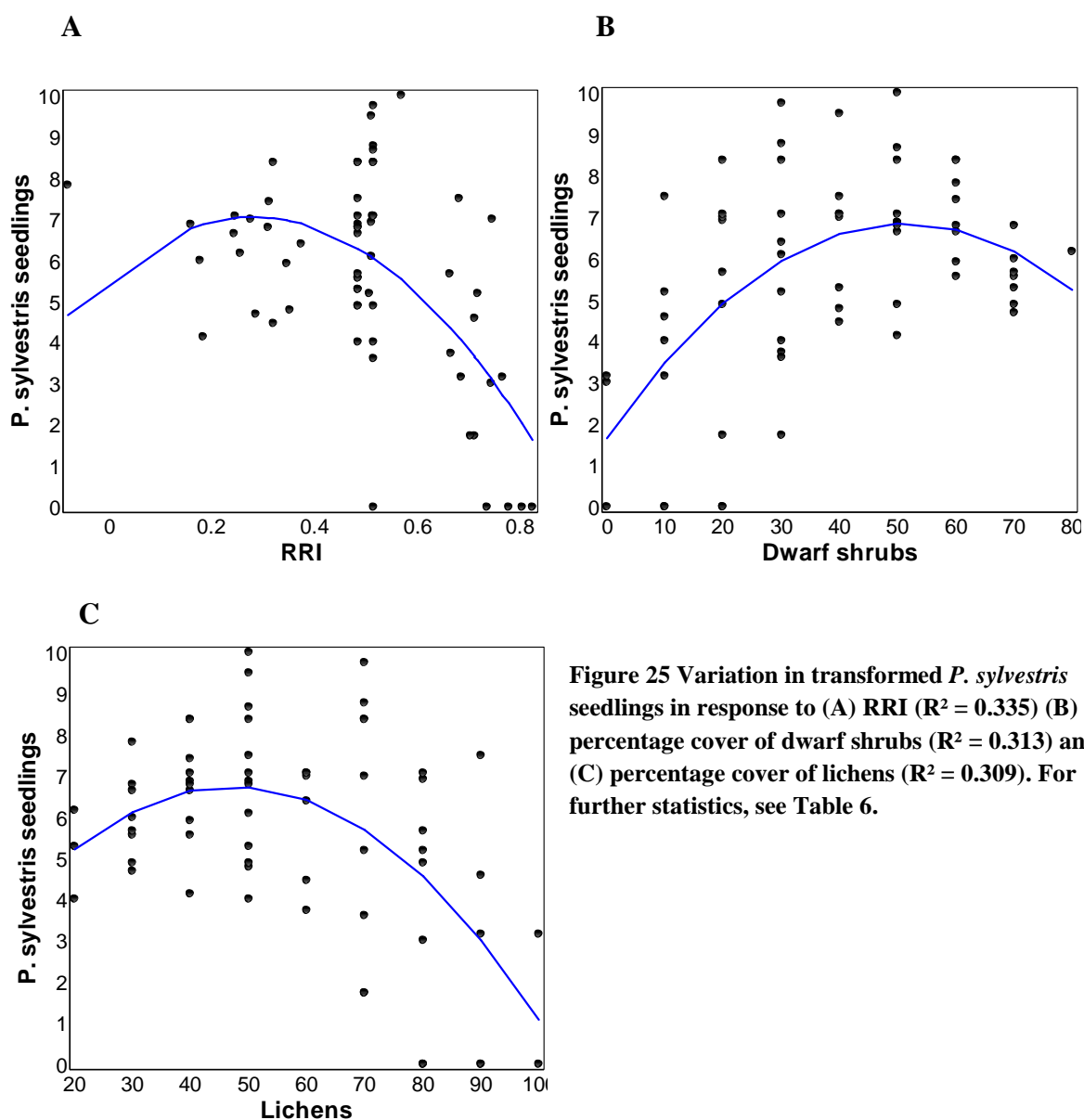


Figure 25 Variation in transformed *P. sylvestris* seedlings in response to (A) RRI ($R^2 = 0.335$) (B) percentage cover of dwarf shrubs ($R^2 = 0.313$) and (C) percentage cover of lichens ($R^2 = 0.309$). For further statistics, see Table 6.

Saplings of *P. sylvestris* had a relatively strong relationship with the majority of the predictor variables. The strongest connections were with biomass index ($R^2 = 0.431$: negative linear), RRI ($R^2 = 0.395$: negative quadratic) and the mutually exclusive dwarf shrub ($R^2 = 0.426$: linear) and lichens ($R^2 = 0.365$: negative linear). A negative, linear relationship was also found with the total number of trees per plot ($R^2 = 0.355$). Unimodal responses were found with respect to the symmetry-variable ($R^2 = 0.118$), adult *P. sylvestris* ($R^2 = 0.254$), adult *P. uncinata* (bimodal), $R^2 = 0.21$) and vaguely on loss on ignition ($R^2 = 0.11$) (Table 6).

P. uncinata recruits, seedlings and saplings, had almost the same response to the predictors. They both had a strong linear relationship to the occurrence of *P. uncinata* trees (seedlings: $R^2 = 0.218$, saplings: $R^2 = 0.251$). Seedlings were also very well explained by the cover of lichens ($R^2 = 0.363$: quadratic), but this variable did not explain the number of saplings very well ($R^2 = 0.193$: linear). To a certain extent they are also explained by the radiation index, which both showed linear relationships to seedlings ($R^2 = 0.191$) and saplings ($R^2 = 0.085$) (Table 7).



Figure 26 Seedling of presumably *P. sylvestris*, on a bed of moss and proximity of heather. Photo: Ole Reidar Vetaas.

Table 6 Regression results - *P. sylvestris* recruits (seedlings & saplings)(Res. Var.) as a possible function of various explanatory variables (Exp. var.).

Resp. var.	Exp. var.	Coeff.	df	t	p (t)	(full model) R-squared	(full model) F	(full model) p (F)
<i>P. sylvestris</i> seedlings	Sym * Sym	-0.133	62	-2.743	0.008	0.108	7.525	0.008
	CC * CC	<0.001	62	-2.063	0.043	0.064	4.255	0.043
	Lich	0.194	62	2.828	0.006			
	Lich * Lich	0.002	61	-3.569	<0.001	0.309	13.623	<0.001
	Hea	0.201	62	4.256	<0.001			
	Hea * Hea	-0.002	61	-3.29	0.002	0.313	13.907	<0.001
	Moss	-0.008	62	-0.274	0.785	0.001	0.075	0.785
	DS	0.045	62	0.443	0.659	0.003	0.196	0.659
	Sytrees	0.699	62	3.071	0.003			
	Sytrees ²	-0.028	61	-2.895	0.005	0.135	4.758	0.012
	Unctrees	-0.545	62	-2.353	0.22			
	Unctrees ²	0.027	61	1.73	0.089	0.128	4.459	0.016
	Trees	-0.072	62	-1.089	0.28	0.019	1.186	0.28
	Moi	-0.058	62	-0.449	0.655	0.003	0.202	0.655
	LOI	0.117	62	0.184	0.854	<0.001	0.034	0.854
	RRI	10.275	62	2.031	0.047			
RRI * RRI	-18.329	61	-3.421	0.001	0.335	15.334	<0.001	
Biomass ²	<0.001	62	-1.89	0.064	0.054	3.572	0.063	
<i>P. sylvestris</i> saplings	Sym	1.427	62	1.862	0.067			
	Sym * Sym	-0.291	61	-2.257	0.028	0.118	4.093	0.021
	CC	-0.024	62	-3.201	0.002	0.142	10.247	0.002
	Lich	-0.037	62	-5.974	<0.001	0.365	35.695	<0.001
	Hea	0.04	62	6.777	<0.001	0.426	45.934	<0.001
	Moss	-0.009	62	-0.61	0.544	0.006	0.372	0.544
	DS	-0.401	62	-2.903	0.005			
	DS * DS	0.029	61	2.415	0.019	0.13	4.539	0.015
	Sytrees	0.411	62	3.69	<0.001			
	Sytrees ²	0.02	61	-4.247	<0.001	0.254	10.369	<0.001
	Unctrees	-0.302	62	-2.605	0.012			
	Unctrees ²	0.013	61	1.618	0.111	0.21	8.111	<0.001
	Trees	-0.164	62	-5.838	<0.001	0.355	34.077	<0.001
	Moi * Moi	0.015	62	1.992	0.051	0.06	3.97	0.051
	Loi	3.732	62	2.711	0.009			
	Loi * Loi	-1.014	61	-2.529	0.014	0.11	3.785	0.028
RRI * RRI	-4.854	62	-6.361	<0.001	0.395	40.458	<0.001	
Biomass	-0.016	62	-6.853	<0.001	0.431	46.964	<0.001	

Abbreviation explanation; refer Table 1

Table 7 Regression results - *P. uncinata* recruits (seedlings & saplings) (Res. var.) as a possible function of various explanatory variables (Exp. var.).

Resp. var.	Exp. Var.	Coeff.	df	t	p (t)	(full model) R-squared	(full model) F	(full model) p (F)
<i>P. uncinata</i> seedlings	Sym	0.24	62	1.86	0.068	0.053	3.459	0.068
	CC * CC	<0.001	62	2.753	0.008	0.109	7.58	0.008
	Lich * Lich	<0.001	62	5.941	<0.001	0.363	35.294	<0.001
	Hea	<0.001	62	-3.943	0.001	0.2	15.547	<0.001
	Moss	-0.016	62	-1.244	0.218	0.024	1.546	0.218
	DS	0.057	62	1.31	0.195	0.027	1.716	0.195
	Sytrees	-0.02	62	-0.742	0.461	0.009	0.55	0.461
	Unctrees	0.112	62	4.152	<0.001	0.218	17.243	<0.001
	Trees	0.078	62	2.891	0.005	0.119	8.358	0.005
	Moi	-0.112	62	-2.079	0.042	0.065	4.323	0.042
	LOI	-0.456	62	-1.689	0.096	0.044	2.852	0.096
	RRI	2.624	62	3.821	<0.001	0.191	14.599	<0.001
Biomass	<0.001	62	3.296	0.002	0.149	10.866	0.002	
<i>P. uncinata</i> saplings	Sym	0.067	62	0.593	0.555	0.006	0.352	0.555
	CC	<0.001	62	0.049	0.961	<0.001	0.002	0.961
	Lich	0.019	62	3.851	<0.001	0.193	14.823	<0.001
	Hea	-0.018	62	-3.638	<0.001	0.176	13.236	<0.001
	Moss	-0.005	62	-0.47	0.64	0.004	0.221	0.64
	DS	0.004	62	0.111	0.912	<0.001	0.012	0.912
	Sytrees	-0.261	62	-3.119	0.003			
	Sytrees ²	0.01	61	2.724	0.008	0.153	5.523	0.006
	Unctrees	0.103	62	4.553	<0.001	0.251	20.733	<0.001
	Trees	0.046	62	1.924	0.059	0.056	3.701	0.059
	Moi	-0.114	62	-2.498	0.015	0.091	6.242	0.015
	LOI	-0.237	62	-1.012	0.316	0.016	1.023	0.316
	RRI	1.5	62	2.399	0.019	0.085	5.757	0.019
Biomass	0.003	62	1.526	0.132	0.036	2.328	0.132	

Abbreviation explanation; refer Table 1

Multiple regression models

The multiple regression aims to build explanatory models by means of the previous regressions analyses, and include at least two predictors. Here I also used the transformed response variables. The model that best explained the occurrence of *P. sylvestris* seedlings included radiation index and cover of dwarf shrubs. The radiation index had a negative quadratic response and dwarf shrubs had a unimodal response. The model has an R²-value of 0.368. It appeared that a few of the variables gained significance when used in a multiple regression. For instance, moisture did not have any statistically significant relationship with *P. sylvestris* seedlings when used as a sole predictor in regression analysis, but when included in a multiple regression, it had the best additional explanation to dwarf shrubs. This was on the non-transformed data and is not included in these results. The model for *P. sylvestris* saplings contained biomass (negative linear) and the radiation index (negative quadratic). This model has an R²-value of 0.532. Both models for *P. uncinata* recruits contained lichens and adult *P. uncinata* trees. Seedlings had a linear response to both and the model had an R²-value of 0.386. Saplings on the other hand, had a linear response to adult *P. uncinata* trees and a unimodal response to lichens. R²-value is 0.347 (Table 8). The variation partitioning and degree of explanation by the multiple regression results are depicted in Figs. 27, 28, 29, and 30.

Table 8 Multiple regression results - *P. sylvestris* and *P. uncinata* recruits (Res. var.) as a function of the two best explanatory variables (Exp. var.).

Res. var.	Exp. var.	Coeff.	df	t	p (t)	(full model) R-squared	(full model) F	(full model) p (F)
<i>P. sylvestris</i> seedlings	RRI * RRI	-4.934	62	-2.292	0.025			
	Hea	0.143	61	2.736	0.008			
	Hea * Hea	-0.002	60	-2.568	0.013	0.368	11.67	<0.001
<i>P. sylvestris</i> saplings	Biomass	-0.011	62	-4.232	<0.001			
	RRI * RRI	-2.951	61	-3.633	<0.001	0.532	34.7	<0.001
<i>P. uncinata</i> seedlings	Lich	0.023	62	4.083	<0.001			
	Unctrees	0.065	61	2.422	0.018	0.386	19.138	<0.001
<i>P. uncinata</i> saplings	Unctrees	0.088	62	3.617	<0.001			
	Lich	0.056	61	2.235	0.029			
	Lich * Lich	<0.001	60	-1.804	0.076	0.347	10.628	<0.001

Abbreviation explanation; refer Table 1

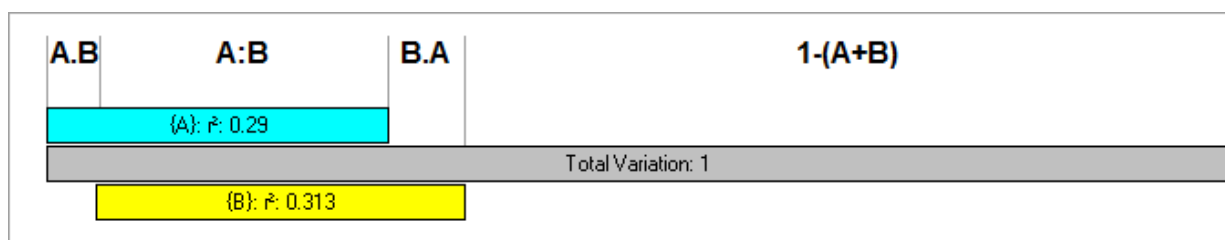


Figure 27 Variation partitioning of *P. sylvestris* seedling multiple regression results: Predictor A: RRI * RRI, Predictor B: D. shrub + D. shrub². Total explained by A = 0.29, Total explained by B=0.313, total explained by A+B=0.368, Unexplained variation = 0.632. Set theory explanation: A.B = variation explained by A, but not B, B.A = variation explained by B, but not A, A:B = variation explained by both A and B.

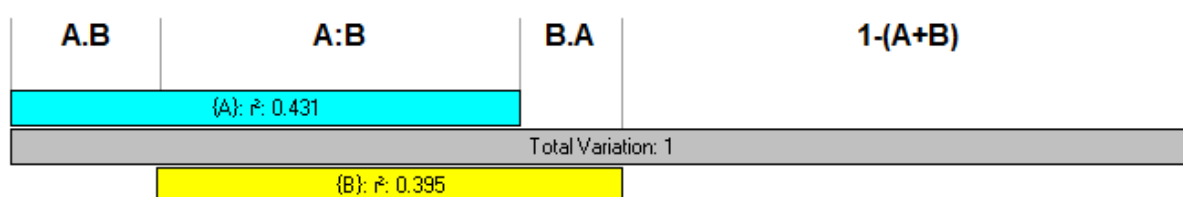


Figure 28 Variation partitioning of *P. sylvestris* saplings multiple regression results: Predictor A: Biomass, Predictor B: RRI * RRI. Total explained by A = 0.431, Total explained by B=0.395, total explained by A+B =0.532, Unexplained variation = 0.468. Set theory explanation; refer Fig. 27.

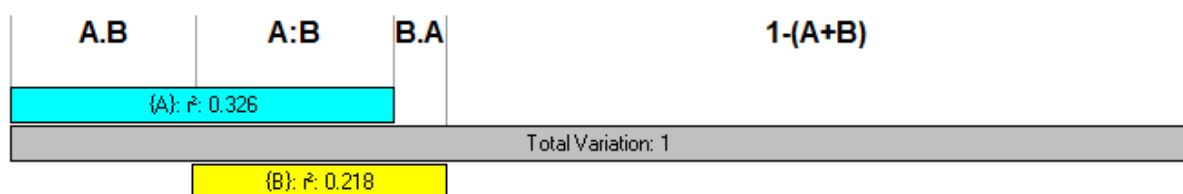


Figure 29 Variation partitioning of *P. uncinata* seedlings multiple regression results: Predictor A: Lichens, Predictor B: Adult *P. uncinata*. Total explained by A = 0.326, Total explained by B=0.218, total explained by A+B=0.386, Unexplained variation = 0.614. Set theory explanation; refer Fig. 27.

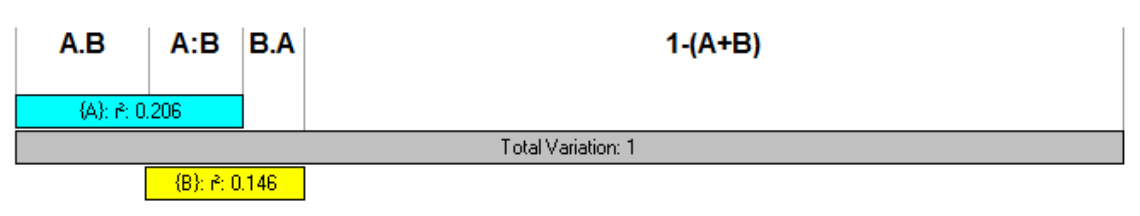


Figure 30 Variation partitioning of *P. uncinata* saplings multiple regression results: Predictor A: Adult *P. uncinata*, Predictor B: Lichens + Lichens². Total explained by A = 0.251, Total explained by B=0.205, total explained by A+B=0.347, Unexplained variation = 0.653. Set theory explanation; refer Fig. 27.

Regression diagnostics on the residuals from the multiple regressions

Distribution of residuals

Residuals after the multiple regressions of *P. sylvestris* recruits were both normally distributed. Residuals of *P. uncinata* recruits, however, were positively skewed. (Figs. 31, 32).

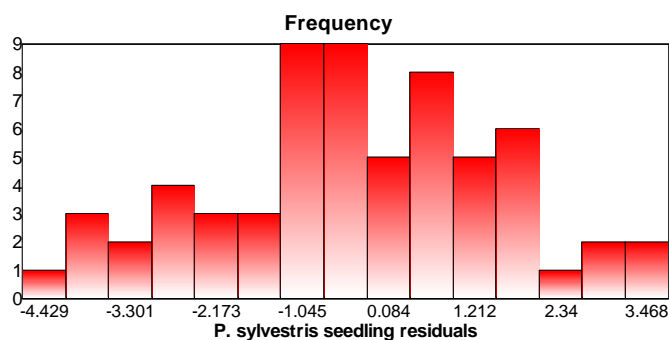


Figure 31 Example of normally distributed residuals of *P. sylvestris* seedlings after multiple regression.

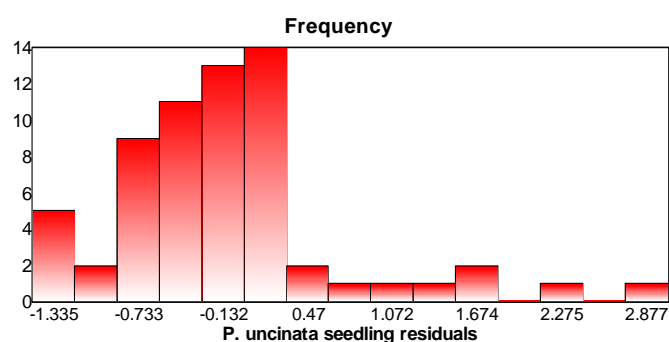


Figure 32 Example of skewed distribution residuals of *P. uncinata* seedlings after multiple regression.

Moran's I

Autocorrelation analysis by means of Moran's I was done on the transformed response variables, as well as the residuals from the previous two-predictor, multiple regression models. By doing this, we could see whether or not the residuals of the two-predictor model were autocorrelated, which may indicate whether there are some important spatially structured explanatory variables missing in the model.

The autocorrelation analysis for *P. sylvestris* seedlings indicated that they were originally not significantly autocorrelated, but after performing the multiple regression, the residuals became autocorrelated. I do not have a good explanation for this. The saplings on the other hand, were highly autocorrelated in the first distance class, meaning they were more alike than expected by chance. They also had an equally significant negative autocorrelation in the fourth distance class. The residuals from the two-predictor model showed no significant autocorrelation. The seedlings

of *P. uncinata* showed high autocorrelation in the first and seventh distance classes and a negative autocorrelation in the third, fourth and sixth distance classes. Also here, the regression residuals were completely free of autocorrelation. The saplings had a similar response with significant autocorrelation in the first and seventh, and a negative autocorrelation in the fourth distance classes. The residuals had no autocorrelation (Fig. 33).

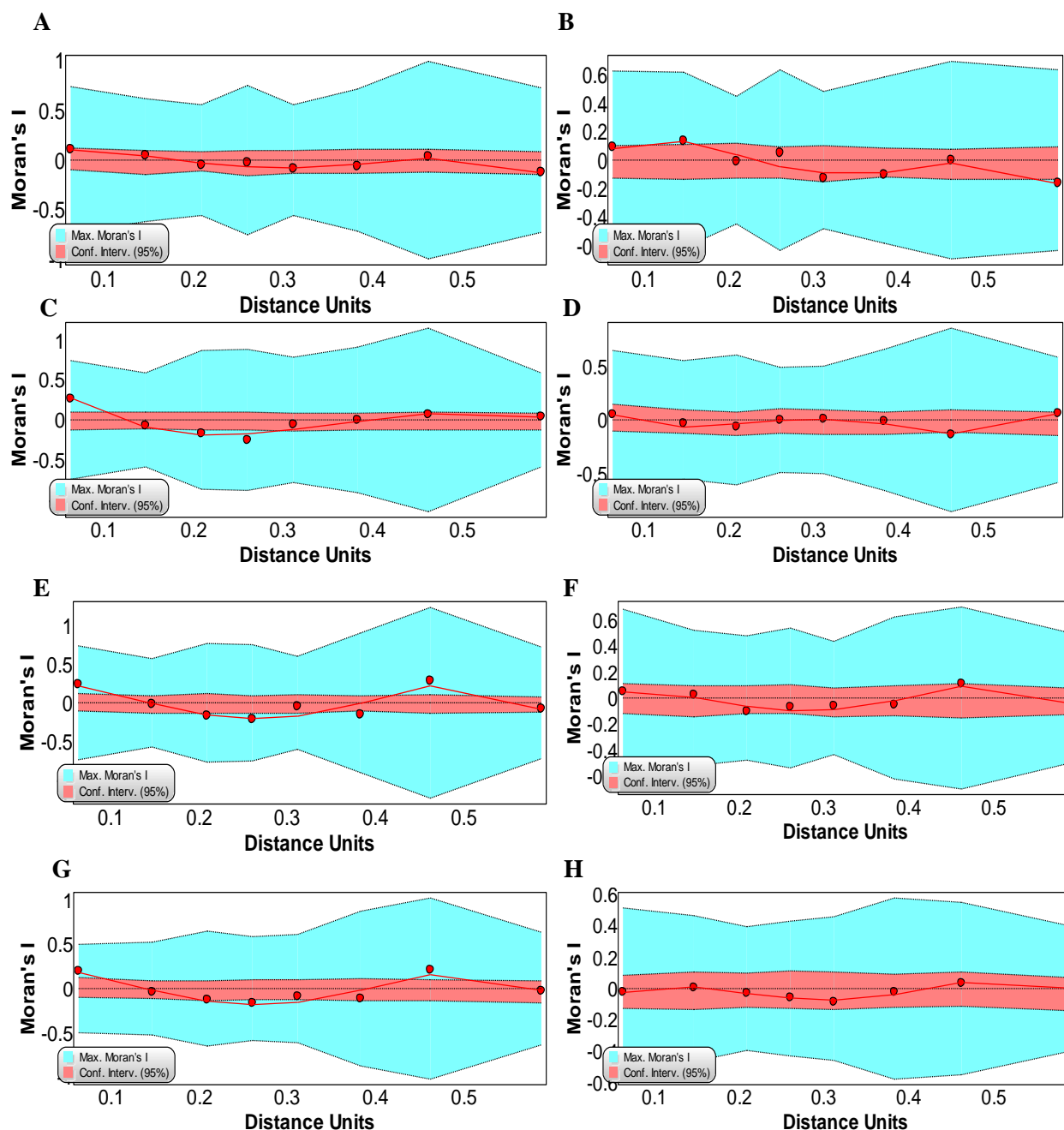


Figure 33 Moran's I (spatial autocorrelation) on (A) *P. sylvestris* seedlings (B) multiple regression residuals of *P. sylvestris* seedlings (C) *P. sylvestris* saplings (D) *P. sylvestris* saplings multi. reg. residuals (E) *P. uncinata* seedlings (F) *P. uncinata* seedlings multi. reg. residuals (G) *P. uncinata* saplings (H) *P. uncinata* saplings multi. reg. residuals.

Discussion

Regeneration of the two pines showed a distinct difference in magnitude and spatial distribution. The main regeneration, seedlings of *P. sylvestris*, had a strong relationship with dwarf shrubs (heather) and lichens, where both life forms predicted a unimodal response of number of seedlings. These two types of ground vegetation showed to be significantly explained by the environmental variables (RRI and soil moisture). These relationships will now be further discussed, along with the research questions and associated hypotheses given in the conceptual framework. I will start with the initial question concerning if the forest regenerates, and to what extent it was planted.

Planting vs. regeneration

There have been a couple of preliminary surveys before the actual fieldwork. The first survey was in wintertime, and it appeared that there was little to no observable regeneration, which would be an understandable observation due to the young age of the forest (36 years), and the fact that *P. sylvestris* might not be able to reach fertility before 30–60 years of age (Øyen 2006). At this time, it was not apparent if the trees had any structure that might resemble planting. There was large variation in the size of the trees, and it looked as if they had germinated rather randomly in the timeframe from the forest fire until now. However, during the second survey, a number of seedlings of various sizes were observed, and a structure of rows and columns that resembled a planting regime could be discerned. At first, this was only apparent on the south-facing slopes and ridges, but during the course of fieldwork, it became clear that these rows and columns were present in all topographic units in the entire study area. The reason why it only looked planted on the south-facing slopes is possibly because both the number of trees and the biomass index had the highest values here. The trees also looked more identical concerning height, shape and DBH. The dendrochronology showed that the majority of trees were in fact 25–27 years old (both species). The first assumption, that the different sizes also imply a variety in age-structure, was thus rejected by the dendrochronological data: 25 year old *P. sylvestris* could vary from 4 cm to 19 cm DBH. Adult *P. uncinata* also had a relatively wide DBH-range of 5 to 19 cm. There were a few trees of older age which are larger, but they are not in the same planted structure as the rest.

It is plausible to suggest that the entire forest was planted 25 to 27 years ago in the standard rows and columns that we can observe today (Fig. 34). The fact that the date varies by 3 years could be caused by errors in the dendrochronology from counting the year rings, or that the planting of trees was conducted over 3 years, e.g. by replanting the spots where the seedlings did not survive.



Figure 34 *P. sylvestris* planted in rows and columns on one of the ridges. Ground vegetations are lichens and patches of moss. Photo: Ole Reidar Vetaas.

The single *P. uncinata* with an age of 19 years is currently unexplained. The few, larger, scattered *P. sylvestris* trees in the area probably regenerated naturally after the fire, but before the planting. Scarce natural regeneration of *P. sylvestris* after a fire is documented e.g. in Spain (Vilá-Cabrera et al. 2012). The largest individual I found, which had a tree-ring age of 55 years, must have been one of the few individuals to have survived the forest fire. It is difficult to give a clear explanation for why *P. uncinata* was only planted on the ridges and south-facing slopes, and in the western

part of the reserve. However, *P. uncinata* is well known to be used for reforestation, especially where soil erosion is an issue, e.g. sand dunes (Øyen 1999). One may therefore speculate that the reforestation regime considered the ridges and south-facing slopes to be the most exposed areas for wind stress. It is questionable if it was ecologically sound to introduce an alien species into an area where *P. sylvestris* seems to be the only native pine.

Concerning the question about regeneration of the forest, the spatial distribution of seedlings indicated that their parent trees are within the study area. If the parent trees were in adjacent plantations one would have expected more seedlings close to the border of the reserve. On average, there were 3.84 seedlings per adult *P. sylvestris* and 0.72 seedlings per adult *P. uncinata*, giving a good image of how well the native species regenerates compared to the alien species. These numbers, however, cannot be said to be perfectly reliable, because of the challenge to separate the two species at an early stage. The seedlings were rather similar, and the clear difference of young individuals is found on the cones (Lid 2005). My initial assumption was that all saplings would be classified as recruits, and an indicator of regeneration. A sapling was defined to be trees higher than 1.3 m, but with a DBH of <5 cm. However, dendrochronological data showed that a measured “sapling” with a DBH of 4 cm was actually a 25-year-old planted individual. It is therefore possible that most of the recorded saplings, or even seedlings (Fig. 35), are actually just small, adult trees (I will not exclude the fact that a few might actually be recruits). The interpretation will therefore be rather different from being an indicator of vital regeneration, since it may now be an indicator of poor growing conditions. If the saplings are only stunted, adult trees, it explains why they showed a strong relationship to the majority of the predictors in the regression analysis, especially the fact that they were negatively correlated with the data for biomass and number of trees per plot, i.e. because a small number of adult trees meant that the planted individuals had not reached the size of what I defined as an adult tree. This also explains why the south-facing slopes were the only topographic unit which seemed to have been planted. If most of the saplings were in fact “small” adult trees, the rows and columns in the plots containing these would appear more asymmetrical. The data of *P. sylvestris* saplings had a significant relationship with 12 of 13 explanatory variables (Table 7). This shows that the saplings are rather dubious when it comes to ecological interpretations, whereas number of seedlings is a more direct response to estimated ecological factors in the area, and provides a more reliable interpretation on how well the forest manages to regenerate itself.



Figure 35 Small, stunted adult *P. uncinata* (see cone) which was by definition classified as a recruit (seedling).

Because most of the adult trees seem to have been planted, one may claim that the initial hypothesis (H1), all trees are planted, was partly supported. Natural regeneration immediately after the forest fire has resulted in a couple of individuals scattered in the study area, but the forest present today is mainly a result of extensive planting. I hypothesised (H2) that the planted trees are producing recruits, and this is fully supported by the results when we look at the extensive spread of seedlings (mostly *P. sylvestris*). Saplings, on the other hand, cannot be regarded robustly as recruits. Although I cannot exclude the fact that a few saplings might actually be the offspring of the planted trees, the age of the planted trees (25–27 years), suggests that it is unlikely that they would have been able to produce offspring such that they appear as saplings today. The third hypothesis (H3), that the forest present today has undergone natural succession with no planting, was therefore completely falsified.

Sand dunes and radiation

I hypothesised that the topographical units would create differences in incoming solar radiation, and thereby influence vegetation and the on-going regeneration. The angle and orientation of a slope, and the resulting variation of incoming radiation, plays a key role in the complexity of varying vegetation cover. This is due to the effect it has on the general energy-distribution, as well as its effect on temperature and soil moisture. These are both factors which widely affect species composition and growth behaviour (Holland and Steyne 1975; Castán & Vetaas 2003). The south-facing slopes received relatively much more solar radiation (0.718) than the north-facing slopes (0.255) for example, although they are just a few metres apart, i.e. over the crest (Fig 36).

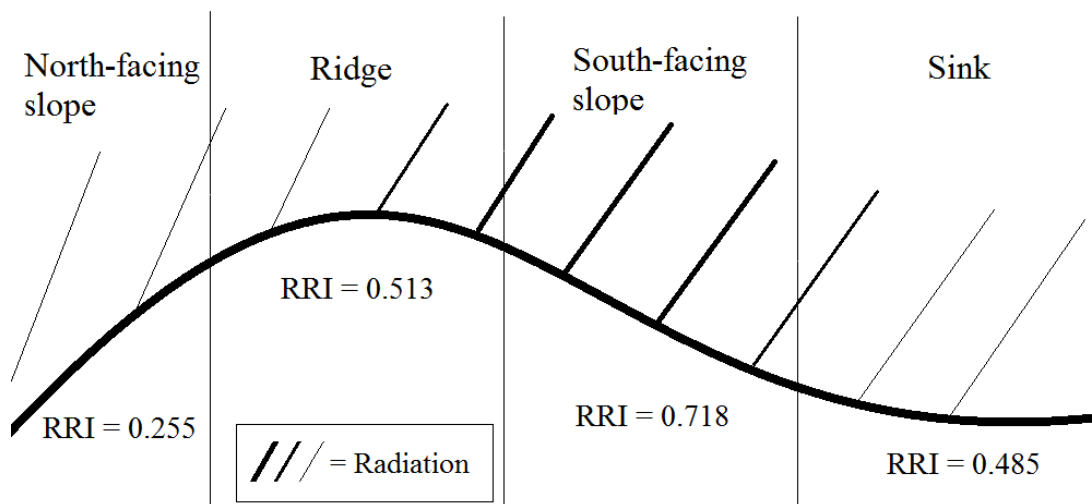


Figure 36 Conceptual cross-section of sand dune with varying incoming radiation (with RRI-values). Thickness of line depict amount of accumulated radiation.

This variation in topography clearly had an effect on the ground vegetation in the area, which can be seen in photos (Figs. 9, 10, 20, and 21). There was a much denser ericaceous understory in the slacks and on the north-facing slopes of the dunes than on the ridges and south-facing slopes. On the south-facing slopes a continuous blanket of lichens was more common. This was also confirmed by the descriptive statistics (Appendix I, II, III, and IV). However, mosaics of both types of ground vegetation were also observed, and seemed to appear on any of the topographic units.

The regression analysis showed a clear and direct effect by RRI on number of *P. sylvestris* seedlings. RRI was the explanatory variable that explained most of the variation in number of seedlings, and was also included in the multiple regression. The response was close to unimodal,

but is better described as a negative quadratic curve (Fig. 25A), meaning that a higher degree of radiation might negatively impact the establishment or survival of the seedlings. This is, in a way, contrary to my initial assumptions from the conceptual framework. Mason (2004) wrote that *P. sylvestris* is generally light-demanding, but Ameztegui (2011) wrote that light-demand is rather a question of survivability than actual growth rate. The negative effect of RRI on *P. sylvestris* seedlings is of course somewhat biased due to the planting of *P. uncinata* on the south-facing slopes or ridges, where RRI-values are highest. The plots on these topographic features with no *P. sylvestris* seedlings affected the regression, and made it look like RRI had a negative effect on number of seedlings. In those plots there is an absence of *P. sylvestris* parent trees due to the exclusive presence of mountain pine. The lack of *P. sylvestris* seedlings is therefore not due to high radiation, but more an effect of a restricted area where the seedlings potentially may have established. However, south-facing slopes actually had a higher total number of adult *P. sylvestris* than the slacks, but only a total of 334 seedlings compared with a total of 643 seedlings in the slacks, showing that poor regeneration on south-facing slopes was apparent also when ignoring plots where *P. sylvestris* was absent. Seedlings of *P. uncinata* had a strong, positive relationship to RRI, but this may be due to the fact that adult *P. uncinata* trees were only planted on ridges and south-facing slopes, with high RRI. However, more radiation meant more seedlings of *P. uncinata* also when the plots with absent values were not included in the analysis.

The next hypothesis under this research question was if the changes in radiation affect the ground vegetation cover. The results from the regression analysis showed that the radiation index explained well both percentage cover of lichens and dwarf shrubs (Table 5). Increasing radiation is related to more lichens, and less dwarf shrubs. A close relationship between variation in vegetation, here the two types of ground vegetation, and the induced radiation gradient, has often been documented at a crude spatial scale, for example in the Himalaya (Vetaas 2000), the Middle East (Boyko 1947), South Africa (Granger & Schulze 1977), the Iberian Peninsula (Dargie 1984, 1987) and Australia (Kirkpatrick et al. 1988). At Starmoen, the uniquely shaped sand dunes provided an opportunity to see the effect of varying degree of incoming radiation at a relatively small spatial scale. The question at hand is whether it is radiation, or another ecological variable that has a causal effect on the ground cover. Heather is not known to be greatly affected by exposure to direct sunlight but the conceptual framework suggests that it needs a large amount of moisture to thrive and reproduce. This will be discussed further in a later section.

The radiation index explained, to a large degree, the biomass index in the regression. This, taken with the light-demanding nature of *P. sylvestris*, makes it plausible to suggest that the adult trees in the forest experience the most optimal conditions on the south-facing slopes, followed by the ridges, slacks, and lastly, north-facing slopes. Such a suggestion is supported by the biomass index, number of adult *P. sylvestris* and the symmetry value having their highest values on the south-facing slopes. Several studies document that the amount of biomass in any forest stand is linearly related to intercepted radiation (Bergh et al. 2005, Monteith 1977, Will et al. 2001).

Without actually testing it, I will also assume that the radiation index positively affects melting of snow, making the optimal period of growth longer for trees located on the south-facing slopes and ridges. This was tested by Gjærevoll (1949), where plants in mountainous areas with different placements in the landscape varied in their length of growing season because the overlying snow melted at different speed.

I hypothesised that increased radiation is either positive (H4) or negative (H5) for regeneration of recruits. Neither of them can be falsified, since radiation appeared to be negative for regeneration of *P. sylvestris* and positive for regeneration of *P. uncinata* (seedlings). However, the small number of *P. uncinata* seedlings does not make this a very robust statement. It is important to note that this is only the direct translation of the covariance in the data, and does not necessarily mean that the radiation affects the survival of seedlings. The hypotheses are therefore not rejected, although they are not very valid statements.

H6 (radiation affects the ground cover) comes under the same category as H4 and H5, with it being indirectly verified. There is a very strong relationship, but it does not necessarily mean that it is an actual causal relationship.

Abiotic and biotic environmental factors

The operational environmental factors that presumably might influence regeneration are soil-moisture and light, expressed indirectly by canopy cover and density of trees. RRI is a consistent, continuous and indirect variable, whereas moisture is a direct factor on the forest's ecological system. There was a strong significant relationship between RRI and %-moisture in the soil, as seen in the regression results. The relationship between these two can also be said to be rather logical. More radiation means more evaporation, thus less soil moisture (Woodward 1987, Castán & Vetaas 2003). From this, it follows that there should have been more moisture on the north side of the slope than in the slacks, and less moisture on the south-facing slopes than on the ridges.

This, however, was not the case, but other factors are likely to be of importance. Higher moisture in the slacks might be a result of drainage from higher to lower elevations, and both the slacks and the shallow-angled south-facing slopes are closer to the level of the underground water-table than the steeper north-facing slopes and ridges. The dryness of the south-facing slopes and ridges may also be influenced by the water-storing abilities of lichens (Porter 1929), making it harder for precipitation to reach the soil.

I hypothesised (H7) that increased radiation means decreased soil moisture, and this is, in my opinion, a verified hypothesis. I base this on the regression analysis which showed a significant relationship between soil moisture and radiation index. By looking at the trends in the basic statistics, one can also see how these two variables co-vary. The final argument for this is that the relationship is highly logical, where more incoming sunlight should mean more evaporation.

Both types of ground vegetation cover (lichens and dwarf shrubs) had strong, but contrary, relationships with amount of soil moisture, as seen in the regression analysis. This means that increasing soil moisture is associated with more ericaceous dwarf shrubs, while less moisture is associated with more lichens. Fægri (1970) writes that heather needs large amounts of moisture to thrive and reproduce. Haaland (2002) also writes that heather's evergreen leaves help the plant to keep moisture during sunny and dry periods. From these statements, one may imagine that the areas which are dominated by dwarf shrubs (heather) are located in habitats with sufficient moisture. Even though it tolerates periods of drought and high radiation, it does not seem to grow in the most sun-exposed parts in the area. That there were areas which were generally dominated by lichens does not necessarily mean that they were the most favourable place for this life form, but that the absence of heather allows it to grow there.

Pinus sylvestris is drought-tolerant, but it is known that the seedlings require a certain amount of moisture to be able to germinate (Oleskog 2000). Surprisingly, the results of the regression analysis did not depict any type of relationship between *P. sylvestris* seedlings and soil moisture. *P. uncinata* seedlings on the other hand, had a significant negative relationship with degree of moisture, meaning that less moisture was positive for regeneration. The latter is biased by the fact that adult *P. uncinata* trees were only planted where there is also the least recorded soil moisture (south-facing hills and ridges). Since *P. sylvestris* seedlings were least commonly found on the south-facing slopes, I thought that this might be due to restricted access to moisture, but, the largest number of seedlings on average was found on the ridges, where there is least access to

moisture. The relationship between moisture and establishment by *P. sylvestris* seedlings has been documented in Mongolia by Dulamsuren et al. (2013), where the emergence of seedlings was shown to be directly limited to access to soil moisture. Mong & Vetaas (2006) also show that pine in the Himalaya has a clear response to moisture, with the majority of seedlings occurring at intermediate or high amounts of soil moisture. Ellenberg et al. (1988), on the other hand, claimed that *P. sylvestris* thrives in either low or high amounts of moisture. Why I did not find this relationship in my area is debateable, but it might mean that there is in fact enough moisture everywhere in the area for *P. sylvestris* seedlings to germinate. So there are probably other variables, and not moisture, which are the limiting factors. Another explanation is that the sampling design did not allow valid recording of the moisture data. With increasing size of the plot, it becomes increasingly difficult to record a value which is representative of the theoretical mean soil moisture of the plot (Reed et al. 1993).

Hypothesis H8 claiming that moisture had an effect on regeneration was not verified, because the null hypothesis in the numerical analysis was not rejected.

Access to sunlight is crucial for the survival of the light-demanding *P. sylvestris*. The variable for incoming radiation does not take into consideration that there is a canopy that might block incoming sunlight from reaching the ground cover and seedlings. The regression indicated that canopy cover had an influence on number of *P. sylvestris* seedlings, with greater canopy cover resulting in fewer seedlings. This fits well with the statements about *P. sylvestris* needing strong sunlight to germinate and survive. An area with a high density of adult trees, and thus a high degree of canopy cover, will not be optimal for regeneration and establishment of new recruits. *Pinus uncinata* seedlings showed the complete opposite reaction, with greater cover of the canopy resulting in higher regeneration. The reason for this might be that the data were less reliable due to the small number of individuals. It might also be because a higher degree of canopy cover also means greater seed production, as each adult *P. uncinata* does not generally produce many offspring.

The regression results depicted that seedlings of *P. Sylvestris* had a significant, unimodal response to density of adult trees of the same species (adult individuals per plot). This means that few or many adult trees correspond to low numbers of seedlings, whereas an intermediate number of trees correspond to a maximum number of seedlings. Hence one may infer that optimal seed production is found where there are a fair amount of adult trees (10–12 individuals per plot), but

beyond this, the density of trees might negatively affect regeneration (probably via the light-deflecting canopy cover). Vickers & Palmer (2000) studied the effect of canopy cover on regeneration of *P. sylvestris* and documented a similar trend, where a canopy cover of 20% was optimal for seedlings of <1 m, due to the proximity to seed sources and undisturbed access to sunlight. Seedlings taller than this and saplings had optimal conditions with zero canopy cover.

Data for *P. uncinata* are relatively inconclusive here, since to a large degree, more adult *P. uncinata* just means that this is where the populations are located, and does not indicate that a higher/lower number is positive for regeneration. Biomass does not seem to explain anything conclusive for the two types of pine.

The hypothesis (H9) that “canopy cover and density of trees have an observable effect on regeneration” is in my opinion verified.

Inhibition

It was hypothesised that both ericaceous dwarf shrubs and lichens might inhibit regeneration of pine species, as explained by the model of inhibition in the conceptual framework (Connell & Slatyer 1977). The two types of vegetation are dominant in the study area. There are arguments for inhibition by both types of vegetation, and because recruits were observed throughout the study area, the question would not be where the inhibition is strongest, but rather what type of ground cover vegetation is optimal for regeneration? I do not include seedlings of *P. uncinata* in this particular discussion, because this species is only located on plots with a large amount of lichens, which may bias the interpretation of the results.

I partly confirmed the hypothesis concerning ericaceous dwarf shrubs. The regression analysis showed that seedlings of *P. sylvestris* had a unimodal response to the ericaceous ground cover. The peak (highest number of individuals) appeared at 50% ericaceous cover within the plot. Further increasing the cover resulted in fewer seedlings. Heather is reported to produce large amounts of allelopathic phytotoxins, known to cause regeneration-failure of conifer (Jalal, 1982). Problems with conifer regeneration in an ericaceous understorey have been widely documented with different types of species, e.g. the negative influence of sheep laurel (*Kalmia augustifolia*) on regeneration of black spruce (*Picea mariana*) (Mallik 1987; Yamasaki et al., 1998) and jack pine (*Pinus banksiana*) (Krause 1986), or how Labrador tea (*Ledum groenlandicum*) has a negative effect also on black spruce (Inderjit and Mallik 1996). Salal (*Gaultheria shallon*) and various species of *Vaccinium* are also reported to inhibit growth of conifer-species such as Sitka

spruce (*Picea sitchensis*), red cedar (*Tsuga plicata*), western hemlock (*Thuja heterophylla*) and amabilis fir (*Abies amabilis*) (Bunnell 1990, Messier 1993, Prescott et al. 1996, Fraser 1993). Growth problems of Sitka spruce (*Picea sitchensis*) and various *Pinus* in the presence of heather is also a well-known phenomenon, extensively documented by several scientists in Britain (e.g. Wheatherell 1953 and Leyton 1954).

I also partly confirmed the hypothesis concerning lichens. The concept here is that lichens might physically hinder seeds from reaching the soil (Porter 1929). It has been questioned if lichens may have allelopathic attributes, as phytotoxins have been isolated from various *Cladonia* species. This, however, was mostly concerning inhibition of other species of *Cladonia* or moss, because the amounts produced are too low to have any effect on other species. This has in later research been partly falsified (Favero-Longo et al. 2010). Conferring with the regression analysis, *P. sylvestris* seedlings had almost the same unimodal response to lichens as they had to the dwarf shrubs, where the largest number of seedlings appeared when the cover of lichens was at approximately 50%. The specific effect that lichens might have on regeneration of pine does not seem to have been previously documented.

One may assume therefore that both the presumed inhibiting agents (*Cladonia*-lichens & heather) are in fact negative for regeneration. A total cover of heather might produce too many allelopathic chemicals for seedlings to thrive, while a total cover of lichens might not make it easy for seeds to reach the soil for germination. However, if a plot has a mosaic of both lichens and heather, the continuous, blocking surface of the lichens is broken by plants of heather, making it easier for seeds to reach the soil. With a lower cover of heather, the amount of phytotoxins might not be large enough to inhibit the seedlings. This trend was, to some degree, observable in the field, where it looked like regeneration was absent when the ground cover consisted only of lichens or heather. Concerning the question of which ground vegetation is optimal for regeneration, I suggest that a mosaic of patches with 50% lichens and 50% dwarf shrubs might create the best habitat for pine seedlings. There were cases outside this trend though, for example, a plot with mainly lichens which had the largest number of pine individuals (100) in the entire study area. The main conclusion illustrates that the models suggested by Connell & Slatyer (1977) are useful for deducing hypotheses, however the empirical results may not be as clear-cut as one may expect (Connell et al. 1987).

Direct and indirect cause of forest regeneration

To explain the different dynamics which has influenced regeneration in the nature reserve, I will use a system of linear causality. By this I mean that there are a number of cause-and-effect relationships in the complex landscape, and although some of the variables may seem to correlate or have a relationship through regression analysis, it may not necessarily mean that they have an operational effect on each other, but just that they are in the same dynamic system. There are numerous variables that appear to affect the degree of regeneration in the area, as well as variables which affect the ones affecting regeneration. Based on observation and the numerical results one may suggest plausible causal links between variables and factors which may have a direct effect on each other, and which variables these again effect in the next step of the linear causality. This may be viewed as a conceptual model (Fig. 37).

It is important to use logical reasoning and be critical of the reliability of the compiled data. If one bases all interpretation on numerical results, it is possible to conclude that the predictor which has the best statistical explanation for a response is also the one which has the largest effect in the ecological system. It is thus possible to blatantly say that radiation has a negative effect on regeneration of *P. sylvestris*, and a positive effect on regeneration of *P. uncinata*. On the other hand, although an area's energy-balance is determined by incoming sunlight, the variation in vegetation should be looked at as a product of not only the varying degree of incoming radiation, but also the effect radiation has on, for example, soil moisture (Woodward 1987, Castán & Vetaas 2003). Another example is that recruits of *P. uncinata* were, unlike initially planned, declared to be an invalid response variable for regeneration. This was due to its limited distribution which gave biased results in the regression analyses. It was also intended to use spatial autocorrelation to elucidate if the regression analysis managed to explain the distribution of response variables. Ultimately, seedlings of *P. sylvestris* were the only recruits which were not rejected as a valid indicator of regeneration. The seedlings were originally not autocorrelated, unlike the other recruits which all were autocorrelated, but the residuals of *P. sylvestris* after the multiple regression appeared to have gained spatial autocorrelation. This does not have a logical explanation, making this analysis irrelevant for further understanding of the forest regeneration.

The system of causality concerning regeneration starts with the degree of incoming sunlight, RRI, because this is the general source of an ecosystem's energy balance. I have elucidated that the radiation index, to a certain degree, explains access to moisture. Here it is important to understand that the measurement of moisture is not highly reliable, and there are other dynamics which

explain the access or absence of moisture than just evaporation caused by incoming solar radiation.

Through logical reasoning, it is plausible to think that the ecosystem's access to moisture is largely decided by the micro-topography, resulting in variation in received radiation and thus evaporation. This micro-topography causes drainage from the ridges/slopes to the slacks, which are closest to the underlying water-table. The water-storing abilities of lichens also cause a reduction in water reaching the soil on ridges and south-facing slopes. Further on, the degree of soil moisture is probably a key factor explaining the cover of lichens and ericaceous dwarf shrubs. This relationship was significant in the regression, and it is documented that heather needs moisture to thrive (Fægri, 1970). The next step of the linear causality is the inhibiting effect the ground cover has on regeneration. It is clear that the optimal habitat for regeneration of *P. sylvestris* seedlings is when there is an equal cover of lichens and ericaceous dwarf shrubs within a plot, which presumably might reduce the potential inhibiting effect of these life forms.

The reason why RRI always had the best explanation for each of the variables within the analyses may be because this is the most accurate and less varying measurement I have estimated, whereas moisture and degree of ground cover could be less accurate. However, moisture and ground cover might be more direct in their influence on regeneration, whereas RRI is an indirect variable. Even if RRI does not directly affect regeneration, it has an effect on moisture, which then again affects degree of vegetation cover, which finally might be an indicator for how well the native *P. sylvestris* regenerates. Degree of canopy cover and density of trees, which are products of the different growth conditions in the forest, also indicated through the regression analysis that they might have an effect on number of seedlings (Fig. 37).

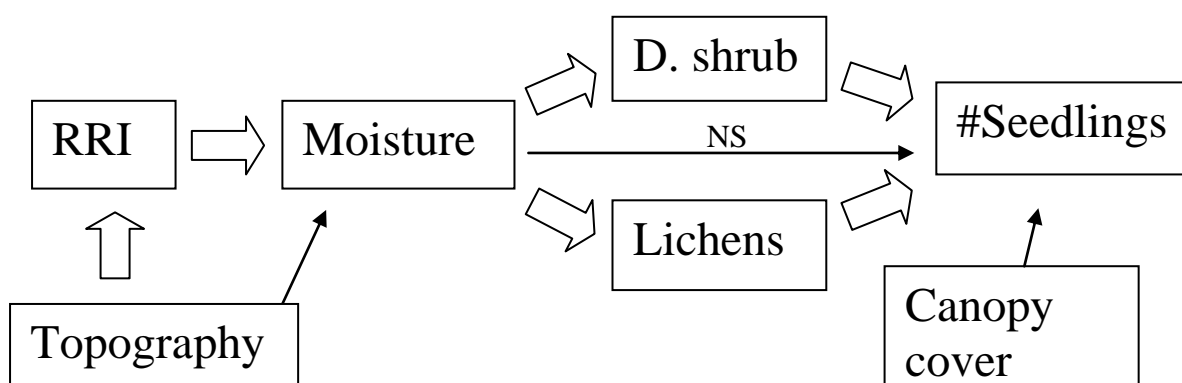


Figure 37 Flow-chart showing the possible casual relationships affecting the regeneration of *P. sylvestris* in the nature reserve.

Management and forest dynamics

The forest we observe in the present nature reserve is influenced by a complex mixture of many different processes. An important aspect of this is human interaction in the form of planting and later management (thinning). The observed dead stumps were more or less randomly scattered within the plots, perhaps due to selective thinning. It was questionable if the symmetry was connected with the variable for dead stumps, where more dead trees would explain the asymmetry. As we can see in the tables (Appendix I, II, III, and IV), this is not the case. The south-facing slopes had a mean of 5.1 dead stumps, while the slacks had a mean of only 2 dead stumps per plot. This shows that management was mostly done where there was the highest number of trees, as well as in the places they originally planted *P. uncinata*. The reason for this is not clear. One reason might be that growth conditions were best on these features, making these places the only ones with enough trees to conduct any thinning on. Another reason might be that the thinning was mostly concerned with conserving the geological formations, which is the reason behind the establishment of this protected nature reserve. It has been documented that thinning in dense forests of Scots pine strongly affects future growth. After selective thinning, the increased area of growth gets distributed among the remaining, largest and fastest growing trees. This increases biomass per tree, as well as making the stand more even-sized (Nilsson et al. 2010, Burns & Puettmann 1996 & Mäkinen et al. 2006 cited in Karlsson et al. 2012). In this study area, due to thinning or ecological conditions, the topographic features which have been subjected to most thinning are also the ones which look the most even-sized, and with the highest biomass index.

From a management perspective, one can question if the conducted planting was optimal for regrowth, conservation and regeneration. To kick-start the secondary succession after the forest fire, the planting was arguably the best thing to do, since a natural regrowth would have taken considerably longer. The vulnerability forests of *P. sylvestris* have to fire has been extensively studied in Spain. Forests which had been burned up to 30 years ago show no observable regeneration. Forest fires older than this, however, show regeneration, but with a relatively low capacity. Even after more than 30 years, 55% of all new recruits were found 10 m away from the undamaged edge of the forest; 90% of all recruits found were 25 m away (Vilá-Cabrera et al. 2012).

Concerning the introduction of *P. uncinata* in Starmoen nature reserve, one can imagine that this was positive for conservation of the protected landforms which were exposed after the fire, due to *P. uncinata*'s ability to reduce soil erosion (Øyen 1999), and the fact that alien species often grow faster than native species (Zobel et al. 1987). However, from the perspective of future regeneration, it appears that *P. uncinata* regenerates to a much lesser extent than *P. sylvestris*. *Pinus uncinata* has not become naturalized, meaning that it will not produce enough offspring to make the population sustainable in the future. This makes it doubtful that planting of an alien species was a good decision for the regeneration of the forest, and thus, conservation of the protected landforms. Unfortunately, the rationale for the planting was not possible to obtain, neither written nor orally from any official institutes. This information was probably lost during the shift of management from the county's environmental department to the municipality. The negative effects of alien pines on an ecosystem (see conceptual framework) have been widely documented in the Southern Hemisphere. A large number (>19) of different alien pine species in Africa have now been classified as invasive. In New Zealand, alien species mainly used for erosion control (*P. sylvestris*, *P. contorta*, *P. nigra*, *P. ponderosa*) are now also considered to be major weeds (Richardson & Higgins 1998).

The question for the future is what actions should be made concerning the alien species and how to ensure the optimal conditions for the future of the nature reserve. One option is to physically remove *P. uncinata* and replant with native *P. sylvestris*. A problem with this is that it would leave the sand dunes exposed for a period of time. If what I presume is correct, *P. uncinata* will not be able to regenerate itself beyond the generation of adult trees present today. According to Booth (1984), *P. sylvestris* seeds can fall up to 30 m away from the parent tree. *Pinus sylvestris* should not have any problems spreading seeds within the areas currently dominated by *P. uncinata*, seeing as the patches of *P. uncinata* only cover parts of the sand-dunes (approximately 20-30 meters in north-south direction). This may take place in the lifespan of *P. uncinata* (100 years (Øyen 1999)), I presume that a natural shift will happen on the south facing slopes and ridges, from the introduced species to the native Scots pine.

Conclusions

This study has analysed the different ecological and human-induced factors which may have influenced the regenerative pattern of a restored pine forest that was planted just after a forest fire (1976). The unique landscape with its topographic features of aeolian sand dunes had a wide variation of abiotic and biotic factors at a fine scale. The gradient induced by variation in topographic relief has often been documented at a broader scale, but this study provided a unique opportunity to see the direct effect of this on a (relatively) fine spatial scale. The micro-scaled topographic relief, induced by the sand dunes, gives a gradient of different exposures to incoming solar radiation. This was expressed by the indirect variable, radiation index, which corresponds to incoming light, but it also corresponds to microclimate temperature and therefore evaporation of moisture, which is a direct resource variable for vegetation growth. The topographic features also cause drainage of precipitation from the ridges/slopes to the slacks, which are also closer to the underlying water-table. The variation in access to soil moisture is a possible reason for the observed variation in ground cover vegetation (dwarf shrubs & lichens). The statistical analyses showed that RRI and moisture influenced the distribution of the two main types of ground vegetation, and this may have affected the number of *P. sylvestris* seedlings. These were not linear relationships, but quadratic, and an intermediate distribution (50%) of both life forms gave the optimal conditions, and thus largest number of seedlings. This was interpreted to be due to a balancing of the inhibiting effects of lichens and dwarf shrubs (mainly heather) found when one life form dominated the ground vegetation. Assuming that the entire nature reserve was planted evenly, then the observed variation in the size of adult trees has been a result of different, internal growth conditions induced by the varying topographical features. Where growth conditions have been less optimal, many of the originally planted trees were stunted. This made them look like saplings, and the area appeared as a more open forest. These variations in growth conditions thus also explained the variations in canopy cover and density of trees, which again had a relationship with number of seedlings, where a compromise between enough incoming sunlight and large enough seed production seemed to be critical.

Human impact on the forest was through initial planting 25-27 years ago and later selective thinning, probably with the idea of protecting the conserved dunes from erosion. The native pine, *P. sylvestris*, was generally planted across in the entire area, whereas the alien species, *P. uncinata*, was planted on ridges and south-facing slopes, presumably in an effort to reduce soil erosion. Although this decision probably had good intentions, it has been shown that this species

has not become naturalized and does not produce enough (if any) reproductive offspring, making its future sustainability doubtful. Although an alien species has qualities and attributes which makes it attractive for reforestation, this study shows that it is questionable to introduce aliens into a nature reserve which already has a well-established native conifer. Concerning future management, given the issues this study has highlighted, it would be preferable to conduct a shift from the alien species to the native Scots pine. However, to physically remove the *P. uncinata* and to replant with *P. sylvestris* would leave the ridges and south-facing slopes exposed to erosion, compromising the landscape which is the reason for the area being a nature reserve. This makes it advisable to let the forest conduct a gradual, natural shift.

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Appendices

Appendix I Descriptive statistics of explanatory and response variables within each plot on ridges.

Ridge:	Variable	Mean	Min	Max	Std. Dev.	S. E. Mean	Kurtosis	Sum
Explanatory:	Sym	2.313	1	4	1.014	0.254	-0.534	
	CC	0.419	0.1	0.7	0.194	0.048	-0.779	
	INC	1	1	1	0	0	0	
	DIR	159.688	115	190	20.49	5.122	-0.002	
	Lich	66.875	50	90	12.5	3.125	-0.834	
	Hea	29.375	10	50	9.975	2.495	0.22	
	Moss	4.375	0	20	7.274	1.819	0.783	
	DS	4.438	0	13	3.723	0.931	1.348	71
	Moi	2.65	0.22	7.61	2.424	0.606	-0.534	
	LOI	1.102	0.61	1.74	0.311	0.078	0.053	
	RRI	0.513	0.506	0.515	0.003	0.001	2.254	
	Sytrees	9.4	1	21	5.795	1.45	-0.2	150
	Unctrees	3.9	0	18	6.17	1.543	1.379	62
	Trees	13.25	6	21	5.132	1.283	-1.297	212
Biomass	121.1	49	191	46.268	11.567	-1.118	1937	
Response:	Syseed	49.5	0	95	28.493	7.123	-0.978	792
	Sysap	3.688	0	8	2.522	0.631	-1.191	59
	Unsseed	1.875	0	6	2.187	0.547	-0.588	30
	Unssap	3.5	0	10	3.033	0.758	-0.432	56

Abbreviation and variable explanation; refer table 1.

Appendix II Descriptive statistics of explanatory and response variables within each plot on "slacks".

Slacks:	Variable	Mean	Min	Max	Std. Dev.	S. E. Mean	Kurtosis	Sum
Explanatory:	Sym	2.438	1	4	0.814	0.203	-0.208	
	CC	0.59	0.1	0.9	0.255	0.064	-0.52	
	INC	1	1	1	0	0	0	
	DIR	1	1	1	0	0	0	
	Lich	38.125	20	50	10.468	2.617	-0.948	
	Hea	53.125	10	70	17.017	4.254	1.301	
	Moss	8.75	0	70	18.212	4.553	9.277	
	DS	2	0	6	1.713	0.428	0.83	32
	Moi	5.719	2.76	8.46	1.622	0.405	-0.953	
	LOI	1.328	0.88	2.08	0.392	0.098	-1.148	
	RRI	0.485	0.485	0.485	NS	NS	NS	
	Sytrees	9.5	5	17	3.633	0.908	0.165	152
	Unctrees	0	0	0	0	0	0	0
	Trees	9.75	5	17	3.856	0.964	-0.294	152
Biomass	97.75	33	195	48.899	12.225	0.073	1564	
Response:	Syseed	40.188	16	70	16.113	4.028	-0.459	643
	Sysap	10.688	3	19	4.285	1.071	-0.334	171
	Unsseed	0	0	0	0	0	0	0
	Unssap	0	0	0	0	0	0	0

Abbreviation and variable explanation; refer table 1.

Appendix III Descriptive statistics of explanatory and response variables within each plot on south facing aspects.

South:	Variable	Mean	Min	Max	Std. Dev.	S. E. Mean	Kurtosis	Sum
Explanatory	Sym	3.5	2	5	1.033	0.258	-0.994	
	CC	0.544	0.2	0.8	0.182	0.046	-0.991	
	INC	17.5	10	26	4.457	1.114	-0.439	
	DIR	168.75	120	195	20.831	5.208	0.496	
	Lich	79.4	50	100	14.361	3.59	-0.302	
	Hea	17.5	0	50	14.376	3.594	0.299	
	Moss	3.125	0	20	6.021	1.505	3.035	
	DS	5.1	1	12	3.193	0.798	-0.186	81
	Moi	3.781	0.483	5.73	1.781	0.43	-0.639	
	LOI	1.454	0.77	3.17	0.647	0.162	2.191	
	RRI	0.718	0.568	0.823	0.062	0.015	1.294	
	Sytrees	11.1	1	20	6.84	1.71	-1.5	177
	Unctrees	3.94	0	13	5.26	1.315	-0.933	63
	Trees	15	7	20	4.258	1.065	-1.205	240
Biomass	156.7	69	262	48.523	12.131	0.417	2507	
Response:	Syseed	20.9	0	100	27.391	6.848	3.792	334
	Sysap	4.2	0	12	4.475	1.119	-0.858	67
	Unseed	3.8	0	25	6.787	1.697	6.199	60
	Unssap	0.95	0	4	1.237	0.309	1.182	15

Abbreviation and variable explanation; refer table 1.

Appendix IV Descriptive statistics of explanatory and response variables within each plot on north-facing aspects.

North:	Variable	Mean	Min	Max	Std. Dev.	S. E. Mean	Kurtosis	Sum
Explanatory:	Sym	3.1	2	4	0.8	0.19	-1.194	
	CC	0.44	0.1	0.7	0.15	0.04	0.413	
	INC	16.3	10	35	6.426	1.607	3.849	
	DIR	203.5	10	355	163.515	40.879	-2.191	
	Lich	42.5	20	70	13.416	3.354	-0.255	
	Hea	53.1	20	80	15.37	3.843	0.298	
	Moss	4.375	0	10	5.123	1.281	-2.219	
	DS	1.125	0	4	1.204	0.301	0.653	18
	Moi	5.224	1.91	9.44	2.584	0.646	-1.546	
	LOI	1.422	0.78	2.87	0.502	0.126	2.771	
	RRI	0.255	-0.08	0.373	0.11	0.027	5.329	
	Sytrees	9.75	3	17	3.376	0.844	0.595	156
	Unctrees	0	0	0	0	0	0	0
	Trees	9	3	14	2.608	0.652	1.036	156
Biomass	75.7	35	121	21.657	5.414	0.382	1211	
Response	Syseed	40.875	17	70	15.108	3.777	-0.491	654
	Sysap	14.5	7	30	6.812	1.703	0.283	232
	Unseed	0	0	0	0	0	0	0
	Unssap	0	0	0	0	0	0	0

Abbreviation and variable explanation; refer table 1.

