Assisted recovery of disturbed arctic and alpine vegetation
- an integrated approach

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PREFACE

Since my first visit to Hjerkinn Firing Range in 1989 I have been captivated by the opportunities of integrating scientific knowledge and practical experience in the management of disturbed wilderness. The fascination of wilderness and wilderness management was further intensified when I visited Svalbard for the first time in 1990. A vague idea of some joint project came into existence already then. However, the real story of this thesis started in 1998, and was financed by the Norwegian University of Science and Technology (Forskningsstrategisk bevilgning 1997) and The Research Council of Norway (Biological Diversity programme and Arctic Scholarship).

My supervisors have been Håkan Hytteborn, Department of Biology, NTNU and Lars Emmelin, Department of Spatial Planning, Blekinge Institute of Technology, the latter also co-writer on Paper IV. Thank you both for contributions and co-operation. I want to express my thanks to Olaf I. Rønning, who introduced me to Svalbard in 1990, and who has shown interest in my work ever since and encouraged and inspired me. My contact with different departments within the Armed Forces has been vital to my research at Hjerkinn. In particular I want to mention The Norwegian Defence Estates Agency. I also want to thank the staff at Hjerkinn Firing Range for their hospitality, practical assistance, and *im*patience for practical and applied results. Thanks to my co-writers: Jørund Aasetre - despite apparently incompatible professional approaches and working habits we really managed to have an interesting and fruitful co-operation, and Elisabeth Cooper and Inger Alsos – your enthusiasm has been a real inspiration.

Colleges, friends, and family have supported me on the way. My good helpers in the field have been numerous: Anne Stine, Heidi, Ingar, Inger Beate, Line (who also offered me accommodation during several field seasons), Reidar, Sverre, and Torhild. Thanks to Olga Hilmo and Tommy Prestø for valuable comments and input, Carolyn Baggerud for helping me with figures and language, PhD-student fellows Linda, Ingar, David, Lene, Kristian and Bård for everyday support, the rest of the staff at Department of Biology for a pleasant time, Vibekke in Tromsø – never more than a phone-call away, and the staff at the former

Centre for Environment and Development (SMU) who contributed to giving this project a positive start.

Thanks to my parents, Tone and Erik, for assistance and practical support during the most busy periods, and to my marvellous supporters Trygve and Marit who keep me going, reminding me that there is much more to life than writing a thesis. Finally, thank you Tommy, for always being there. Without you this would have been a different story!

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CONTENTS

LIST OF PAPERS

The thesis is based on the following individual papers

I. Cooper, E.J., Alsos, I.G., Hagen, D., Smith, F.M., Coulson, S.J. & Hodkinson, I.D. Reproduction by seed in Svalbard: seedling emergence in the field and in soil samples studied in laboratory trials. Manuscript.

II. Hagen, D. 2002. Propagation of arctic and alpine native species with a possible restoration potential. *Polar Research* 21: 37-47.

III. Hagen, D. Arctic and alpine restoration using native species transplants. Submitted to *Restoration Ecology*.

IV. Hagen, D., Aasetre, J. & Emmelin, L. 2002. Communicative approaches to restoration ecology: a case study from Dovre Mountain and Svalbard, Norway. *Landscape Research* 27: 359-380.

V. Hagen, D. Restoration by willow (*Salix* spp.) cuttings as a management strategy in Hjerkinn Firing Range, Dovre Mountain, Norway. Manuscript.

The papers are referred to in the text by their Roman numerals.
Paper II and Paper IV are included with permission from the publishers.

INTRODUCTION

PROBLEM DESCRIPTION

Arctic and alpine plant communities are today under influence of more extensive anthropogenic disturbances than any time in history (Walker & Walker 1991; Reynolds & Tenhunen 1996; Crawford 1997). These areas are traditionally perceived as wilderness, and they still represent some of the most untouched landscapes on earth (Hannah et al. 1994; CAFF 2001). Today, we face cumulative impact from small-scale disturbances, and increased diversity of disturbances on a wide range of scales, from small spots up to large landscapes (Walker & Walker 1991; Forbes et al. 2001). In a situation with short growing seasons and a severe physical environment, natural recovery is limited by slow vegetative growth (Crawford 1989; Billings 1992), low and unreliable seed production (Chambers 1989; Oksanen & Virtanen 1997; Bliss & Gold 1999), and shortage of safe sites for seedling establishment (Urbanska 1997a).

In traditional nature conservation severely disturbed areas can easily be considered as “lost” (Hendee et al. 1990; Anon. 1995). The increased pressure on wilderness areas has raised the question of using restoration as a management strategy (Walker 1997; Edwards et al. 1997; Forbes & Jefferies 1999). By restoration of disturbed sites the landscapes can retain important nature and social values.

The science of ecology is essential to any restoration project. Ecological terms are needed to describe the status of a site, and knowledge of ecological processes is needed to set up realistic goals for restoration and to evaluate ecological effects of the restoration enterprise (e.g. Jordan et al. 1988; Forbes & Jefferies 1999; Urbanska & Chambers 2002). However, successful restoration requires an expanded and interated approach including technological, social, political, economical and aesthetical aspects (e.g. Diamond 1987; Edwards & Abivardi 1997; Higgs 1997). An integrated approach is essential to the application of scientific knowledge into practical restoration enterprises with a time frame, cost and scale that is relevant for the management of each specific area (Figure 1).

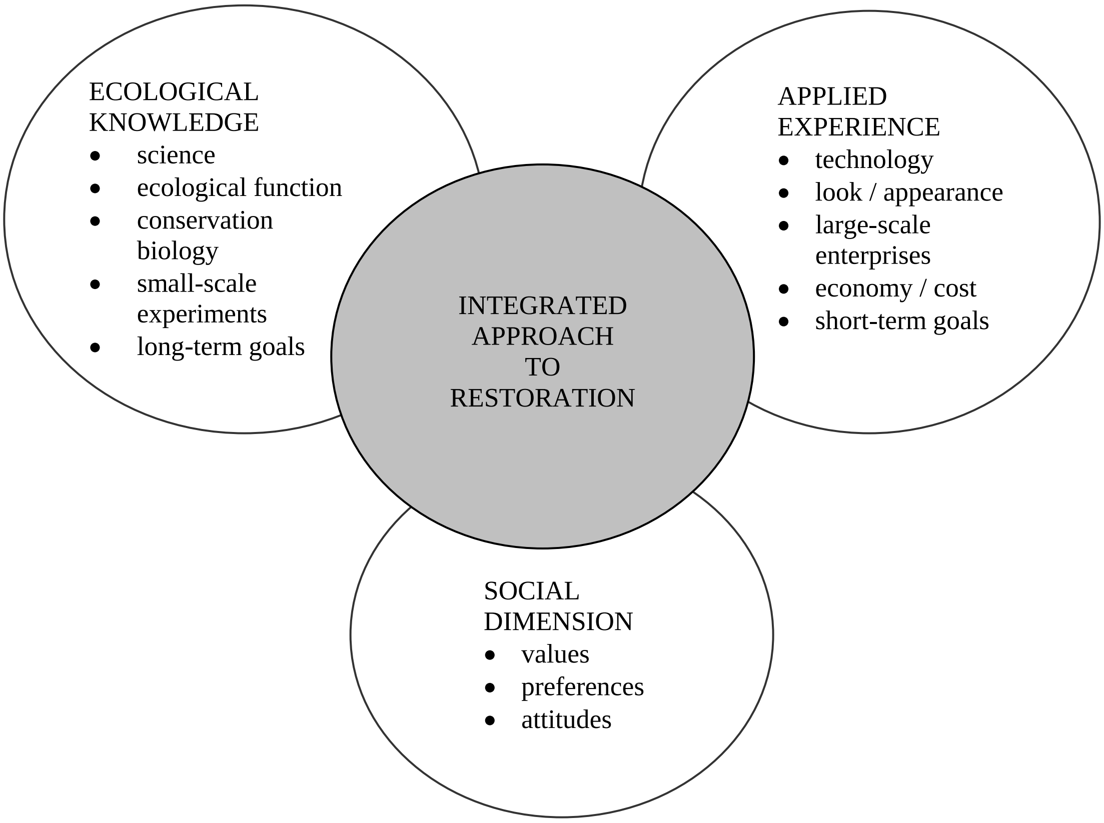

Figure 1: Ecological knowledge, both from pure scientific studies and from restoration research is the basis for restoration. For the application of restoration in management of arctic and alpine areas, the ecological knowledge must be integrated with experiences from practical enterprises, and also focus on the social dimensions of management, such as values and preferences of involved users and stakeholders. The size of circles is adjusted to fit the text, and is not related to their relative importance.

ECOLOGICAL BASIS FOR RESTORATION OF ARCTIC AND ALPINE VEGETATION

Natural disturbances causing habitat instability occur frequently within temporal and spatial scale in arctic and alpine ecosystems (Walker & Walker 1991), and these processes play an important role in creating community structures (Pickett & White 1985). Anthropogenic disturbances in arctic and alpine vegetation are in general small, but dramatic. Even though frequencies and sizes can be very different, the study of responses can be of interest to detect similarities and differences between natural and anthropogenic disturbances (Webber & Walker 1987; Forbes & Jefferies 1999). The severity of disturbances is of vital importance to the effect of damage and the rate of recovery (Emers et al. 1995; Vavrek et al. 1999; Forbes et al. 2001). This thesis focuses on severe anthropogenic disturbances in dry arctic and alpine areas where the vegetation cover is mechanically removed and the underlying mineral soil is exposed. They can be categorised as having a very high disturbance level (cf. Emers et al. 1995), or as extensively disturbed areas (cf. Urbanska 1997b), on the meso- and macro-scale (Walker & Walker 1991). In such sites natural recovery is virtually absent within the range of decades (Urbanska 1997b; Forbes & Jefferies 1999).

Recovery is the process by which an ecosystem achieves relative biological and physical stability following disturbance (Webber & Walker 1987). The main sources for establishment of new vegetation are from lateral clonal growth in adjacent vegetation, rooting of vegetative fragments, germinating seeds, or buried seed bank (e.g. McKendrick 1987; Stöcklin & Bäumler 1996; Urbanska & Chambers 2002). Established individuals have a nurse effect that allows survival and establishment of other species (Urbanska 1997a; Nunez et al. 1999). Recolonisation tends to occur by species in adjacent communities (Emers et al. 1995). When the disturbed area is large, vegetative growth is relatively unimportant for natural recovery, and input of seeds or plant fragments is necessary to establish new individuals (Forbes & Jefferies 1999; Ebersole 2002).

Reproduction by seed occurs frequently in arctic and alpine vegetation, but seed production and viability vary between years and sites (e.g. Sørensen 1941; Bliss & Gold 1999; Molau & Larsson 2000). At Svalbard presumably over 60 % of the vascular species reproduce mainly by seed (Eurola 1972; Brochmann & Steen 1999). Over half of the tundra plant species have viable seed banks (reviewed in McGraw & Vavrek 1989), and arctic seed banks are generally larger than previously assumed (e.g. Ebersole

1989; Lévesque & Svoboda 1995; Larsson 2002). Density of seedlings in the field shows large variability among and within sites, and seedling survival rates are in general very low (Bell & Bliss 1980; Chambers 1995; Bliss & Gold 1999). The relative importance of vegetative regeneration increases towards higher latitudes and altitudes, and about 50 % of Svalbards' vascular species have the ability of asexual reproduction (Brochmann & Steen 1999).

A good understanding of species reproductive behaviour, vegetative growth, and initial phases of succession are essential for development of methods for restoration by native species (Urbanska 1997c). Mechanisms of natural succession can be used to predict patterns of recovery, and are important for formulation of realistic goals for restoration. Early successional arctic and alpine communities can be self-perpetuating, and pioneer species in such marginal systems can be long-lived perennials that persist into later successional stages (Svoboda & Henry 1987; Forbes 1996; Forbes et al. 2001; Ebersole 2002). These species can have a long-term effect in restoration situations.

RESTORATION ECOLOGY – SCIENCE AND TECHNOLOGY

In severely disturbed dry arctic and alpine sites, assisted recovery seems to be necessary to initiate establishment of a new vegetation cover within a human time-scale. Deciding when restoration is actually needed is the initial phase of action, and ecological, ideological, and social considerations are part of this (Edwards & Abivardi 1997; Lackey 1998; Forbes & Jefferies 1999). The development of improved methods for assisted recovery, and how to accomplish restoration are the next phases.

Approaches to restoration

Restoration ecology arose from the need to rehabilitate highly disturbed ecosystems, and contains a scientific, an applied and a social basis (Bradshaw 1995; Clark 1997; Edwards et al. 1997), and some claim even an artistic (Turner 1987). A wealth of definitions and terms are used to describe different approaches to the artificial establishment of a new vegetation cover on disturbed sites. Two main traditions, or approaches, are the scientific approach of ecological restoration and the more applied approach of practical and technical rehabilitation.

Ecological restoration is a scientific approach to the process of restoring the function of ecosystems (Bradshaw 1997; Jordan et al. 1988; Webb 1997). The science of ecology and ecological knowledge is the basis for this approach, and its main focus is the upper left circle of Figure 1. Restoration ecology is considered a part of conservation biology, and restoration projects are often closely connected to conservation of biodiversity at all levels (e.g. Heywood & Watson 1995; Hobbs 2002). In the more *applied approach* of rehabilitation, the focus is more in the direction of creating a certain look or appearance, and originality or vigour of ecosystems is not stressed (Bradshaw 1984; Harper 1987; Harker et al. 1993). The main focus in this approach is the upper right circle of Figure 1. Technical and practical projects are often carried out by engineers, gardeners or landscape architects, and can often be large in scale (e.g. Bradshaw & Chadwick 1980; Schichtl & Stern 1996). Documentation from applied, large-scale projects is often poor. Both the scientific and the applied approaches have subjective components, like asserting problems, suggesting solutions and evaluating success. There is a large potential for mutual support between the approaches, as science can apply ecological principles to the well-established technology of the reclaimers (Allen & Hoekstra 1987; Webb 1997). The scientific language of restoration ecology increases the distance to practical approach, as reclaimers often use a more technical language dealing with similar problems and solutions (Clark 1997).

Implementing restoration in arctic and alpine areas

Restoration in arctic and alpine areas imply special problems and challenges, due to low temperatures, limited water availability during part of the year, and low levels of soil nutrients (Chapin & Shaver 1985; Forbes et al. 2001; Urbanska & Chambers 2002). There is a need to develop new and improved methods for site-specific restoration, particularly in dry vegetation types with slow natural recovery. The aim of assisted recovery can be the establishment of a new plant cover, or to prepare for increased natural recovery, or a combination of these.

Selection of species for restoration depends on environmental characteristics of the disturbed site, ecological and physiological qualities of single species, and the goals for restoration (Chambers et al. 1984). Poor availability of plant material has traditionally prevented the use of native species in restoration (Miller et al. 1983; Forbes & Jefferies 1999). The use of native species becomes more feasible as restoration methods are improved, and as ecological and ideological arguments against introduced species become more outspoken (Lesica & Allendorf 1999). The effect of introduced species on local vegetation development is often unpredictable (Cargill & Chapin 1987; Densmore 1992), and there is concern that introduced species can displace original vegetation or breed with locally adapted taxa (Parker & Reichard 1998).

A wide range of more or less successful methods for restoration has been used during the last decades. Seeding of grass is an established method reported to result in rapid development of a plant cover (e.g. Younkin & Martens 1987; Jorgenson & Joyce 1994), but the long-term effect of grass in enhancing native colonisation is disputed (e.g. Densmore 1992; Helm 1995; McKendrick 1997). Use of native species transplants in restoration is expected to be favourable compared to seeding under extreme environmental conditions, as the most vulnerable stages of germination and recruitment are circumvented (Urbanska 1997d; Fattorini 2001; Davy 2002). Collecting transplants adjacent to the disturbed site (e.g. May et al. 1982; Tishkov 1997; Shirazi et al. 1998) suffers from the problem of inflicting damage at new sites (Urbanska & Schütz 1986). Raising new plants propagated from seeds and cuttings of native species under horticultural conditions, and transplanting these into disturbed sites can be an alternative (e.g. Densmore & Holmes 1987; Urbanska et al. 1987; Fattorini 2001). Integration of applied experience from large-scale cultivation, and scientific knowledge about species and site conditions will be of vital importance for the development of this restoration method.

Soil attributes are essential to natural recovery, and hence for planning and accomplishing restorations. This topic has not been treated explicitly in this thesis, but effects of different soil treatments on survival and growth of transplants have been investigated (Papers III & V).

RESTORATION IN A SOCIAL CONTEXT

Though ecological knowledge is fundamental, social conditions are often the limiting factor to success in restoration projects (Edwards et al. 1997; Hobbs 2002). The social meaning of restoration is a complex of values, attitudes, beliefs and preferences. Even though several authors point at social issues as important and critical parts of restoration projects (e.g. Baldwin et al. 1994; Edwards et al. 1997), this is often seen merely as a way to convince people in an area to support a solution prescribed by ecologists (Cairns 1995; Macdonald et al. 2002). Active involvement from local people and stakeholders in goal formulation and success evaluation is indeed an exception in restoration projects.

How to decide what to do? The formulation of goals

Management in general, and restoration in particular, is a value question. The questions of who determines what is worthy of restoration, and how restoration should be accomplished will then be essential to the outcome (Pierce 1994; Lackey 1998). The value of a restored ecosystem compared to a "natural" one depends on the viewer and problem perception (Loucks 1994), and thus restoration ecology can never give one objective right answer to what is the best solution. Political and management decisions prior to restoration provide guidelines for an enterprise, and obviously influence goal formulation (e.g. Maguire 1995; Lackey 1998). Goals can vary over time for one particular problem or situation (Magnusson 1997). Defining site or situation specific goals are essential to restoration projects, both for ecological and social reasons (Jackson et al. 1995; Slocombe 1998; Ehrenfeld 2000).

The restoration ecology literature deals with theoretical and practical problems of identifying an "original state" that can be re-established through restoration (e.g. Cairns 1990; Inouye, 1995), and also more modified descriptions of the ideal ecosystem following recovery is defined by ecological terms (Strandberg 1997; Forbes & McKendrick 2002; Urbanska & Chambers 2002). The focus of an indigenous or original ecosystem seems to lead to a scientific search for a single best solution rather than to the examination of alternatives (Bradshaw 1995; Higgs 1997). The goal for restoration can alternatively be described as a “desired state”. While the effects of any single attempt at restoration may be analysed in ecological terms, criteria for choosing a desired state can not simply be derived from an ecological analysis of the landscape, but must also refer to what is desirable to stakeholder groups or the community. Defining desired states includes social, ideological, and technical considerations, in addition to ecological.

What is good restoration?

Ecology as a science is crucial in describing the effects of any restoration enterprise, and success evaluation has traditionally focused on technical solutions or pure scientific results (Higgs 1997). In order to extend the view on success evaluation, the distinction between ecological effect and environmental impact can be useful. The *ecological effect* of restoration can be described as actual change in the environment, and it is scientifically observable and predictable. The normative concept of *environmental impact* raises the question of whether the effects of restoration matter to society, evaluated against some value norm (Munn 1979; Emmelin 1996). In order to understand the environmental impact of restoration it is necessary to look into the values and considerations of affected groups and stakeholders. Some projects address social benefits as a goal. In this perspective the best decisions in a management situation are described as those “*that appear to best respond to society’s current and future needs*” (Lackey 1998). On the contrary, it has been claimed that rehabilitation of land back to a socially acceptable condition falls short of restoring a native plant community, and consequently this condition is of less value to the scientist, but perhaps of equal value to the user (Jordan et al. 1988).

Successful restoration depends on the contribution from a broad range of interests, traditions and sciences. In a management situation an integrated approach to restoration is essential, in order to obtain an optimal utilisation of ecological, social and technical qualifications during the management process, including goal formulation, planning and accomplishing the restoration enterprise, and success evaluation.

OBJECTIVES

The main objective of this thesis is to contribute to the development of an integrated approach to restoration in the management of arctic and alpine areas, with a focus on severely disturbed dry sites. An integrated approach must include ecological, applied, and social aspects of restoration when proposing management solutions in disturbed vegetation.

The specific aims of this thesis are:

1. To study arctic species' potential of recruitment from seeds, by examining germination of fresh seeds, germination from soil seed bank trials in greenhouse, and seedling occurrence under natural conditions in the field (Papers I & II).
2. To examine prospects for propagation and cultivation of selected arctic and alpine species from seeds, bulbils, and cuttings, and to recommend species for future restoration (Papers II, III & V).
3. To develop restoration methods using cultivated transplants of native species, with focus on survival and growth of transplants under various environmental conditions (Papers III & V).
4. To examine the attitudes towards restoration as a management strategy among stakeholders and local people in one arctic and one alpine area, and to see how these attitudes are influenced by attachment to the area and view of nature (Paper IV).
5. To discuss how a social and communicative approach can be an integrated part of goal formulation and success evaluation of restoration projects, without loosing ecological fidelity (Papers IV & V).

STUDY AREAS

One arctic and one alpine area were used in this study. Both areas have short, dry, and cold growing seasons, though environmental conditions are in general more severe in the arctic area, see below. Historic and present use and future management perspectives are very different for the two areas, but concurrent problems related to disturbance and recovery makes a joint focus interesting. A major problem in both areas has been that the thin vegetation layer on exposed ridges and dry heaths is removed or torn off, uncovering dry mineral soil. Natural recovery is virtually absent for decades, and assisted recovery seems to be necessary to initiate the establishment of a new vegetation cover within a human time scale. Results presented in Papers II, III and IV are based on investigations in both study areas. Paper I is based on an investigation from the arctic area, while Paper V is based on a study in the alpine area.

The arctic study area is the Svalbard archipelago in the northern Barents Sea, with the main focus on disturbed areas inside and outside the settlement Longyearbyen on the west coast, 78°N 16°E (Figure 2). In Papers I and IV data involving other parts of Svalbard are also included. Longyearbyen is situated in the middle-arctic vegetation zone, and the growing season is about 70 days long (number of days with an average temperature of ≥ 5°C) (Moen 1999). Summer (May to September) precipitation is 77 mm and average summer temperature is 1.8°C (S.-E. Øines, Norwegian Meteorological Institute, personal communication). *Dryas* heath communities (Rønning 1965) dominate the area, but a variety of heath, wetland and snow-bed communities occur (Brattbakk 1984).

Longyearbyen is the largest settlement on Svalbard with approximately 1600 inhabitants. It was founded as a coal mining town in 1901 (Arlov 1996). During the last decade economic life has shifted from coal mining as the completely dominating activity towards increasing investments in research and tourism. Today 60 % of Svalbard is protected by law as National Parks or Nature Reserves. Human disturbances are mostly related to expanding settlements, and most technical installations are located in heath communities. Vehicle tracks and trampling paths exist locally in the wilderness (Råheim 1992). Restoration activities have been accomplished on Svalbard. Large-scale restoration was initiated in Longyearbyen, by the local authority in the 1980's, and has mainly included seeding of introduced grass species (Låg 1986, unpublished data). Some limited research on native species exists (Tishkov 1997; Brosø 2001; unpublished data).

The alpine study area is Dovre Mountain on the mainland of Norway, with focus on the 165 km^2 large military training area Hjerkinn Firing Range, 63°N 10°E (Figure 3). Hjerkinn is mainly situated in the low alpine vegetation zone, and the growing season is about 115 days long (Moen 1999). Summer (May to September) precipitation is 248 mm, and average summer temperature is 7.2°C (S.-E. Øines, Norwegian Meteorological Institute, personal communication). Coarse, calcium-poor glacial sediments dominate in the area, and vegetation is characterised by lichen and dwarf shrub heaths, *Salix* spp. meadows, and scattered bogs and fens (NIJOS 1999).

The military activity at Hjerkinn has existed since 1923, and is of economic and social importance to the neighbouring communities. Today 90 km of roads, more than 100 buildings, several target ranges and other military installations fragment the area (Jacobsen & Skattum 2002, Anon. 2003). Hjerkinn Firing Range is surrounded by several protected areas and a turnpike road through the military area improves accessibility into large wilderness areas. The Armed Forces took the initiative to restoration activity within the firing range in the late 1980's, and since then small-scale experiments and large-scale restoration have been carried out, involving a wide range of restoration methods (e.g. Hagen 1994; 2003). In 1999 the Norwegian Parliament decided to establish a new military training area in southern Norway, and as a consequence the Hjerkinn Firing Range will be closed down during 2005-2008. The Parliament decision gives instruction concerning future management, and the main focus is to ”*restore the area in a way that entails considerable profit for the nature*” (Anon. 2001; Faye-Schøll & Martinsen 2002).

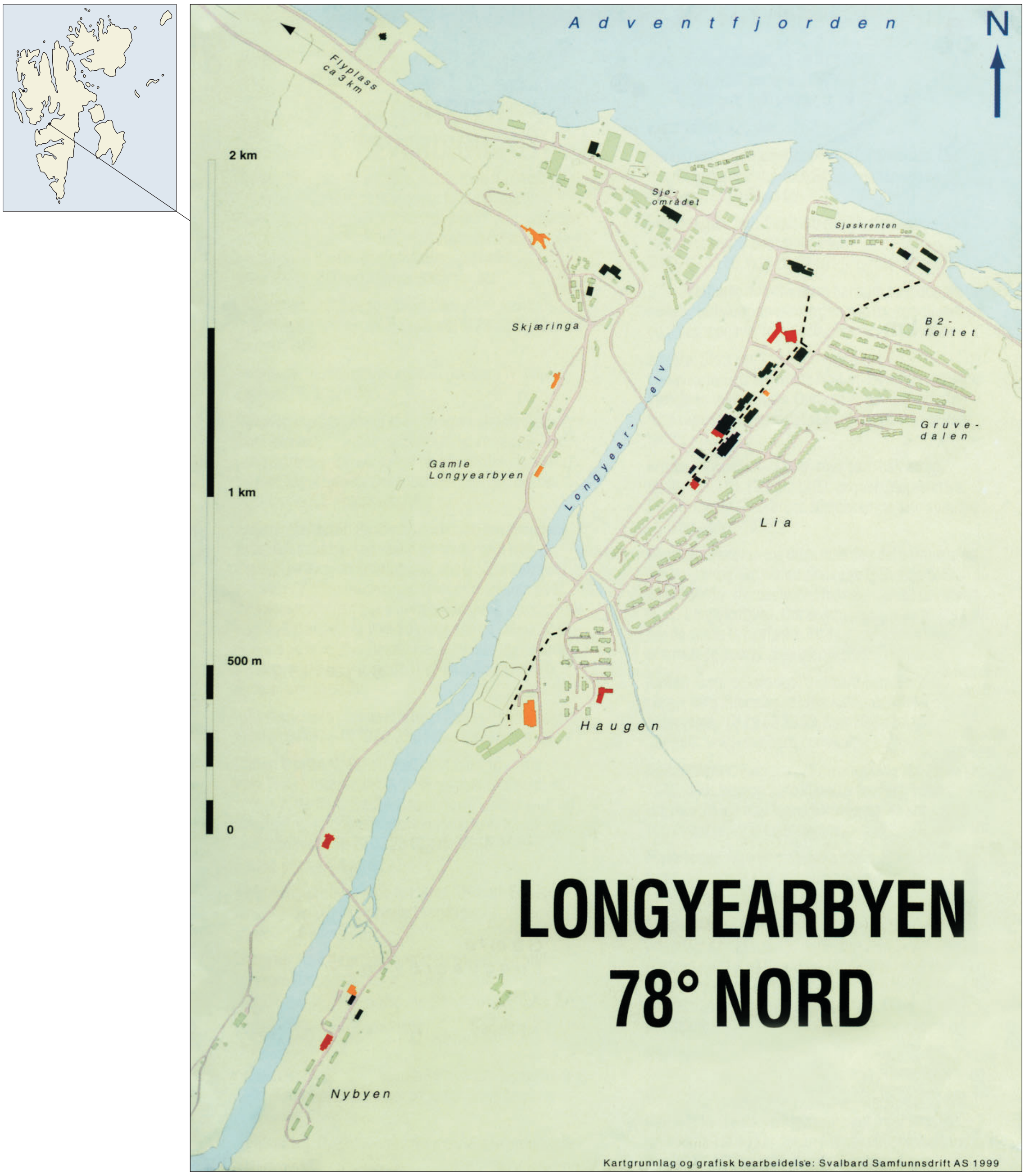

Figure 2: The settlement Longyearbyen is situated on Svalbard archipelago in the northern Barents Sea. Local infrastructure, such as roads, buildings, and sanitary installations are well developed, and dominate the settlement area. The majority of Svalbard is wilderness, with few new traces of human activity. All remnants of human artefacts on Svalbard dated from before 1945 are protected by law as cultural heritage monuments.

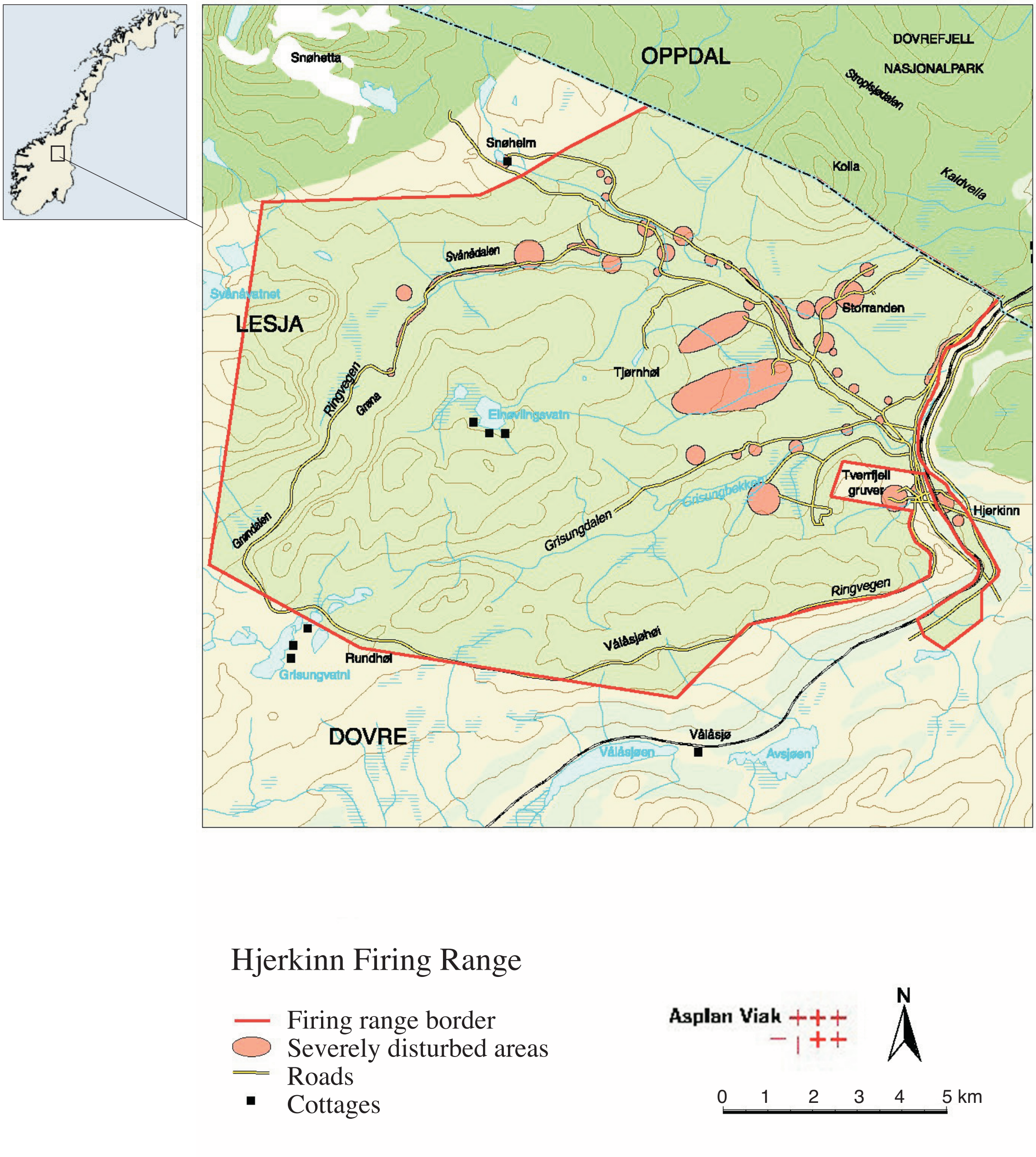

Figure 3: Hjerkinn Firing Range is situated on Dovre Mountain in Central Norway, at 1000 – 1400 m a.s.l. Roads and military installations fragment the area, and are mainly situated in the western part of the firing range. Several protected areas surround the firing range, and the largest is Dovrefjell National Park (dark green areas on the map). Since this map was made the national park has been extended, and now adjoins the firing range border in the north, including Snøheim.

METHODS

A broad range of quantitative and qualitative methods has been used in this thesis. In Papers I and II soil seed bank and fresh seeds were germinated in the greenhouse (cf. Thompson et al. 1997; Hartmann et al. 2002). Permanent plots were established in disturbed and intact sites of *Dryas* heath, to study seedlings emerging in the field, and detailed mapping of individual seedlings was necessary to carry out recordings during three field seasons (Paper I). Current vegetation cover in the disturbed site was less than 10 %, compared to 90 % in the intact *Dryas* heath.

In Papers II and V horticultural techniques, according to Hartmann et al. (2002), were used to propagate and cultivate transplants from cuttings and seeds. The cultivated transplants were planted into disturbed sites. Data for survival, reproduction, and growth was recorded during three field seasons, and randomly selected transplants were collected for biomass measurement (Papers III & V). Simple and multiple regressions (Zar 1996) were computed to uncover the combination of non-destructive growth variables that best corresponded to the total biomass for each species (Papers III & V). These outlined combined variables were comprehended as expressions of plant size. In Paper III root segments were stained by Trypan blue for examination of mycorrhiza (e.g. Kormanick et al. 1980), and infection level counted according to Allen et al. (1987) and Magnusson (1994).

Qualitative methods from behavioural and social sciences were used in Paper IV. Focus group technique (Kreuger 1994) was used to capture the diversity of perceptions, attitudes and preferences among involved groups and stakeholders. Contact meetings based on the focus group technique were organised at each study area, supplemented by personal interviews with persons from groups poorly or not represented at the meetings.

RESULTS AND DISCUSSION

ASSESSMENT OF RECOVERY POTENTIAL

Seeds germinating from persistent seed banks are in general important for species establishment at disturbed sites, and even in arctic communities this can be crucial for initial succession and recovery (Freedman et al. 1981; Shaver et al. 1983; Ebersole 1989; Thompson et al. 1997). Knowledge of the composition and density of the seed bank, and of seedling occurrence in the field on Svalbard have up to date been very limited.

Seedlings from 50 of the 161 native Svalbard vascular plant species were identified in the germinable seed bank from a range of mesic-dry habitats (Paper I). Several of these species have, as far as known, not been reported in soil seed bank studies from other arctic areas, such as *Draba nivalis*, *Papaver dahlianum*, *Sagina nivalis*, *Saxifraga rivularis*, and *Trisetum spicatum*. Seedling density varied considerably between species and habitats (Paper I), as reported from other comparable studies (e.g. Freedman et al. 1981; Bliss & Gold 1999; Larsson 2002). Seedlings from 27 species were recorded in permanent plots in disturbed and intact *Dryas* heath during three growing seasons (Paper I). Seedlings of several common species, such as *Bistorta vivipara, Cerastium arcticum, Dryas octopetala, Luzula* sp. and *Saxifraga cernua* were recorded in the field at both sites in all three years.

Generally the seed bank represented the established vegetation in the sample areas, for herbs, but not for shrubs, sedges or thermophilic plants which may have special requirements for germination or seed formation (Paper I). Several species were observed in the vegetation but not in the seed bank. This could be due to local or scattered distribution (e.g. *Polemonium boreale*) (Elven & Elvebakk 1996), low seed germinability (e.g. *Ranunculus sulphureus, Taraxacum arcticum*) (Eurola 1972), failure to break dormancy (e.g. *Carex* spp.) (Schuetz 2000), or inadequate climate conditions for seed production (*Betula nana, Vaccinium uliginosum, Campanula rotundifolia*) (Alsos et al. 2002).

Fresh seeds of *Papaver dahlianum, Oxyria digyna* and *Luzula arcuata* ssp. *confusa* had high germination in the greenhouse (Paper II), and in general exceeded what has been reported from other arctic studies (Eurola 1972; Bell & Bliss 1980; Bliss & Gold 1999). Seeds were collected in a warm summer, compared to the average mean for the area. Seeds of *Dryas octopetala* had low germination (Paper II), as also reported by Eurola (1972) and Khodachek (1997). Seedlings of *D. octopetala* were present in both intact and disturbed *Dryas* heath in all three years (Paper I), while seedlings rarely occur in the field on the north-west coast of Svalbard (P.A. Wookey and E.J. Cooper, personal communication). A thermophilous nature of seed production has been found in this species (Wookey et al. 1995), while seedling survival seemed to be less temperature limited (Paper I). Fresh bulbils of *Bistorta vivipara* had very high germination in the greenhouse (Paper II). This was also the most abundant species in the seedbank, both in the greenhouse and in the field (Paper I), germinating from bulbils (cf. Söyrinki 1939; Molau 1993). “Seedling” density was higher in the field than in the greenhouse trials for both intact and disturbed *Dryas* heath (Paper I), probably due to high mortality rates of bulbils during storage (Elmqvist & Cox 1996). *Bistorta vivipara* had almost total replacement of individuals in the field from one year to the next (ca. 100% mortality) (personal observation).

A comparison between seedling density in the field and in the greenhouse was done for intact and disturbed *Dryas* heath. The density of seedlings emerging in the field was higher in intact than disturbed *Dryas* heath, while no significant difference between these habitats was found in the greenhouse trials. The disturbed *Dryas* heath had a higher density of seedlings emerging from soil samples in the greenhouse than the field, while in intact *Dryas* heath seedling density is higher in field (Paper I). This indicated that growing under greenhouse conditions was an advantage for seeds from soil collected at disturbed sites, while this advantage was limited for the seeds from intact *Dryas* heath. The intact heat had 90 % vegetation cover, and probably had an abundance of safe sites for seedling in the field. Summer mortality of seedlings in field was expected to be higher in disturbed habitats, linked to desiccation (Jumpponen et al. 1999; Schlag & Erschbamer 2000) and poor seedling growth (Bell & Bliss 1980;

Chambers et al. 1990). Seedlings are most likely to establish near adult plants in the field. These provide more safe sites with a more stable microclimate than bare or disturbed ground (Urbanska 1997a; Bliss & Gold 1999). Seedlings in the field were recorded within six weeks after germination, whereas those in the greenhouse were recorded within a week (Paper I), and mortality of very young seedlings in the field probably influenced this result.

This study has emphasised the value of recording seedlings in the field, when describing seed bank diversity in intact and disturbed *Dryas* heath. While 70 % of the species present in mature vegetation in intact and disturbed *Dryas* heath showed ability to germinate in the field, only 39 % of the species present in mature vegetation in these two habitats germinated in the greenhouse study (Paper I).

Species like *Cerastium arcticum, Draba nivalis, Luzula arcuata* ssp. *confusa, Saxifraga cernua,* and *S. oppositifolia* had high density of seedlings in most habitats in the greenhouse trials, and they were frequently observed as seedlings in the field during every summer, 1998-2000 (Paper I). A majority of these species have high germination of fresh seeds (Eurola 1972; Paper II) suggesting that they reproduce regularly by seed on Svalbard. Despite the relatively high seed bank diversity and density in the disturbed *Dryas* heath (Paper I), vegetation recovery has been almost absent during the last 30 years. This indicates that recovery has been limited by seedling survival and availability of safe micro-sites rather than the presence of viable seeds (Paper I & II). If native seeds are to be considered a source for restoration in *Dryas* heath, the critical seedling period should be circumvented.

IMPROVED METHODS FOR ASSISTED RECOVERY

Due to the slow rates of natural recovery, artificial establishment of new vegetation is a highly relevant topic in arctic and alpine areas. Seed bank or *in situ* sown seeds have been used for restoration purposes (Chambers et al. 1990; Forbes & Jefferies 1999), but seem to be unreliable in dry arctic and alpine vegetation (Papers I & II). This thesis has focused on the development of methods using transplants of native species in the restoration of severely disturbed, dry sites, as this is one way to circumvent the most critical stages of seedling mortality in the field.

Generating plant material

This investigation has shown that greenhouse propagation and cultivation from seeds or cuttings of several common arctic and alpine species is practicable, and can be conducted during the period between two growing seasons (Papers II, III & V). Greenhouse cultivation is a resource demanding technique, but holds good prospects for producing numerous plants for restoration purposes.

Selection of plant species for propagation must be based on field observations of natural recovery in an area, and ecological and physiological qualities of single species. The species included in this thesis were common, native, drought tolerant, and occurred naturally in or immediately next to disturbed sites. The species either had high seed/bulbil production, or horticultural experience indicated that they were easy to propagate as cuttings (Papers II & V). Clonal material may lack genetic variation, and to prevent negative effects on long-term persistence (Davy 2002), a high number of source plants was used for each species (Papers II & V).

The potential for recruitment by seed has been discussed earlier in this thesis, and several common species had high and quick germination in the greenhouse (Paper II). Cuttings from *Arctostaphylos uva-ursi, Empetrum nigrum* ssp. *hermaphroditum, Vaccinium vitis-idaea, Salix herbacea, S. polaris,* and *S. phylicifolia* had good rooting capacity in the greenhouse (*S. phylicifolia* from Paper V, others from Paper II). High rooting capacity for *Salix* spp. was expected from previous studies (e.g. Chmelar 1974; Silvola & Ahlholm 1993; Hartmann et al. 2002), while limited or ambiguous experiences existed for heath species (Nelson 1987; Lehmushovi 1993; Hartmann et al. 2002). Cuttings from *Dryas octopetala* and *Cassiope tetragona* had poor rooting capacity (Paper II), although under natural conditions these species spread laterally along the ground, and weak adventive roots are formed (Söyrinki 1939; Oksanen &

Virtanen 1997). Cuttings from *Saxifraga oppositifolia* showed large rooting variation (Paper II), possibly related to ecotype variation (Crawford 1997; Kume et al. 1999).

Greenhouse cultivation produced a new generation of individuals of all propagated species, with the exception for *Bistorta vivipara*. During a four-month period (eight months for evergreen species) cultivated individuals attained the size of several year old plants in the study areas (Papers II, III & V). Cultivation of *B. vivipara* failed due to almost complete 'seedling' mortality during the first two weeks after germination, possibly due to high temperature and dehydration in the greenhouse (Paper II). High mortality of young *B. vivipara* was also observed under natural conditions in the study area (Paper I).

Fresh, woody *Salix* spp. cuttings planted in the field immediately after cutting had high rooting ability during one growing season, but very high mortality and slow growth rates during the years after planting (Paper V). Consequently, this was not a good method for restoration of the dry sites used in this experiment.

Field planting of cultivated transplants

Greenhouse propagated transplants were planted in disturbed sites in the field, near the original source for seeds and cuttings, and survival and growth were recorded during three growing seasons. Transplant survival was high in 8 of the 11 examined species (Paper III & V). All species with high survival occurred naturally in the disturbed sites or in a transition zone to intact vegetation. The three species with low survival mainly occurred naturally in intact *Dryas* heath vegetation (*Cassiope tetragona* and *Salix polaris*), or had variable transplant qualities (*Saxifraga oppositifolia*) (cf. Kume 1999; Paper II). Transplant mortality was highest during the first months after planting, and almost no mortality was observed during the subsequent seasons (Papers III & V). For the majority of species transplant size increased during the experiment (Paper III). This result showed that early survival is a critical stage for establishment for the transplants, as it is for naturally occurring seedlings in arctic and alpine vegetation (Bell & Bliss 1980; Bliss & Gold 1999; Paper I).

In the alpine study area jerking and browsing by muskox and sheep immediately following planting were the major death causes for *Salix phylicifolia* (Paper V). Later browsing seemed to increase lateral branching (Paper V), as also found by Tolvanen et al. (2001) and Bergmann (2002).

Planting in late summer had positive effects on transplant survival and growth, compared to planting in spring, for several of the Dovre species (Paper III), and this is also found in other studies (Urbanska & Chambers 2002). Low precipitation just before and after the early plantings can partly explain this result. Larger mean plant size for late planted transplants, observed in some species (Paper III), can be an advantage for further survival and growth.

Planting of transplants into peat soil had ambiguous effects on survival and growth in this investigation. Transplants of *Empetrum nigrum* ssp. *hermaphroditum*, *Papaver dahlianum* and *Oxyria digyna* grown in commercial peat soil were larger than those grown in natural soil (Paper III). The commercial peat soil had a supply of nitrogen, phosphorus and potassium, and minor additions of these nutrients increase vegetative growth in arctic and alpine vegetation (e.g. Klokk & Rønning 1987; Parson et al. 1994). The separate effect of nutrient supply was not tested in this study, but should be considered for future experiments. Transplants of *Salix phylicifolia* grown in native peat soil had lower survival and growth at exposed sites, compared to those planted in the original soil at the site (Paper V). Different capillary conductivity in the peat compared to the underlaying original soil at the site seemed to be a barrier to water transport between soil layers, causing drought in exposed localities (Bradshaw & Chadwick 1980). Tearing by wind during winter and soil desiccation during summer further reduced vitality of *S. phylicifolia* plants at exposed sites (Paper V), and this species can only be recommended for restoration in leeward sites with a stable snow layer during winter, which is the natural habitat for this species.

The use of native soil or roots for mycorrhiza inoculation were superfluous for the species in this study (Paper III). At the end of the third growing season mycorrhiza was present in all examined transplants of species known to have mycorrhiza (Miller 1992;

Väre et al. 1992), and infection level was independent of soil treatment (Paper III). Quick colonisation of mycorrhiza following plant establishment is in agreement with other studies (Allen et al. 1987; Jumpponen et al. 2002).

Results described in Papers II, III and V can be used for further development of methods using transplants in restoration. Further experiments should consider adding water at planting time, extended cultivation to increase initial planting size, nutrient supply, and protection against browsing animals. Established transplants can contribute further to recovery by creating safe sites for plant establishment (Urbanska 1997a; d), by influencing soil nutrient concentration and soil activity (Onipchenko et al. 2001), and by physical stabilisation of the environment (Whisenant 2002). However, despite improved methods for restoration, the recovery of severely disturbed sites in arctic and alpine vegetation has to be seen in a long time perspective due to the slow rates of natural succession, and slow vegetative growth (e.g. Urbanska 1997b; Forbes & Jefferies 1999; Forbes & McKendrick 2002).

RESTORATION IN MANAGEMENT OF ARCTIC AND ALPINE VEGETATION

As Clark (1997) pointed out, restoration ecology faces the double challenge of ensuring that ecologists are aware of the social context in which restoration is carried out, while at the same time ensuring that society is aware of the ecological possibilities and limitations of restoration. Any defined goal in restoration is only one of many alternative solutions, and the choice is based on values (Diamond 1987; Bradshaw 1997). Accordingly, goals will represent management ideals of the actual participants in a goal-formulating process.

In Paper IV a social, communicative approach was used to involve local people and stakeholders in generating future desired states for the study areas, based on the existing situation or “present state”. The results from Paper IV were further applied in Paper V to integrate the communicative approach in a site-specific restoration enterprise. The main focus was to investigate the participants’ attitudes towards using restoration ecology as part of a management strategy. Both the hands-off strategies of letting nature heal itself, and at the same time a wish to restore natural functions were recognised (Paper IV). The view on future management in general, and restoration activity in particular, seemed to be influenced by participants' relationship to the area and their view of nature (Paper IV). This is accordance with literature within the topics of place attachment (e.g. Buttimer & Seamon 1980; Sandell 2000), and view of nature (e.g. Passmore 1980; Emmelin 1993).

Participants on Dovre had to deal with specific management challenges related to the closedown of the firing range, and they had a pragmatic view on the use of restoration as a management strategy (Papers IV & V). Practical solutions, economic considerations, need for some immediate results, and some acceptance for introduced species was a part of this attitude. The participants on Svalbard had less defined management challenges to face, and their statements were less consistent and more divergent than on Dovre (Paper IV). Both strong support and total resistance to restoration as a management strategy were stated at Svalbard. The opponents claimed that a restored ecosystem in the wilderness is unnatural, and that restoration caused worse damage than the original traces of human impact. Arguments to support restoration were very similar in the two areas, focusing on ecology and aesthetics, but pure aesthetic arguments were more broadly accepted among the participants at Dovre. The satisfaction level of inhabitants and visitors was stated as a success-criteria; *"When people like it - it is a success"* (Paper IV).

Based on the statements from local people and stakeholders it is possible to formulate different scenarios or desired states, for future management of an area. In Paper IV a pragmatic scenario with a high acceptance level to restoration, and a puristic scenario with a restrictive use of restoration were outlined for each area. Accordingly there is no "right" alternative, but several possible courses of action depending on how the "desired state" is formulated. Which alternative to implement is often a political or economic decision, even though ecological knowledge is essential for formulation of realistic goals and for evaluating long-term ecological effects.

One characteristic of the statements supporting practical restoration was the strong belief that restoration will be successful (Paper IV). The original vegetation cover was considered the ideal success, and a majority of the participants expected restoration efforts to lead to this in the long run. The reality is that long-term ecological effects of restoration in arctic and alpine vegetation are hardly documented. However, based on existing ecological knowledge, restoration efforts compensating natural recovery can hardly be expected within a time scale of 100 years (Crawford 1997; Forbes & Jefferies 1999). Making society aware of the ecological possibilities and limitations of restoration seems to be an essential part of realistic goal formulation (Clark 1997; Higgs 1997; Ehrenfeld 2000), and requires serious focus in practical restoration enterprises.

Planting of willow (*Salix* spp.) cuttings was used to show how an integrated approach could be applied in the restoration of an area (Paper V). The ecological contribution was to develop a method using willow cuttings, and to evaluate the ecological effects of this method following field plantings. This included species selection, propagation and cultivation methods, site characteristics, and evaluation of survival and growth in the field. The technical or applied contribution was related to the logistics of production and planting of numerous willows, and economic calculations for this type of enterprise given the site-specific goals. Ecological and technical contributions dealt with *"What is possible?"*. The social or communicative contribution was to formulate goals including users and stakeholders desired states, or *"What is wanted?"* (Paper IV). In this particular case, this included the consideration of whether there is a need for restoration at all, demand for some immediate aesthetical effect, and selection of sites for restoration. The integrated approach used in this study (Paper V) made the willow cuttings interesting for future restoration in the study area, as it was both "possible" and "wanted". The long-term ecological effect of the method must be further evaluated. Implementation of the willow method in future management of this area will be a political and economic decision (Edwards & Abivardi 1997; Faye-Schøll & Martinsen 2002).

CONCLUSION AND FUTURE PERSPECTIVES

MAIN FINDINGS

Together the main findings in this thesis contribute to an integrated approach on restoration. However, several of the single items focus on either ecology, practical application, or social aspects.

- Recordings of seedlings naturally occurring in the field, and greenhouse germination of soil seed bank trials and fresh collected seeds showed that several common species reproduce regularly by seed on Svalbard.
- Natural recovery seems to be limited by seedling survival rather than the availability of viable seeds, and if native seed should be considered a source for restoration the critical seedling period must be circumvented.
- Greenhouse propagation and cultivation of plant individuals from seeds or cuttings of several common arctic and alpine species is practicable.
- Survival and growth transplants planted in the field are closely related to species-specific ecological preferences. Initial plant size and water and nutrient availability influence development of transplants, but should be further investigated.
- Browsing by wild and domestic herbivores can be a problem immediately after planting of large transplants.
- Peoples' attitude to the use of restoration as a management strategy is related to their attachment to an area, and their view of nature. Those facing specific management challenges are in general more focused on finding good solutions.
- Stakeholders and local people mainly use ecological and aesthetical arguments to support restoration, and some immediate effects of the enterprise are requested.
- There seems to be a contrast between the very strong belief among stakeholders and local people, that restoration will be successful and the "original" vegetation completely restored, compared to what is realistic in ecological terms.
- It is possible to integrate ecological, technical, and social considerations in evaluation of a restoration method applied in a specific site or situation.

FURTHER DEVELOPMENT OF AN INTEGRATED APPROACH

A declaration from the Parliament in 1999 was the first real initiative for using restoration of disturbed wilderness as a management strategy in Norway. The area concerned was Hjerkinn Firing Range on Dovre Mountain, and the goal for the restoration was to "*restore the area in a way that entails considerable profit for the nature*". In accordance with this, the Norwegian Ministry of the Environment in 2001 affirmed a national strategy to increase the total area of wilderness in Norway. Restoration of wilderness areas brings forward new perspectives on nature management. The traditional approach to nature conservation has been a clearly minimalistic "hands-off" approach (Emmelin 1986, Aasetre 2000). The active intervention that is essential in restoration can be a contrast to this approach, as it implies "hands-on" management to restore "hands-off" wilderness characteristics (Noss 1995). Restoration of wilderness will thus influence our perception of these areas.

An integrated approach is essential to the application of restoration ecology in future management of arctic and alpine areas. There is a need for further research both within the separate subjects of restoration, and on the actual integration *per se*. Future research should focus on processes of natural recovery, long-term ecological effects of restorations, further improvement of restoration methods (including those described in this thesis), and single species' qualities for restoration purposes. For the application of restoration in large-scale enterprises, the integration of scientific and technical knowledge, including economic issues, should be brought into focus. Society's demand for plain answers and immediate results will be a challenge in future management. The identification of alternative desired states as a planning tool should be further investigated. This thesis has shown that when facing a concrete management challenge, people feel committed to come up with good solutions. The contrast between *"What is possible?"* and *"What is wanted?"* must be enlightened, and include contributions from ecology and social sciences.

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Paper I

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Plant recruitment in the High Arctic: Seed bank and seedling emergence on Svalbard

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Abstract. Composition and density of the soil seed banks, together with seedling emergence in the field, were examined on Svalbard. 1213 soil samples were collected from six dry-mesic habitats in three regions representing various stages of colonization from bare moraines to full vegetation cover and spanning a range of typical nutrient and thermal regimes. Of the 165 vascular plant species native to Svalbard, 72 were present as mature plants at the study sites and of these 70% germinated seed. Proglacial soil had 12 seedlings per m^2, disturbed *Dryas* heath 131, intact *Dryas* heath 91, polar heath 715, thermophilic heath 3113, and a bird cliff 10437 seedlings. Highest seed bank species richness was at the thermophilic heath (26 species). Seedlings of 27 species emerged in the field, with fewer seedlings in disturbed habitats (60 seedlings per m^2) than in intact *Dryas* heath (142), suggesting that an absence of 'safe sites' limited seedling establishment in disturbed habitats. Measurement of seedling emergence in the field increased awareness of which species are able to germinate naturally. This may be underestimated by up to 31% if greenhouse trials alone are used, owing partly to unsuitability of greenhouse conditions for germination of some species and also to practical limitations of amount of soil sampled. Most thermophilic species failed to germinate and some species present at several sites only germinated from the thermophilic heath seed bank, suggesting that climate constrains recruitment from seeds in the High Arctic.

Keywords: Colonization; Disturbance; *Dryas octopetala*; Reproduction; Safe site; Species diversity; Species richness.

Nomenclature: Elven & Elvebakk (1996).

Introduction

Habitat disturbance through overgrazing, freeze-thaw action and periglacial processes, as well as anthropogenic disturbance, is common in the Arctic (Forbes et al. 2001), providing enhanced opportunities for seed germination (Freedman et al. 1981). Changing climate also creates new areas for colonization following glacier regression. Germination from seed banks is thus important for species establishment in these disturbed or recently exposed areas (Ebersole 1989).

Most Arctic plant species have viable seed banks (review by McGraw & Vavrek 1989). These are generally larger than previously assumed and are of comparable size with those of temperate forests, although of lower species richness (e.g. Larsson & Lévesque in press). Nevertheless, there is wide spatial variation, with the largest and most diverse seed banks found beneath snow bed and heath vegetation (Fox 1983) or solifluction lobes (McGraw et al. 1991). Similarly, seedling density varies widely among and within sites and is generally highest in disturbed communities (Bliss & Gold 1999). Seed bank size is often greater beneath intact vegetation than disturbed or fragmented heaths or newly deglaciated areas, owing to the proximity of dispersal sources. Competition, however, may reduce the number of surviving seedlings.

There are 165 vascular plant species native to Svalbard (Elven & Elvebakk 1996), a greater species richness than other areas at similar latitudes (Kartesz 1994; Vechov & Kuliev 1996). Knowledge about their recruitment, however, is limited. Eurola (1972) found germinable seeds in 60% of 63 species collected and Brochmann & Steen (1999) estimated that over 60% of the total vascular species reproduced sexually. However, they did not investigate seed banks or which species germinate in the field in Svalbard.

Knowledge of the recruitment potential of Svalbard plants by seeds and bulbils is essential to understand plant population dynamics and responses to climate change or physical disturbance. This paper integrates data from different geographical regions of Svalbard to provide a broad picture of recruitment. We integrate data from four studies to determine which species recruit from seeds and bulbils on Svalbard. The following questions are addressed: 1. What is the diversity and density of the seed banks in mesic-dry vegetation types? 2. Does the seed bank represent the established vegetation in the habitats studied? 3. Which factor most limits seedling emergence in the field?

Study locations

Six different habitats (Table 1) were studied in three geographical regions on Spitsbergen, Svalbard. These were polar heath, bird cliff and proglacial habitats adjacent to the NW coast (Brøggerhalvøya and Sarsøyra, 78°43'-57' N, 11°20'-12°20' E), intact and disturbed *Dryas* heath in Adventdalen (78°11' N, 15°40' E) and thermophilic heath in Colesdalen (78°7' N, 15°8'-16' E), both in central Spitsbergen. These habitats constitute a climatic and nutrient gradient from the thermophilic heath, through the relatively warmth demanding *Dryas* heath, to the widespread polar heath and finally the proglacial habitat. The bird cliff represented climatically intermediate but highly nutrient-enriched habitat.

NW coast: Polar heath was sampled on the Brøggerhalvøya and Sarsøyra peninsulas (vegetation detailed by Nilsen 1997). The bird cliff lay under Simlestupet (390 m a.s.l.) along Kjærstranda, NW Brøggerhalvøya. Vegetation cover, dominated by mosses and members of the *Ranunculaceae*, *Saxifragaceae* and *Poaceae*, was 100%. Proglacial habitats lay in front of Midtre Lovénbreen, 4 km east of Ny-Ålesund, Brøggerhalvøya. Here sites (vascular vegetation cover 0-11%) with little fluvial re-working were selected, allowing surface ages to be estimated from aerial photographs (Norwegian Polar Institute) at ca. 2 to 100 yr (Hodkinson et al. 2003).

Adventdalen: Sites were dominated by *Dryadion* communities (Rønning 1965), together with heath, wetland and snow-bed plant associations (Brattbakk 1984). *Dryas* sites were situated in intact heath (ca. 90% cover), dominated by *D. octopetala*, *Cassiope tetragona* and *Salix polaris*. Disturbed sites were within a *Dryas* heath area, one by a roadside, the other next to a mining installation. Distances between individual sites was ca. 30 m and thus transmission of seeds and bulbils between the intact and disturbed areas was expected to be frequent. Physical disturbance occurred > 20 yr ago with the removal of the surface organic layer but re-vegetation is slow, with cover < 10%.

Colesdalen: A thermophilic south-facing valley slope site, the only Svalbard location of *Campanula rotundifolia*. *Vaccinium uliginosum* is known to flower and fruit here and *Betula nana* is abundant (Alsos et al. 2003).

Material and Methods

Our integration of four studies presents some variation in sampling and germination methods as described in Table 1 and below. How these differences impact on the germinable seed bank observed is unknown but similar variations in sampling dates and germination methods exist among previous studies (e.g. Archibold 1984; McGraw et al. 1991). Thus, our inter-habitat comparisons compare in accuracy with inter-study comparisons made by, for example, McGraw & Vavrek (1989). Our purpose was to identify species capable of reproducing by seeds in Svalbard, and this variation in methodology may increase the chance of meeting the germination requirements for individual species.

Table 1. Collection details for soil seed bank samples from Svalbard.

Study region	Habitat	Number of sites	Soil cores per site	Total number of cores	Core diameter cm	Total area sampled, m^2	Collection date
Colesdalen	Thermophilic heath	4	50	200	3.5	0.20	26 - 29 August 1999
NW coast	Polar heath	32	25	792 [1)]	3.5	0.76	9 July - 7 August 2000
	Bird cliff	1	25	25	3.5	0.02	19 July 2000
	Proglacial	5	20	100	6.5	0.33	27 July 2000
Adventdalen	*Dryas* heath						
	Intact	2	24	48	7 × 7 [2)]	1.29	2 July 2000
	Disturbed	2	24	48	7 × 7 [2)]	1.29	2 July 2000

[1)] 800 cores were sampled but eight were lost in transit; [2)] Seven cores of diameter 7 cm were taken and merged to form one sample.

Organic soil accumulates slowly in nutrient-poor areas on Svalbard (2000 yr for 5-7 cm soil, Hodkinson et al. 2003) and was less than 2 cm deep at many sites. For a 4 cm deep organic soil in Adventdalen, 88% of emerging seedlings and the highest species diversity was in the top 2 cm (D. Hagen unpubl.). Therefore, the soil layers and the transient, short-term and long-term persistent components of the seed bank were not differentiated (see Thompson et al. 1997). The top 2 cm of organic soil was collected together with bryophytes and litter.

In polar heath and thermophilic heath habitats, soil samples were collected (Table 1) within 10 cm of focus species to maximize the chance of capturing dispersed seeds. In the polar heath, samples were taken adjacent to *Dryas octopetala, Luzula arcuata* ssp. *confusa, Saxifraga oppositifolia* and *Silene acaulis,* all species that are grazed by floral herbivores such as reindeer and geese (Cooper & Wookey 2003). Similarly, in thermophilic heath *Betula nana, Campanula rotundifolia* and *Vaccinium uliginosum* were the focus species. Separation between samples varied between 0.4 and 5 m according to the distribution of the focus species. Bird cliff samples were collected 2-10 m apart without a target focus species whereas proglacial samples were taken from five sites approximately equally spaced over an 800 m distance away from the glacier snout. At each site replicate samples were taken 2-10 m apart. Intact *Dryas* heath and physically disturbed sites in Adventdalen were ca. 30 m apart, and within each site the samples were taken ca. 5 m apart. Site size was ca. 50 m × 50 m for the polar heath, bird cliff and thermophilic sites, and 20 m × 20 m for the proglacial, intact and disturbed *Dryas* heath sites. Samples were cooled (2-6 °C) during transport and stored in paper bags at 0.5 °C for 5-7 wk. Species lists were compiled of the surrounding vegetation within each sampling site and compared with existing lists (Herbarium TROM).

Greenhouse germination of seeds from soil collected on Svalbard

Samples were kept at – 5 °C for 5 wk, then thawed at 0.5 °C for 3 d and acclimatized at 4 °C for 4 d. Volumes of soils from intact and disturbed *Dryas* heath sites were reduced by sieving and washing (see Thompson et al. 1997). Soil samples from the polar heath, bird cliff, proglacial habitat and thermophilic heath were spread thinly on filter paper in plastic petri dishes and germinated at 18 °C in a greenhouse, using a 24-hr photoperiod (150 µmol) over 12 wk (11 for thermophilic heath) simulating the maximum Svalbard summer period. Samples from intact and disturbed *Dryas* heath were placed on commercial sterilized soil in aluminium foil boxes and germinated at 22 °C in a greenhouse over 14 weeks. These samples were stirred in weeks 3 and 11, and gibberillic acid (1 ppm) was added in week 12. All samples were moistened every second day, and seedlings counted weekly. Unidentified seedlings were transplanted to a mixture of peat and perlite and grown at 15 °C until identification was possible. Some graminoids were cold treated (0.5 °C) to initiate flowering and thus facilitate identification. Seedlings that died before identification were recorded. For simplicity, the term 'seedling' is used for germination both from seeds and asexual bulbils, including those of *Bistorta vivipara, Saxifraga cernua* and *S. foliolosa*.

Plate 1. Dryas heath at Ossian Sarsfjellet, Kongsfjorden, North West coast of Svalbard. Photo: Inger Greve Alsos.

Seedling emergence in the field

Three intact and three disturbed *Dryas* heath sites (each ca. 20 m × 20 m) were established in Adventdalen, next to the seed bank sampling sites. At each site ten permanent plots (0.5 m × 0.5 m) were located randomly and the identity and number of seedlings emerging within them recorded in early August each year from 1998 to 2000. Seedlings were mapped to avoid repeated counting in subsequent years.

Statistical analysis

The Mann-Whitney *U*-test was used to compare two independent samples for differences in seedling density between the intact and disturbed *Dryas* heath habitats and to compare seedling emergence in the field and greenhouse for these habitats. Statistical tests were not applied to differences between other sites owing to variation in sampling methods used.

Results

Germination of soil in the greenhouse

Seed bank diversity

The germinable seed bank comprised 50 species from 11 families (Table 2). Families with the highest richness and density of seedlings were the *Caryophyllaceae, Brassicaceae* and *Saxifragaceae*. All but two germinating species were recorded from the surrounding vegetation (Table 2). Six families, *Betulaceae, Polemoniaceae, Scrophulariaceae, Campanulaceae, Asteraceae* and *Cyperaceae*, were found in surrounding vegetation but not in the germinable seed bank. Seed bank diversity increased with that of the surrounding vegetation, with the relationship between number of species in the seed bank (S) and in the surrounding vegetation (V) expressed by the equation

$$S = 0.68V - 5.62 \ (n = 6, R^2 = 0.91) \qquad (1)$$

Seed bank size

Germinable seed bank (Table 2) size was lowest in the proglacial habitat (12 seedlings m^{-2}) and highest at the bird cliff (10437). Thermophilic heath had a larger seed bank (3113 seedlings m^{-2}) than polar heath (715), disturbed *Dryas* heath (131) and intact *Dryas* heath (91). Density of germinating seeds was not significantly different between disturbed and intact *Dryas* habitats (Mann-Whitney $U = 961.00$; $P = 0.157$). Highest densities of seedlings of individual species were at the bird cliff and included *Saxifraga cespitosa* and *Cochlearia groenlandica* (4366 and 2827 seedlings per m^2, respectively). Other species with ≥ 100 seedlings per m^2 at any habitat were *Bistorta vivipara* (bulbils), *Cerastium arcticum, Draba daurica, Luzula arcuata* ssp. *confusa, Saxifraga cernua* (bulbils), *S. cespitosa,* and *S. nivalis*. No seeds of the woody shrubs, *Cassiope tetragona, Dryas octopetala* or *Salix polaris*, germinated from the soils of the NW coast although these species were often dominant. *Dryas octopetala, Luzula arctica, Stellaria longipes* and *Trisetum spicatum* were common in the vegetation at most habitats, but germinated only from thermophilic heath. By contrast, *Betula nana, Campanula rotundifolia* and *Vaccinium uliginosum* failed to germinate even from the thermophilic heath.

Seedlings recorded in the field

Seedlings of 27 species from 12 families were recorded in permanent plots in 1998-2000, with a mean of 19 and 15 species at the disturbed and intact *Dryas* heath respectively (Table 3). Seedlings of the common species, *B. vivipara, C. arcticum, D. octopetala, Luzula* spec. and *S. cernua* were recorded in all three years. The highest numbers of species, and the only germination of *C. tetragona,* occurred in the exceptionally warm summer of 1998, although most species germinated in both habitats every year. *B. vivipara* showed near total replacement of individuals between years (i.e. ca. 100% mortality). *B. vivipara* had the highest seedling density in both intact *Dryas* heath (69 seedlings per m^2) and disturbed habitat (24). *Oxyria digyna* (12) and *Luzula* spec. (10) had the second highest density in intact and disturbed *Dryas* heath respectively. Numerous species displayed low seedling densities (mean < 1 seedling per m^2). Total seedling density was higher in the intact *Dryas* heath (142 seedlings per m^2) than the disturbed heath (61) (Table 3) (Mann-Whitney $U = 155.00$, $P < 0.001$).

Comparison between seed germination in the field and greenhouse

All species with germinable seeds in the intact and disturbed *Dryas* heath soils in the greenhouse were present as seedlings on field plots and as mature plants in the surrounding vegetation. Seedlings of *Pedicularis hirsuta* and *Silene uralensis* ssp. *arctica*, emerged in the field but not the greenhouse. Seedlings of 17 species germinated from all *Dryas* heath soils in the greenhouse compared with 27 species in the field, but only 14 were common to both studies (Tables 2 and 3). These were *B. vivipara, C. arcticum, Sagina nivalis, Ranunculus nivalis, Papaver dahlianum, Cardamine bellidifolia, Draba* spec., *S. cernua, S. cespitosa,*

Table 2. Seedling germination from soil samples collected from six habitats on Svalbard. Density values (mean and SE) are expressed as seedlings · m^{-2}. All germinating species except the two marked † from proglacial samples were found as mature plants in the surrounding vegetation. Species observed in the surrounding vegetation but not as seedlings germinating from the collected soils are marked with x in the table. Those marked by * did not germinate from soil collected from any habitat. Species are organised by families, according to Lid & Lid (1994).

Habitat / Area NW coast	Polar heath NW coast	Bird cliff NW coast	Proglacial Colesdalen	Thermophilic heath Adventdalen	Intact *Dryas* heath Adventdalen	Disturbed *Dryas* heath
Species	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
*Salix reticulata**	x					
Salix polaris	x		x	62 ± 24	x	x
*Betula nana**				x	x	
Bistorta vivipara (bulbils)	13 ± 5	x	x	327 ± 84	3 ± 2	10 ± 3
Koenigia islandica				21 ± 21		
Oxyria digyna	3 ± 2	x			x	x
Arenaria spec.*			x			
Cerastium arcticum	11 ± 4	x	x	114 ± 35	3 ± 2	2 ± 1
Cerastium arcticum × *regelii*	3 ± 3			36 ±18		
Cerastium regelii	x			26 ± 12		
Cerastium spec.				21		
*Minuartia biflora**				x		
Minuartia rossii†	x		2 ± 2			
Minuartia rubella	1 ± 1		x			x
Minuartia spec.	1 ± 1					
Sagina nivalis	x		x	x	1 ± 1	10 ± 6
Silene acaulis	4 ± 2		x		x	x
Silene furcata ssp. *furcata*				5 ± 5		x
Silene uralensis ssp. *arctica**	x					x
Stellaria longipes				5 ± 5	x	x
Ranunculus nivalis	x			x	6 ± 3	2 ± 2
Ranunculus pygmaeus	3 ± 2	x		21 ± 16		
*Ranunculus sulphureus**		x		x		
Papaver dahlianum	x			x	2 ± 1	3 ± 2
Braya purpurascens		x	2 ± 2			
Cardamine bellidifolia	14 ± 4			26 ± 12	1 ± 1	
Cochlearia groenlandica	20 ± 8	2827 ± 1574				x
*Draba alpina**			x		x	x
Draba arctica†	x		7 ± 5			x
Draba corymbosa	3 ± 2					
Draba daurica	x	624 ± 232		5 ± 5		5 ± 2
Draba lactea	5 ± 3					
Draba nivalis	x	42 ± 42		16 ± 9		x
Draba norvegica	x	42 ± 42		68 ± 21	1 ± 1	2 ± 1
Draba oxycarpa	4 ± 2			x	1 ± 1	2 ± 1
*Draba subcapitata**						x
Draba spec.				5		
Chrysosplenium tetrandrum		790 ± 390				
*Saxifraga aizoides**	x					
Saxifraga cernua (bulbils)	16 ± 5	166 ± 78			5 ± 2	4 ± 3
Saxifraga cespitosa	205 ± 48	4366 ± 1359		343 ± 82	12 ± 4	26 ± 8
Saxifraga foliolosa (bulbils)	1 ± 1					
Saxifraga hieracifolia	x	42 ± 42		x	x	
Saxifraga hyperborea	4 ± 4	x		5 ± 5		
Saxifraga hyperborea × *rivularis*	151 ± 35					
Saxifraga nivalis	4 ± 2	541 ± 318		395 ± 111	x	
Saxifraga oppositifolia	39 ± 10	x	x	5 ± 5	x	
Saxifraga rivularis	3 ± 2	83 ± 83		16 ± 12		
Saxifraga tenuis	25 ± 10			16 ± 16		
Dryas octopetala	x		x	135 ± 32	x	x
Potentilla hyparctica		x		10 ± 7		3 ± 2
Potentilla pulchella						1 ± 1
Cassiope tetragona				x	4 ± 2	4 ± 2
*Vaccinium uliginosum**				x		
*Polemonium boreale**				x		
*Euphrasia frigida**				x		
*Pedicularis hirsuta**	x		x	x	x	
Pedicularis lanata ssp. *dasyantha**					x	

Table 2. *(cont.)*

Habitat / Area NW coast	Polar heath NW coast	Bird cliff NW coast	Proglacial Colesdalen	Thermophilic heath Adventdalen	Intact *Dryas* heath Adventdalen	Disturbed *Dryas* heath
Species	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
*Campanula rotundifolia**				x		
*Taraxacum arcticum**				x		
*Juncus biglumis**	x			x		
Luzula arctica	x			31 ± 16	x	x
Luzula arcuata ssp. *confusa*	39 ± 8			369 ± 44	48 ± 8	35 ± 8
*Carex misandra**	x				x	
*Carex nardina**	x					
*Carex rupestris**	x		x		x	
Alopecurus borealis	3 ± 3			x	x	
*Festuca edlundiae**						x
Festuca rubra ssp. *arctica*				31 ± 13	x	x
*Hierochloë alpina**				x		
Phippsia algida	7 ± 4					
Poa alpina var. *alpina*					2 ± 1	18 ± 7
Poa alpina var. *vivipara**	x			x		
Poa arctica			x	5 ± 5	x	1 ± 1
Poa pratensis ssp. *alpigena**		x		x		
Trisetum spicatum				31 ± 15	x	x
Germinable seed bank density						
Unidentified (seedling.m^{-2})	135 ± 19	915 ± 330	–	961 ± 162	3 ± 2	4 ± 3
Identified to species (seedling.m^{-2})	580	9522	12	2126	88	127
Total density (seedling.m^{-2})	715 ± 76	10437 ± 2773	12 ± 7	3113 ± 327	91 ± 13	131 ± 18
Species richness						
Number of seed bank species in germinable seed bank	25	10	3	26	13	16
Number of additional species in surrounding vegetation	22	10	13	19	20	17
Total number of species in surrounding vegetation	47	20	14	45	33	33

Potentilla hyparctica, P. pulchella, C. tetragona, Luzula spec. and *Poa* spec. *Draba, Luzula* and *Poa* spec. were difficult to determine in the field, but species germinating in the greenhouse were *L. arcuata* ssp. *confusa, Poa alpina* var. *alpina, P. arctica, Draba daurica, D. norvegica, D. oxycarpa*. It is reasonable to presume that the same species germinated in the field. Thus, 31 of the 44 species (70%) present among the mature vegetation in *Dryas* heath in Adventdalen showed ability to germinate in the field. Seventeen of the 44 (39%) germinated in the greenhouse, suggesting that the germination trials under-represented seed diversity by 31%.

The density of seedlings recorded in disturbed *Dryas* heath soils in the greenhouse was higher than in the field (131 and 61 seedlings per m^2, respectively; Mann-Whitney U = 498.00, P = 0.022). By comparison, for intact *Dryas* habitats, seedling density was higher in the field (142 versus 91 seedlings per m^2; Mann-Whitney U = 461.00, P = 0.008).

Discussion

Seed bank diversity

This study covers 72 of the 165 native Svalbard vascular plants, 50 of which germinated from soil seed banks or in the field. Thirty-five of these species (or congeners) have been recorded elsewhere at similar densities (e.g. in Thompson et al. 1997; Bliss & Gold 1999; Larsson & Lévesque 2003). The germination of a further 14 taxa, *Cerastium arcticum* × *regelii*, *Draba daurica, D. norvegica, D. oxycarpa, Minuartia rossii, Papaver dahlianum, Potentilla hyparctica, Ranunculus pygmaeus, Sagina nivalis, Saxifraga hyperborea* × *rivularis, S. rivularis, S. tenuis, Silene furcata* and *Trisetum spicatum* appear unreported in the Arctic literature.

Apparent lack of a germinable seed bank for 24 species may result from local or scattered distribution (e.g. *Polemonium boreale*) (Elven & Elvebakk 1996), low seed germinability (e.g. *Ranunculus sulphureus, Taraxacum arcticum*) (Eurola 1972), failure to break dormancy (e.g. *Carex* spp.) (Schuetz 2000), or inad-

Table 3. Seedlings observed in the field in intact and disturbed *Dryas* heath in Adventdalen, Svalbard. Mean and standard error of seedling densities (number of seedlings m^{-2}) during three years (1998-2000). The number of years when seedlings were present is indicated. Species organised by families, according to Lid & Lid (1994). Number of plots of each habitat = 30. Total area studied in each habitat = 7.5 m^2. Species which also germinated in the greenhouse trials from these habitats are marked with *.

	Intact *Dryas* heath			Disturbed *Dryas* heath		
Species	Mean	± SE	Years	Mean	± SE	Years
Salix polaris	1.7	± 0.5	2	1.1	± 0.4	3
*Bistorta vivipara**	68.8	± 8.2	3	23.6	± 7.9	3
Oxyria digyna	12.1	± 3.3	3	0.1	± 0.1	1
*Cerastium arcticum**	0.4	± 0.2	3	0.4	± 0.2	3
Minuartia cf. *rubella*				0.3	± 0.1	2
Sagina cf. *nivalis**	0.6	± 0.6	1	1.4	± 0.6	3
Silene acaulis	0.1	± 0.1	3	0.1	± 0.1	1
Silene uralensis ssp. *arctica*				0.7	± 0.2	3
Stellaria longipes	2.6	± 0.6	3	0.3	± 0.2	2
*Ranunculus nivalis**	0.1	± 0.1	1			
Ranunculus spec.	0.1	± 0.1	1			
*Papaver dahlianum**				6.0	± 1.4	3
*Cardamine bellidifolia**	3.4	± 0.8	3			
Draba nivalis				0.6	± 0.3	2
Draba spec.*	0.6	± 0.2	3	1.9	± 0.4	3
*Saxifraga cernua**	1.1	± 0.8	3	3.7	± 0.8	3
*Saxifraga cespitosa**				0.8	± 0.3	2
Saxifraga oppositifolia	0.5	± 0.3	2	0.5	± 0.3	3
Dryas octopetala	7.6	± 1.8	3	2.3	± 0.8	3
*Potentilla hyparctica**	0.1	± 0.1	1	0.4	± 0.1	3
*Potentilla pulchella**				0.3	± 0.2	3
*Cassiope tetragona**	0.1	± 0.1	1			
Pedicularis hirsuta	13.1	± 2.8	3			
Luzula spec.*	14.3	± 2.8	3	9.8	± 1.5	3
Festuca cf. *rubra*	0.1	± 0.1	1	1.3	± 0.4	2
Poa sp.*	0.2	± 0.1	2	0.1	± 0.1	3
Trisetum spicatum				0.3	± 0.2	2
Seedling density						
Unidentified density	12.9	± 3.8	3	4.5	± 1.4	3
Total density	141.6	± 11.9		60.5	± 10.3	
Species richness						
Number of species: 3-yr total	20			22		
Mean no. species.yr^{-1}	15			19		

equate climate conditions for seed production (*Betula nana, Vaccinium uliginosum, Campanula rotundifolia*) (Alsos et al. 2003). Rare and thermophilic species appear poorly represented owing to their scattered distribution within Svalbard (Elven & Elvebakk 1996).

Seed bank density

Some species found below the bird cliff had a much higher density of germinable seeds in Svalbard than reported elsewhere, e.g. *Chrysosplenium tetrandrum* 790 seedlings per m^2 compared with 39 - 204 (Leck 1980), *Cochlearia groenlandica* 2827 per m^2 compared with 752 (Freedman et al. 1981) and *Saxifraga cespitosa* 4366 per m^2 compared with 10 - 80 (Larsson & Lévesque 2003) and 33 (Bliss & Gold 1999). This probably results from the warm southern exposure and high levels of nutrients (Wookey et al. 1995). Density of germinating seeds varied among habitats, with bird cliff soils having three times more seedlings per m^2 than the thermophilic heath, 10 × more than the polar heath, 100 × more than the *Dryas* heaths and 1000 × more than the proglacial habitat. Thus, bird cliff habitats, though limited in area, may represent important seed sources, especially when uphill of coastal plains.

The large seed bank at the thermophilic heath may reflect both favourable microclimate and sampling date. This habitat, sampled in autumn, included short-lived seeds that normally germinate in spring and therefore may not remain in the seed bank by the time of sampling (mid-summer) at the other habitats e.g. arctic *Salix* spp. (Densmore & Zasada 1983). Nevertheless, the seed bank was large compared to other arctic habitats where soil was sampled after seed maturation (Fox 1983; Archibold 1984), suggesting a local climate impact.

Seed bank representation of established vegetation

Seed banks generally represented the established vegetation of sample areas, with the noticeable exception of dwarf shrubs. *Salix polaris, Dryas octopetala* and *Cassiope tetragona* were common in the vegetation but were poor germinators in seed bank trials. Svalbard *Dryas* normally has low germinability (Cooper unpubl.) but this increases under experimental warming (Wookey et al. 1995) or exceptionally warm summers (Hagen 2002), suggesting a thermophilous response.

Lack of a germinable seed bank for *C. tetragona* at the thermophilic slope may relate to germination requirements (Eurola 1972) or to its transient nature (Fox 1983). The short-lived nature of its seeds, its abundance in the seed rain, rarity in the total seed bank and absence/sparseness in the germinable seed bank elsewhere evidences this idea (McGraw et al. 1991; Lévesque & Svoboda 1995; Molau & Larsson 2000). On our thermophilic site this may have been compounded by low plant densities.

Two species, *M. rossii* and *Draba arctica,* germinated from proglacial soils but were unrepresented in the surrounding vegetation, suggesting longer distance (> 20 m) seed dispersal. The apparent germination from seed of *Minuartia rossii* is surprising since it rarely flowers on Svalbard (Elven & Elvebakk 1996), although seeds of related species may survive in soil for 100 yr (Thompson et al. 1997).

Seed banks and recruitment on disturbed and proglacial areas

Of the 14 species present as mature plants on the proglacial areas, 11 were recorded in germinable seed banks from other habitats, but two, *Pedicularis hirsuta* and *Carex rupestris*, did not germinate from any soil. The remaining *Braya purpurascens* was present in both mature vegetation and seed bank. Three proglacial species, *D. arctica*, *B. purpurascens* and *M. rossii* are only locally abundant in Svalbard (Elven & Elvebakk 1996) and were absent from germinable seed banks of other habitats. All species present as mature plants must have colonized within the last 100 yr and have thus reproduced under the prevailing climate.

Proglacial habitats and disturbed *Dryas* heath represent pioneer stages of community assembly, predominantly bare ground supporting scattered individual plants. Differences in community development relate to distance from dense vegetation (Ryvarden 1971), sources of seed and a developed seed bank (Stöcklin & Bäumler 1996) and the influence of the glacier on microclimate (Matthews 1992). Nine species of plant common to the proglacial areas and disturbed heath were found as seedlings in the field and in greenhouse studies. These species, *Bistorta vivipara, Cerastium arcticum, Draba alpina, D. octopetala, Minuartia rubella, Poa alpina, S. nivalis, S. polaris* and *Silene acaulis,* thus have high recruitment potential.

Seedling recruitment in intact versus disturbed Dryas heath

Common species in greenhouse trials were frequently observed as seedlings in the field in 1998-2000, e.g. *C. arcticum, Draba nivalis, Luzula arcuata* ssp. *confusa, Saxifraga cernua* and *S. oppositifolia* (Tables 2 and 3). Most have high fresh seed germination (Eurola 1972; Hagen 2002) suggesting regular reproduction by seeds in Svalbard. A higher number of species germinated in the field than in the greenhouse, indicating soil germination trials alone may underestimate seed bank species richness by up to 31% (see also Thompson et al. 1997; Molau & Larsson 2000). The greater soil area studied in the field than the greenhouse (7.5 m^2 vs. 1.29 m^2, respectively) probably accounted for some of the difference. In addition, greenhouse trials failed to meet the germination requirements of some species that successfully germinated in the field, such as *Pedicularis hirsuta,* possibly due to its hemiparasitic association with *S. polaris*.

Seedling density in the field was higher in intact than disturbed *Dryas* heath but differences in greenhouse trials was not significant. Disturbed *Dryas* heath had a higher seedling density in greenhouse versus field measurements whereas for intact *Dryas* heath the relationship was reversed, suggesting that enhanced early growth under greenhouse conditions was advantageous to seedlings from disturbed heath. By contrast, seedlings from intact heath probably had an abundance of 'safe germination sites'. Thus, seedling mortality, linked to desiccation (Jumpponen et al. 1999) and poor growth (Bell & Bliss 1980) may be higher in disturbed habitats. Mature vegetation provides microclimatically stable safe sites compared with bare or disturbed ground (Coulson et al. 1993). The most abundant species, *B. vivipara,* had lower germination density in the greenhouse than in both field habitats ($P < 0.001$), which may result from high bulbil mortality and death during storage (Elmqvist & Cox 1996).

This higher germination from disturbed sites in greenhouse trials suggests that initial colonization is from the seed bank (see also Leck 1980) rather than freshly dispersed seeds or vegetative runners. However, vegetation cover in the disturbed *Dryas* heath remains low after 20 yr, suggesting that recruitment is limited by the availability of microsites rather than the presence of seed.

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Paper II

Propagation of native Arctic and alpine species with a restoration potential

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Arctic and alpine plant communities today are subject to an increasing frequency and intensity of anthropogenic disturbances. Good understanding of reproductive behaviour and regenerative capacity of native species is important in a restoration situation following human disturbance in Arctic and alpine vegetation. Seeds, bulbils or cuttings from 12 native Arctic and alpine species were collected from Longyearbyen in Svalbard and Dovre Mountain on the Norwegian mainland. Propagation ability was tested in greenhouse conditions. Seeds of *Papaver dahlianum*, *Oxyria digyna*, *Luzula arcuata* ssp. *confusa*, and bulbils of *Bistorta vivipara* all had more than 50 % germination. *Dryas octopetala* had less than 10 % germination. Both quick and slow germinators were identified among the tested species. Seed storage temperature (+4 °C, -1 °C and -20 °C) showed no overall effect on germination. The rooting capacity of cuttings from evergreen and deciduous species was tested. *Arctostaphylos uva-ursi*, *Empetrum nigrum* ssp. *hermaphroditum*, *Vaccinium vitis-idaea*, *Salix herbacea* and *S. polaris* had more than 70 % rooting ability, while *Dryas octopetala* and *Cassiope tetragona* had less than 10 %. *Saxifraga oppositifolia* showed large variation in rooting ability, ranging from 20 - 90 %. The species with high germination and rooting ability are used in an extended restoration experiment in the study areas.

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Physical stress and habitat disturbances are the dual adversities that Arctic and alpine plants must adapt to and survive under (Billings 1992; Crawford 1997a). Low temperatures, short growing seasons, low resource availability, and oscillating environmental conditions are the most striking physical characteristics of Arctic habitats (Billings 1974, 1987; Crawford 1997a; Shaver et al. 1997). Habitat instability—both temporally and spatially—is an additional factor affecting Arctic plant survival (Murray 1987; Oksanen & Virtanen 1997), and plays an important role in creating community structures (Picket & White 1985*). Cryoperturbation, solifluction, water and ice movements bring instability to the surface (Walker & Walker 1991), and can bring changes in soil and vegetation qualities (Walker 1997). The survival of plants in the Arctic is probably more related to their ability to resist fluctuations and environmental uncertainties than their ability to adjust to harsh physical conditions (Crawford 1997b).

In addition to natural disturbances, Arctic and alpine plant communities are today subject to an increasing frequency and intensity of anthropogenic disturbances (Reynolds & Tenhunen 1996; Crawford 1997b; Forbes et al. 2001). The scale, frequency and intensity of anthropogenic disturbances are essential to describe their effect on Arctic communities (MacMahon 1997; Shaver et al. 1997). Direct anthropogenic disturbances (Forbes 1997), related to human settlements, mining, military activity and tourism have occurred in the Svalbard archipelago and Dovre Mountains on the Norwegian mainland. Roads, houses and technical installations are traditionally placed on dry, exposed ridges with short snow cover duration compared to the surrounding communities, and relatively minor drainage problems. Human disturbances, varying in size from a few to several hundred m^2, have removed the organic layer and uncovered coarse gravel material in these areas. According to Forbes et al. (2001) dry sites in the high Arctic are a worst case situation when it comes to recovery, and dry sites in general take longer to regenerate than wet sites. Even small-scale human disturbances of vegetation and soil layer might seem harmless to plant communities or landscapes, but cumulative impact from such perturbations can eventually cause severe damage (Forbes et al. 2001).

The main sources for establishment of new vegetation in disturbed sites are from lateral clonal growth in adjacent undisturbed sites, vegetation fragments rooting in the site, germinating seeds, or buried seedbank. Recovery is limited by slow vegetative growth (Crawford 1989; Billings 1992), low and unreliable seed production (Chambers 1989; Oksanen & Virtanen 1997; Bliss & Gold 1999), and shortage of safe sites (Urbanska 1997a). Few native species and irregular seed production have traditionally prevented the use of native species in Arctic and alpine restoration efforts (Miller et al. 1983; Younkin & Martens 1987; Magnusson 1997). The effect of introduced species to local vegetation development is often unpredictable (Cargill & Chapin 1987; Densmore 1992; Forbes & Jefferies 1999). There is also a concern that introduced species can displace original vegetation or breed with locally adapted subspecies (Parker & Reichard 1998). Restoration experiments using native grass species have reported graminoids displacing other species (Densmore 1992; Chambers 1997; Strandberg 1997). Examination of restoration potential in other native species is therefore required.

Good understanding of reproductive behaviour and regenerative capacity of native species is important in a restoration situation following human disturbance in Arctic and alpine vegetation (Urbanska 1997b). Arctic and alpine species are generally characterized by vegetative reproduction, low seed production, and low seedling recruitment (Marchand & Roach 1980; Sonesson & Callaghan 1991). However, the importance of sexual reproduction must not be underestimated in Arctic and alpine ecosystems (Söyrinki 1939; Chapin & Shaver 1985; Murray 1987; McGraw & Fetcher 1992; Oksanen & Virtanen 1997). Establishment from propagules is unreliable and low in tundra vegetation (MacMahon 1987), and seedling recruitment shows large interannual variations (Chambers 1989; Bliss & Gold 1999). Germination success is affected by characteristics of the seeds, such as seed morphology and germination responses (Chambers & MacMahon 1994). In addition, various environmental factors at the microsite, for example, surface attributes, microclimatic conditions, presence of animals, and mycorrhiza status, influence the probability of each seed to germinate (Matthews 1992; Chambers & MacMahon 1994; Chambers 1995a, b). Only a minority of Arctic species exhibit seed dormancy (Amen 1966; Billings 1974; Gartner 1983). Harper (1977) distinguishes between innate, induced and enforced dormancy, and there are examples of Arctic and alpine species within all these types (Urbanska & Schütz 1986). Meso- and macroclimatic conditions of a particular year or of previous years influence seed development, since flower development starts the previous season, or seasons, in several Arctic plants (Bell & Bliss 1980; Diggle 1997; Khodachek 1997). A favourable combination of environmental conditions for germination may not occur every year under Arctic and alpine conditions (Billings 1974; Bell & Bliss 1980).

Vegetative regeneration plays an important role in the establishment and recovery of Arctic and alpine ecosystems. Production of vegetative units, like bulbils, is one adaptation to short and cold growing seasons (Crawford 1989). Viviparous species are able to produce propagation units even in years unfavourable for seed production (Forbes & Jefferies 1999), and are shown to establish successfully on Arctic disturbed patches (Forbes 1996). Rooting from lateral branches or from branches in contact with soil are other ways of vegetative reproduction. Propagation of new plants from cuttings is a well established technique in horticulture, and is based on the natural rooting potential of lateral branches. A cutting is a vegetative part separated from a mother plant, which under certain environmental conditions forms new roots (Hartmann et al. 1997). The balance of root-promoting hormones and carbohydrates in individual cuttings is crucial to rooting capacity. The level of these components depends on such factors as species, genotype, generative state, age of mother plant, time of year, etc. (e.g. Ericsson 1988; Hartmann et al. 1997). Rooting ability of cuttings varies within families, genera and even species (Hartmann et al. 1997).

The aim of this study is to deduce the restoration potential of several native Arctic and alpine species by examining reproductive capacity, involving both seeds and vegetative reproduction units. The questions asked are:

1. What is the germination ability of seeds and bulbils in selected Arctic species under greenhouse conditions, and how is germination affected by seed storage temperature?

2. What is the rooting capacity of woody cuttings from selected Arctic and alpine species under greenhouse conditions?

This study is part of a more extensive project, where the species with high germination and rooting ability are used in a restoration experiment in the study areas from which the propagules and cuttings were collected (Hagen in prep).

Materials and methods

Study areas

Seeds, bulbils and cuttings were collected from the Svalbard archipelago and on Dovre Mountain, Norway. The Svalbard study area (78° N, 16° E) is a high Arctic, permafrost area. Plant material for this study was collected within 1 km from the settlement of Longyearbyen, at 20 - 40 m asl. Roads, mining and infrastructure installations fragment the settlement surroundings, and there is a growing tourist industry in the area. Dryadion communities (Rønning 1965) dominate, but a variety of heath, wetland and snow-bed communities are also reported (Brattbakk 1984). Most technical installations are located in Dryas heath communities, but are expanding into wetland vegetation (personal observations).

The Dovre Mountain is an alpine area in central Norway (63° N, 10° E). Cuttings for this experiment were collected inside a military firing range at 1000 m asl. Forest limit in the area is about 900 m asl. The site is covered with lime-deficient gravel and sand material, dominated by *Salix* bushes and heath vegetation (Larsson et al. 1985). Roads, vehicle tracks, firefields and military installations fragment the 165 km^2 military area, and the most severe disturbances are located in dry heath communities.

In both study areas individual disturbances vary in size from a few m^2 to several km in length, and in several cases the organic layer has been completely removed, exposing coarse gravel material. In several disturbances additional gravel has been supplied on top of the existing vegetation layer.

Propagation

Collection and storage—Twelve species were selected (Table 1). *Papaver dahlianum, Luzula arcuata* ssp. *confusa* and *Oxyria digyna* are typical pioneer species in disturbed dry sites

Table 1. Species and propagation units, origin of plant material, and sample size (N) used in the experiment. Nomenclature follows Lid & Lid (1994).

Species	Plant group	Origin	Propagation unit	N
Arctostaphylos uva-ursi	evergreen shrub	Dovre	cuttings	756
Bistorta vivipara	forb	Svalbard	bulbils	1200
Cassiope tetragona	evergreen shrub	Svalbard	cuttings	687
Dryas octopetala	evergreen shrub	Svalbard	cuttings	674
Dryas octopetala	evergreen shrub	Svalbard	seeds	1200
Empetrum nigrum ssp. *hermaphroditum*	evergreen shrub	Dovre	cuttings	756
Luzula arcuata ssp. *confusa*	forb	Svalbard	seeds	1200
Oxyria digyna	forb	Svalbard	seeds	1200
Papaver dahlianum	forb	Svalbard	seeds	1200
Salix herbacea	deciduous shrub	Dovre	cuttings	390
Salix polaris	deciduous shrub	Svalbard	cuttings	640
Saxifraga oppositifolia	forb	Svalbard	cuttings	644
Vaccinium vitis-idaea	evergreen shrub	Dovre	cuttings	601

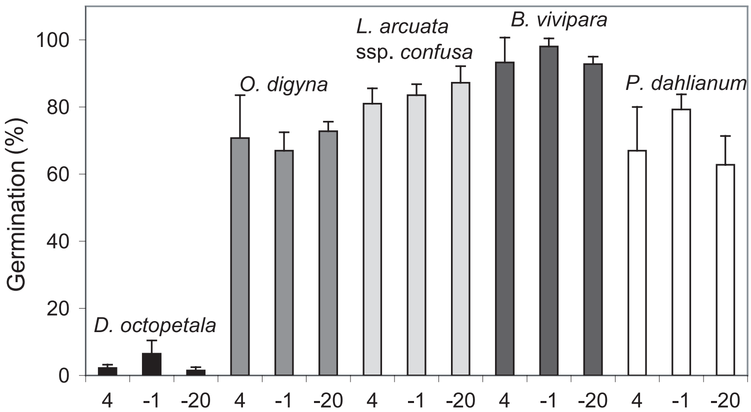

Fig. 1. Germination (%) for five species at three storage temperatures (+4, -1 and -20 °C) at the end of the experiment (99 days). Each bar shows average germination and s.d. of four replicates (sample sizes shown in Table 1).

in Svalbard; they are also common species in undisturbed ridge and heath communities in the area. Seeds were collected within or adjacent to disturbed sites. Seeds and cuttings from *Dryas octopetala* and cuttings from *Salix polaris* were collected in undisturbed Dryas heath. The species had high seed production, and sufficient seed quantity for this study was easily accessible. Cuttings of *Saxifraga oppositifolia* were collected from unstable gravel localities along a riverbed. Dovre cuttings of *Salix herbacea* were collected from undisturbed snow-bed vegetation, and cuttings of dry tolerant evergreen species were collected in low alpine heath vegetation adjacent to human disturbed sites. The heath species are late invaders in disturbed sites, but *Arctostaphylos uva-ursi* and, rarely, *Empetrum nigrum* subsp. *hermaphroditum* occur as survivors in disturbed sites at Dovre. Cuttings from Svalbard and all seeds and bulbils were collected in the middle of August 1998. Cuttings from Dovre were collected in September 1998. The deciduous species had senesced at collection and the majority of leaves had fallen. Cuttings from all species were about 5 cm long, and taken from the outermost 10 cm of main and lateral branches. No roots were present at planting time. Plant material was collected from ten or more mother plants per species.

Collected seeds were dried at room temperature and stored at three different temperatures (+4 °C, -1 °C and -20 °C) until February 1999. All cuttings were wrapped in moist mosses and transported in plastic bags. Cuttings from evergreen species were not stored before planting. Cuttings from deciduous species were wrapped in moist cloths and stored at -1 °C until March 1999.

Greenhouse germination and rooting—No examination of seeds with respect to germination viability was carried out prior to the germination experiment. Seeds were sown in peat soil covered with a thin layer of sand, at 22 °C. Four replicates of 100 seeds were sown for each species and storage temperature. The seeds were allowed to germinate in three consecutive periods. These germination periods lasted 33, 35 and 31 days and were divided by close-down periods of 4-5 weeks at 4 °C with no light or water. During the first three weeks in each germination period pots were kept in darkness and 14 hours of daylight were offered for the remainder of the periods. The samples were stirred every third week. Germination data were collected every third day during the most intensive germination activity, otherwise once a week. Seeds with any cotyledon emergence were considered germinated.

Cuttings of the evergreen species were planted a few days after collection in peat soil mixed with perlite (2:1 volume ratio) covered by a thin layer of sand, in 4 × 4 cm peat pots. An equal number of cuttings were placed under two different moisture regimes, one with a fog system and the other with saturated moist air in an enclosure tent of polyethylene (see Hartmann et al. 1997). The fog system is the most advanced method, offering a smooth and stable supply of foggy conditioned water. The polyethylene tent was used to test the adequacy of a simpler method. All cuttings were kept under low temperature (0-4 °C) during winter; the temperature was gradually increased from February to March (up to 22 °C).

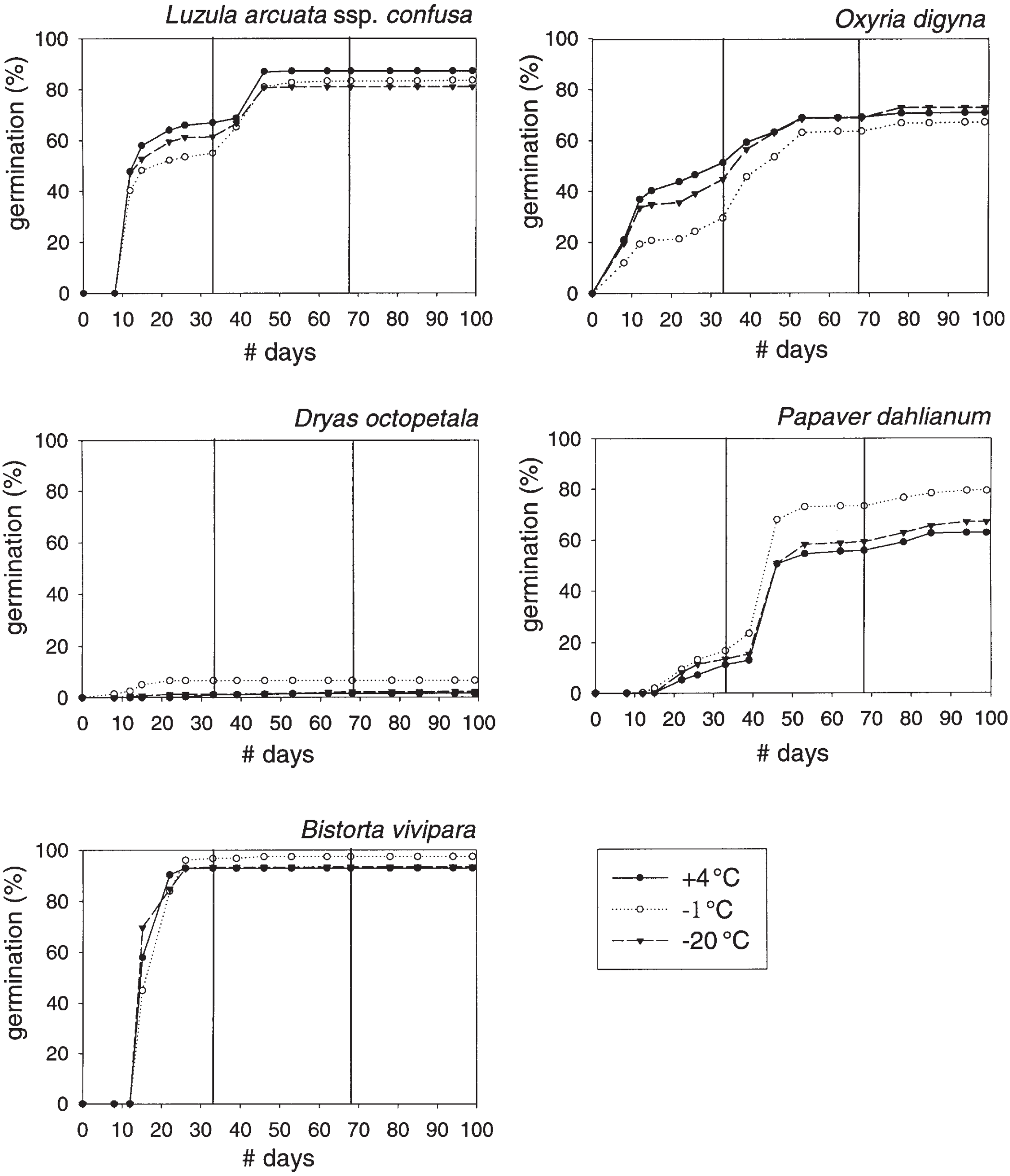

Fig. 2. Germination progress for each species and storage temperature (+4, -1 and -20 °C) during the experiment. Each curve is the mean value of four replicates. The vertical lines illustrate 4-5 week long breaks separating three germination periods. Horizontal axes show number of days from sowing, excluding the breaks.

No artificial light was supplied, and normal day-length increased from 8 to 11 hours during this period. From March to April the cuttings were kept at a stable temperature of 22 °C with 18h photoperiod; a fungicide treatment was offered to repulse mould attack. Cuttings from the deciduous species were planted and treated as the evergreen species after the six month storage period, but only at saturated moist air conditions. All cuttings were examined for emerged roots at the end of April 1999. All cuttings with visible roots were considered rooted.

Data analysis

Repeated measures analysis of variance (ANOVA) (Zar 1996) was used to test the effects of species, storage temperature and time on germination proportions. Time (the end of each germination period) was considered a three level factor. Statistical analysis of the data was performed using SPSS, version 10.0 for Windows (SPSS, Inc. 1999). To improve the normality and homogeneity assumptions, *Dryas octopetala* was not included in this test.

Results

Seeds and bulbils

Most species had between 60 % and 98 % germination (Fig. 1). Highest total germination rate was observed in bulbils from *Bistorta vivipara*, while *Luzula arcuata* ssp. *confusa* had the highest level of seed germination rate. With less than 10 % germination, *Dryas octopetala* showed weaker germination than the other species (Fig. 1).

The species effect on germination was significant (Table 2). A post hoc Tukey test for multiple comparisons suggested that the germination level of each species differs significantly from all other species ($p < 0.001$). Seed storage temperature had no separate effect on germination, but the species by treatment effect was significant (Table 2). *Papaver dahlianum* had the highest germination proportion for seeds stored at -1 °C, while *Oxyria digyna* had the lowest germination proportion for this storage temperature (Fig. 2).

Time affected germination, and the germination progress was both species and treatment (seed storage temperature) specific (Table 2). All species started to germinate during the first two weeks of the experiment (Fig. 2). For *Bistorta vivipara* and *Dryas octopetala* no further germination was observed in subsequent germination periods. More seeds of *Luzula arcuata* ssp. *confusa* germinated during the second period (34 - 68 days), and for *Oxyria digyna* and *Papaver dahlianum* germination was also observed during the third period (69 - 99 days).

Table 2. Repeated measures ANOVA of the effect of species, treatment (seed storage temperature) and time to seed and bulbil germination. Time levels are defined as germination at the end of three germination periods (33, 68 and 99 days).

Source of variation	df	MS	F	Sign.
Species	3	14437.581	125.300	<0.001
Treatment	2	10.549	0.092	0.913
Species * treatment	6	392.345	3.405	0.009
Error	36	115.225		
Time	2	10488.757	742.080	<0.001
Time * species	6	1863.275	131.827	<0.001
Time * treatment	4	125.601	8.886	<0.001
Time * species * treatment	12	19.675	1.392	0.190
Error (time)	72	14.134		

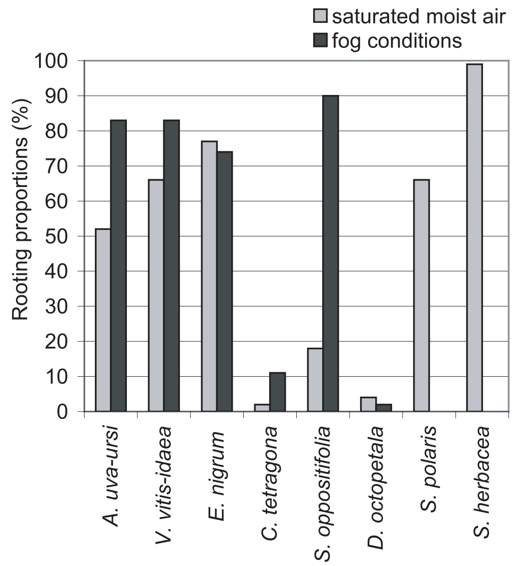

Fig. 3. Rooting proportions of species propagated by cuttings. The experiment was conducted at two different moisture regimes: saturated moist air and fog conditions. However, *Salix polaris* and *S. herbacea* were propagated only under saturated moist air conditions. For N, see Table 1.

Cuttings

Roots were observed on selected cuttings from all evergreen species within two months after planting. During winter further development was restricted due to low greenhouse temperature and short day-length. Root development continued as temperature increased during spring. Root growth and development of the already rooted cuttings continued from April, but no additional cuttings developed roots. At the end of April roots were observed in all species, but in very different proportions (Fig. 3). The “good rooters” in this study (with more than 50 % rooting under both moisture conditions) are *Arctostaphylos uva-*

ursi, Empetrum nigrum ssp. *hermaphroditum* and *Vaccinium vitis-idaea*. The "weak rooters" (with less than 10 % rooting) are *Dryas octopetala* and *Cassiope tetragona* (Fig. 3). *Saxifraga oppositifolia*, which responded differently to the two conditions, is a "good rooter" at fog conditions (Fig. 3).

Cuttings from the deciduous *Salix polaris* and *S. herbacea* showed spontaneous rooting and bud break immediately after planting. Two months after planting both species had more than 60 % rooting (Fig. 3).

Discussion

Seeds

The species in this germination experiment were offered optimal environmental conditions for seedling emergence: high temperature, sufficient moisture and stable soil. The optimum germination temperature for most non-dormant seeds is between 20 and 25 °C (Hartmann et al. 1997), and this is also the situation for Arctic plants (Gartner 1983; Khodachek 1993).

Seed storage temperature had no separate effect on germination in this experiment, although a "time × treatment" interaction existed. Most alpine species require high temperature to germinate, and only a few germinate at low temperatures (Bliss 1985). This can be a selective mechanism to prevent fall or spring germination, when high frost frequency will increase seedling mortality (Bliss 1985). In general, Arctic species have weak or no seed dormancy (Amen 1966; Gartner 1983; Chapin 1993), allowing germination whenever physical conditions permit. Non-dormant seeds tend to germinate simultaneously and have higher mortality rates (Amen 1966; Gartner 1983). *Oxyria digyna* is described as both non-dormant (Mooney & Billings 1961; Bonde 1969) and with a slight cold-moist stratification requirement (Eurola 1972; Bell & Bliss 1980). However, the chilling temperature required is fulfilled by normal Arctic summer temperature, and thus does not block germination (Bell & Bliss 1980). Both *Luzula arcuata* ssp. *confusa* and *Papaver dahlianum* had a marked peak in the germination rate at the start of the second germination period of the experiment. *L. arcuata* ssp. *confusa* seeds are suggested to have dormancy related to repeated winter frost (Eurola 1972; Khodachek 1993), while other studies indicate that *L. arcuata* ssp. *confusa* and *P. radicatum*, a close relative to *P. dahlianum*, are non-dormant (Bell & Bliss 1980). The germination proportions in the present experiment are higher than in the other cited experiments without close-down periods. This indicates some partial dormancy in seeds from *L. arcuata* ssp. *confusa*, possibly further released by close-down periods. *P. dahlianum* also seem to have partial dormancy. Germination is slow, starting at the end of the first germination period, and was possibly suspended by the close-down period. It is uncertain whether the germination in the second and third periods is just a continuation of the first germination period, or reflects further released dormancy from the close-down period.

Among the Arctic species there are both good and weak, and quick and slow germinators (Eurola 1972; Khodachek 1993; Bliss & Gold 1999). Other studies confirm *Dryas octopetala* as a weak germinator (Eurola 1972; Khodachek 1997). Seed viability was not examined before the germination experiment. Injured or immature seeds might have influenced the total germination level. Natural occurrence of *D. octopetala* seedlings in Svalbard differs considerably among undisturbed sites, and between disturbed and undisturbed sites (pers. obs.; E. J. Cooper, pers. comm. 2001). Seed viability in *D. octopetala* is markedly improved by elevated ambient air temperature (Wookey et al. 1995). *Oxyria digyna, Papaver dahlianum* and *Luzula arcuata* ssp. *confusa* are among the most common pioneer species in Svalbard, and all had high germination rates in this experiment. They are all wind dispersed and produce numerous seeds, a feature proposed to characterize species frequently found in early successional stages (Matthews 1992). All seeds in this study were collected at the end of a warm summer (average air temperature June–August was 6.0 °C, whereas the normal summer average is 4.2 °C) (data available from Norwegian Meteorological Institute). Increased air temperature has a positive influence on seed viability and germination ability in several Arctic and alpine species (Urbanska & Schütz 1986; Chambers 1989; Khodachek 1997; Bliss & Gold 1999). Slow germinators can be defined as those with most germination more than two weeks after sowing (Eurola 1972). According to this definition *P. dahlianum* and *D. octopetala* are slow germinators, and *L. arcuata* ssp. *confusa* and *O. digyna* are quick germinators.

Bulbils

The quick and high proportion of bulbil germination of *Bistorta vivipara* in this experiment corresponds with other studies (Söyrinki 1939; Bonde 1969; Molau 1993). As an adaptation to stress and disturbance, development of vegetative units increases the plants' ability to reproduce successfully even in short and cold summers (Billings 1974; Murray 1987; Crawford 1989). *B. vivipara* reproduces almost exclusively asexually by bulbils, but the development of seeds can occasionally be observed in Arctic and alpine populations (Söyrinki 1989; Bauert 1996), and the fact that populations are often genetically variable indicates that sexual reproduction plays a role (Diggle 1998; Karlsson 2000). Viviparous species are late flowering, and the bulbils have a higher germination rate than seeds from the same species (Molau 1993). The "seedlings" from bulbils of *B. vivipara* in this experiment had very high mortality, and most individuals died during the first ten days after germination. Environmental conditions, such as high temperature and dehydration are possibly the reason for high greenhouse mortality. High mortality of small *B. vivipara* plants was also observed under natural conditions at the study site (Hagen in prep.).

Cuttings

Most *Salix* species are easy to propagate via cuttings, and this is also the case for several Arctic and alpine willows (Chmelar 1974; Densmore et al. 1987; Keigley 1988). The high rooting ability observed for *Salix herbacea* and *S. polaris* in this experiment was therefore expected. Optimum growth temperature of 15 °C and increased growth at long photoperiods (more than 18h) is reported in *S. polaris* (Paus et al. 1986). Rooting capacity varies among seasons, and collecting cuttings in late winter might have increased the rooting rate (Houle & Barbeux 1998). The gender of the mother plant was not taken into consideration in this experiment, but female mother plants of other *Salix* species have been reported to root more profusely than male plants (Singh 1986; Houle & Barbeux 1998).

Saxifraga oppositifolia exhibits great ecotypic variation, and is by several authors recognized as two morphs, prostrate and cushion (Brysting et al. 1996; Rønning 1996; Crawford 1997). Kume et al. (1999), in a Svalbard study, found that the prostrate form was superior in vegetative propagation by shoot fragments, while the cushion form was superior in sexual reproduction. Cuttings from both morphs were collected in this experiment, and unequally separated between the two greenhouses, probably causing the different rooting rates.

Both *Cassiope tetragona* and *Dryas octopetala* showed weak rooting capacity in the present study. Under natural conditions both *C. tetragona* and *D. octopetala* spread laterally by vegetative ramets along the ground, and weak adventitious roots are formed (Söyrinki 1939; Oksanen & Virtanen 1997). For many clonal plants recruitment from seeds is important only during the initial colonization, and thereafter the species spreads largely by clonal growth (Bazzaz 1996).

Vaccinium vitis-idaea, *Arctostaphylos uva-ursi* and *Empetrum nigrum* ssp. *hermaphroditum* were all good rooters in this experiment. Under natural conditions these species have a prostrate growth, and form new roots along the branches. The use of cuttings is a recognized propagation method for *V. vitis-idaea* (e.g. Lehmushovi 1993). *A. uva-ursi* is not reported to be a particularly good rooter, but can be improved by selected treatment combinations, like mycorrhiza inoculation (Linderman & Call 1977; Nelson 1987; Hartmann et al. 1997). Propagation of *E. nigrum* ssp. *hermaphroditum* by cuttings is rarely described in the literature. However, some practical experience exists, indicating both good (Salemaa in prep.) and poor (I. Fredriksen, pers. comm. 1999) rooting capacity. Additions of auxins or mycorrhiza inoculation are possible ways to improve root formation in cuttings (Norton & Norton 1985; Verkade 1986; Ripa 1993), although *E. nigrum* ssp. *hermaphroditum* and *A. uva-ursi* are reported to root well without any additional auxin (Salemaa in prep.). The selection of mother plants is reported to have a significant effect on rooting capacity, as hormon content and other physiological traits has individual variation within species (e.g. Snow 1939; Hartmann et al. 1997).

Relevance for restoration

The results of this experiment permit the evaluation of some species' suitability for restoration endeavours. Seeds of *Luzula arcuata* ssp. *confusa, Oxyria digyna*, *Papaver dahlianum* and bulbils of *Bistorta vivipara* germinated well in this experiment, however the bulbil "seedlings" had high mortality. Cuttings of *Salix herbacea, S. polaris, Vaccinium vitis-idaea, Arctostaphylos uva-ursi, Empetrum nigrum* ssp. *hermaphroditum* and probably a prostrate morph of *Saxifraga oppositifolia* root well. During the greenhouse propagation period, lasting between two field-growing seasons (8 months), it was possible to produce new plants attaining the same size as several-year-old congeners in nature. These species are easy to propagate and can be used in further restoration research; the results are currently being utilized in an extended restoration project in the two study areas (Hagen in prep.). The ability of the propagated individuals to survive, grow and reproduce in the field will be crucial in evaluating the species' utilization in restoration.

Due to high population sizes and high morphologic diversity in the selected species, this experiment did not pay any attention to the genetic aspect of conservation. However, this must be taken into consideration in a possible large-scale restoration project (see Fenster & Dudash 1994; Frankham 1995).

Restoration projects based on the use of native species propagated in greenhouses are few, but important, and such experiences can contribute to the development of self-sustaining plant coummunities, and reduce the use of commercially available invasives traditionally used in Arctic and alpine restoration (e.g. Urbanska et al. 1987; Urbanska 1995). In addition to the ecological evaluations, economic considerations, local cultural preferences, time limitations etc. must be given serious attention prior to practical use of these species in restoration projects (Hagen et al. in prep.). Transplanting propagated material is a rather costly solution and has to be balanced against an increased revegetation success.

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Paper III

Arctic and alpine restoration using native species transplants

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ABSTRACT

The combination of increased anthropogenic disturbances and slow natural recovery of dry sites in arctic and alpine areas has increased the interest of using assisted recovery as a management strategy. Transplants from native species may be used for restoration of the vegetation cover. In this experiment greenhouse propagated transplants of five heath species, two willows, one graminoid and three herbs were transplanted into one low alpine and one middle arctic area. Transplants were offered three different soil treatments, and were planted early or late in the summer. Transplant survival, growth, and reproduction were recorded during three growing seasons. Transplants of the dry-tolerant shrubs *Arctostaphylos uva-ursi, Empetrum nigrum* ssp. *hermaphroditum,* and *Vaccinium vitis-idaea* and the willow *Salix herbacea* had more than 80 % survival in the alpine site. Transplants of *Luzula arcuata* ssp. *confusa, Oxyria digyna* and *Papaver dahlianum* had more than 75 % survival in the middle arctic site. *Saxifraga oppositifolia* and *Salix polaris* had less than 50 % survival, while all individuals of *Cassiope tetragona* died during the experiment. A majority of the surviving transplants became larger during the experiment. The observed effects of planting date indicated that transplant survival and growth can be increased by planting in late summer, rather than in the spring, and this could be related to both water supply during the first growing season and transplant size at planting date. Commercial plant soil with additional nutrients had a positive effect on growth in some species. The inoculation method used had no effect on the presence or level of mycorrhiza. This experiment has generated input concerning transplantation as a future alternative to traditional revegetation methods. However, the recovery of severely disturbed sites in arctic and alpine vegetation has to be seen in a long time perspective due to the naturally slow rates of vegetation change.

Key words: arctic/alpine, greenhouse cultivation, mycorrhiza, planting season, soil type, restoration, transplant growth, transplant survival

INTRODUCTION

Arctic and alpine plant communities are today under influence of increasing anthropogenic disturbances (Reynolds & Tenhunen 1996; Crawford 1997; Forbes et al. 2001), and natural recovery is generally very slow (Forbes 1996; Harper & Kershaw 1996). Dry sites are a worst case situation when it comes to recovery (Forbes et al. 2001). The combination of increased disturbances and slow natural recovery has increased interest in considering assisted recovery as a management strategy in future landscape planning.

Arctic and alpine species are well adapted to physical stress and natural habitat disturbances (Crawford 1989; Walker & Walker 1991; Oksanen & Virtanen 1997). Many anthropogenic disturbances have natural analogs, and many species colonizing natural disturbances are also found colonizing anthropogenic disturbances (Walker et al. 1987; Forbes & Jefferies 1999). The ecological conditions and naturally establishing species on disturbed sites should be the basis for assessment and for selection of species and technology for restoration (Urbanska et al. 1997). Morphological and physical adaptations in plants can be considered an advantage when selecting species for a restoration program, as they can respond, and even profit from environmental uncertainties (Crawford 1997). This contributes to making native species better suited for restoration than exotics under marginal environmental conditions (Urbanska et al. 1987). In addition, the use of native species makes it possible to avoid any unfortunate or unexpected consequences of introductions (Ehrlich & Mooney 1983; Parker & Richard 1998).

Seeding can be a viable restoration strategy in arctic and alpine ecosystems (Chambers et al. 1990). Several restoration projects report that seeding of native or introduced grass resulted in development of a plant cover following severe disturbance (e.g., Arnalds et al. 1987; Younkin & Martens 1987; Jorgenson & Joyce 1994). However, the long-term effect of grass to enhance native colonization is disputed (e.g., Cargill & Chapin 1987; Densmore 1992; Helm 1995). Demographic studies of seedlings and juvenile plants in arctic and alpine vegetation indicate high risk of mortality early in the life of a plant

(Bell & Bliss 1980; Bliss & Gold 1999). The use of native species transplants in restoration is suggested to have advantages compared to seeding, particularly under extreme environmental conditions, as the most vulnerable stages of germination and recruitment are circumvented (Urbanska 1997; Handa & Jefferies 2000; Fattorini 2001). Transplants collected from sites adjacent to the disturbed locality have been used directly for arctic and alpine restoration (e.g., May et al. 1982; Tishkov 1997; Shirazi et al. 1998). However, this method suffers from the problem of repairing damage at one site by inflicting damage upon another (Urbanska & Schütz 1986). The use of individuals propagated or cloned from native species can be one solution to this problem. A few such case studies have been carried out in arctic and alpine vegetation (Densmore & Holmes 1987; Urbanska et al. 1987; Brosø 2001; Fattorini 2001). The prospect of this method needs to be further extended for additional vegetation types and species.

In dry alpine and arctic areas, species potentially available for natural or assisted recovery are limited (Forbes 1996). Anyway, the native species' characteristic is the obvious basis for selecting individual species for restoration. In these ecosystems pioneer species are often maintained in the sites during succession, expanding and coexisting with later invaders (Svoboda & Henry 1987; Bliss & Peterson 1992; Forbes 1996). Using pioneer species in restoration can thus contribute to long-term vegetation establishment. Willow shrubs have been used in several restoration projects in arctic and alpine areas, because they are easy to propagate as cuttings (e.g., Chmelar 1974; Densmore et al. 1987; Hagen unpublished). Dry-tolerant species able to survive in coarse gravel are also of special interest for restoration in "worst-case" disturbances where natural recovery is very limited (Forbes et al. 2001).

The presence of mycorrhiza is reported to have positive influence on establishment, survival and plant production (Haselwandter 1987; Smith & Read 1997). Level of mycorrhiza is reported to increase during succession or recovery stages, and is probably important in recovery of disturbed vegetation (e.g., Allen & Allen 1980; Allen et al. 1987). Pioneer species occupying sites with a low content of organic soil seem to be less dependent on mycorrhiza (Read & Haselwandter 1981; Miller 1982; Onipchenco &

Zobel 2000). Mycorrhiza inoculation as a method to improve transplant success must be examined.

The necessity to define and agree upon a common goal is essential to all restoration projects, as revegetation can have a variety of objectives, such as erosion control, restoring biodiversity, esthetical motives, or achieving social benefits (Lackey 1998; Slocombe 1998; Forbes & Jefferies 1999; Hagen et al. 2002). Restoration success must be evaluated in agreement with the objectives of the individual projects (Forbes & Jefferies 1999, van Diggelen et al. 2001). Extreme environmental conditions and severe anthropogenic disturbance at the sites in the present study contribute to virtually no natural recovery. Under such circumstances, any establishment of native plant individuals can be considered a success, and can be formulated as the initial step in a long-term goal for restoration.

A transplant experiment was performed to identify the suitability for a number of native species for restoration of arctic and alpine vegetation. The principle questions are:

- Are there any species-specific characteristics in the establishment success of transplants?
- Do soil type and planting season affect survival and growth of transplants?
- Is it possible to inoculate mycorrhiza from native soil or roots, and what is the effect of this inoculation on the survival and growth of transplants?

The results of the experiment will be evaluated regarding practical restoration in severely disturbed xeric arctic and alpine vegetation.

STUDY AREAS AND METHODS

Study area

This experiment was conducted on the Svalbard archipelago and on Dovre Mountain, Norway (Figure 1, Table 1). Both places have relatively short and cold growing season and low precipitation (Table 1). During the initial field season (1999), summer precipitation was higher than the average mean on Svalbard and lower than the average mean on Dovre (Figure 2). The experimental site on Svalbard was located near the settlement Longyearbyen, along a roadside slope with coarse and dry lime-rich gravel soil. The experiment was performed within an area of 10 m x 20 m, to keep the natural environmental variation as low as possible. The road was built about 1950, and natural recovery was mainly restricted to a few individuals of *Luzula arcuata* ssp. *confusa*, *Oxyria digyna* and *Papaver dahlianum*. On Dovre Mountain two sites were selected within a military firing range. One site, called "heath", was a flat roadside with coarse and dry lime-poor gravel soil. The experiment was performed within 10 m x 20 m, of the same reason as described above. The road was built about 1960 and natural recovery was restricted to scattered individuals of *Festuca ovina*, *Rumex acetosella*, *Stereocaulon* spp., and few other species (Figure 3). The other Dovre site, called "*Salix*", was along the same road, and had extensive natural recovery due to favorable moisture conditions. The experiment was performed within an area of 8 m x 12 m.

Species selection and transplant cultivation

Selection of plant species for the propagation experiment was based on field observations of natural recovery in the area, and ecological and physiological qualities of single species. Species included in the experiment had to be common, native, dry tolerant, and occur naturally in or immediately next to disturbed sites. The species should either have high seed production or horticultural experience should indicate that they were easy to propagate as cuttings. During a previous experiment the propagation ability of seeds, bulbils and cuttings from common native species in the study sites was tested in greenhouse conditions (Hagen 2002), and made up the basis for the selection of species for the transplant experiment (Table 2).

The graminoid *Luzula arcuata* ssp. *confusa* and the herbs *Oxyria digyna* and *Papaver dahlianum* are common species on severely disturbed soil at Svalbard, and they all have high seed production. All are reported to be non-mycorrhizal (Väre et al. 1992). Seeds of these species were collected in August 1998, stored until February 1999 and then sown in peat soil and kept at 22°C until germination, see Hagen (2002) for further details. *Arctostaphylos uva-ursi*, *Empetrum nigrum* ssp. *hermaphroditum* and *Vaccinium vitis-idaea* are common, dry tolerant, woody species in the heath vegetation adjacent to the ”heath” experimental site on Dovre. *Cassiope tetragona* is a common, woody species in heath vegetation adjacent to the experimental site on Svalbard, while the herb *Saxifraga oppositifolia* is a common species in both heath vegetation and on severely disturbed soil at Svalbard. Cuttings from all Dovre species were collected in September 1998, and cuttings from the Svalbard species were collected in August 1998. All these evergreen cuttings were immediately planted in a mixture of peat soil and perlite and kept at 0-4°C during winter, and then at a stable temperature of 22°C with 18-h photoperiod from March to April, see Hagen (2002) for further details. Cuttings of the deciduous *Salix polaris* from Svalbard and *S. herbacea* from Dovre were collected in August and September1998, respectively. *Salix polaris* is a common species in the heath vegetation adjacent to the experimental site on Svalbard, while *S. herbacea* is a common species in snow patch vegetation adjacent to the ”*Salix*” site on Dovre. Willows are known to be easy to propagate as cuttings, and is a familiar genus in restoration. The deciduous cuttings were stored at -1°C until March 1999, and then treated as the evergreen cuttings. All woody heath species and willows used in this experiment are reported with mycorrhiza (Miller 1982; Kohn & Stasovski 1990; Väre et al. 1992). Successfully propagated transplants were further cultivated following normal horticultural principles (according to Hartmann et al. 1990, new edition 2002) at 12-15°C until May 1999, and then placed outdoors for hardening.

Experimental design

The three experimental sites were selected to represent different environmental characteristics, and the choice of experimental species was based on each site’s characteristics and the species occurrence in the site or in adjacent vegetation.

Accordingly, each site had its specific set of species. The sites were divided into plots of 0.5 m x 0.5 m, with a 0.5 m distance to the next plot in all direction. In each plot 9 transplants of the same species were planted (Figure 4). Two treatment variables were used within the sites: planting date and soil treatment. In half of the plots transplants were planted in early summer 1999 (= planting date 1), May 31 on Dovre and June 22 on Svalbard. In the rest of the plots transplants were planted later in summer 1999 (= planting date 2), September 8 on Dovre and July 19 on Svalbard. The soil treatments were commercial organic soil (C), native soil from adjacent vegetation (N), and commercial organic soil mixed with native roots from the same species (R). Each plot assigned a specific combination of *species* x *planting date* (early or late) x *soil treatment* (S, R or N). Each specific combination was replicated 4-9 times within the site, number of replications differed between species (Table 2). All plots within a site were distributed by complete randomized design. On Dovre only soil types C and N were offered at planting date 1. *Cassiope tetragona* from Svalbard was difficult to propagate, and due to low availability of transplants this species was only planted in early summer and all transplants received soil treatment N. As there is no replication of sites the results should be interpreted cautiously (Hurlbert, 1984). However, the large number of randomly distributed and replicated plots is considered sufficient to discuss the questions asked in this study.

All transplants were propagated and grown in one operation, and transplants planted in autumn were kept under hardening conditions during the time between the two planting events. This implies that the early- and late-planted transplants were offered different conditions during this period. Late planted transplants of *L. arcuata* ssp. *confusa, O. digyna, P. dahlianum* and *V. vitis-idaea,* were larger at planting date than those planted in early summer ($p \leq 0.001$). Transplants from the other species had similar sizes at both planting dates. At planting *Luzula, Oxyria* and *Papaver* transplants had numerous flowers, average plant diameter was about 5 cm and height was 5-10 cm, the heath species transplants (Table 2) were on average 7-10 cm long with 2-7 branches and no flowers observed, and willow transplants were on average 3-4 cm long with no flowers observed. Transplants were planted so the root ball was covered and soil tamped around them.

Field and laboratory registrations

Survival and growth measurements

During the experiment period non-destructive registration of survival and growth of each individual transplant were accomplished four times: at planting time (1999), at the beginning and the end of the second growing season (spring and autumn 2000), and at the end of the third season (2001). Survival was registrated as the absolute number of surviving transplants within each plot at each registration time. Growth parameters were species-specific. In *Papaver dahlianum*, *Luzula arcuata* ssp. *confusa* and *Oxyria digyna* total diameter (*diameter*) were measured, and number of rosettes/shoots (*rosettes*) (*Papaver* and *Luzula*) and total number of leaves (*leaves*) (*Oxyria*) were counted. Diameter was the projected width of the transplant in north-south direction. For all other species, number of main branches (*mainbra*), number of secondary branches (*secbra*), and length of longest branch (*longbra*) were measured. Other growth parameters were considered (e.g., Paus et al. 1986; Parson et al. 1994; Chapin & Shaver 1996), but regarded less suitable for repeated, non-destructive measurements of numerous transplants. Mean size of transplants within each plot was used in the statistical testing. Effects of treatments on growth were tested for each species separately. A direct comparison of growth parameters among species was not considered useful because growth is more related to morphology and size of a plant than to plant physiology.

Four replicates of each specific treatment combination were selected randomly, and one transplant within each plot was sampled systematically for biomass measurements. This was done three times during the experiment. Sample size was according to e.g. Parson et al. (1994). *Cassiope tetragona* was not included in this part of the experiment due to low number of transplants and high mortality rate. The sampled transplants were stored at -20°C until further examination. In the laboratory transplants were washed, dried at 70°C for 24 h, and weighed.

Preparation of mycorrhiza samples

Root fractions were randomly sampled from all transplants collected for biomass measurements at the last sampling event, and used for examination of mycorrhiza. Roots were shaken to remove soil and roots from other species, and preserved in 45 % ethanol. Preserved roots were bleached in 10 % KOH at 60°C for 10 minutes and soaked into a mixture of 30 % H_2O_2 and 20 % NH_3, and then stained in Trypan blue (e.g., Kormanick et al. 1980). After staining roots were stored in a lactic acid, glycerol and water solution. Fifty 1 mm fine root segments of each plant were scored for presence or absence of mycorrhiza infection, and the number of infected segments was expressed as a percentage of total segments observed (e.g., Allen et al. 1987; Magnusson 1994).

Statistical analysis

Kruskal-Wallis non-parametric test for several independent samples was used to test differences in survival between species and treatments within the sites, and the Mann-Whitney U test was used for consecutive testing of pairwise differences (Zar 1996). The measurements of biomass from selected transplants were used to calculate a combined growth variable for individual species, based on the non-destructive measurements of all transplants. Simple and multiple regressions (Zar 1996) were computed to uncover the combination of growth variables that best correspond to the total biomass for each species (expressed by R^2). This outlined, combined variable is denoted *bmcorr* (Table 3), and is comprehended as an expression of transplant size. Repeated measures analysis of variance, general linear model (GLM) procedure, was used to test the effect of soil type and planting season on growth (*bmcorr*) for each species separately during the experiment (Zar 1996). Registration time was considered the repeated within subject factor. A post hoc Tukey test was performed to test pairwise differences between soil types when significant effects were found. Only transplants surviving during the entire experiment were included in statistical testing of growth. *Salix polaris* and *Cassiope tetragona* are not included in the growth testing due to low number of surviving transplants. One way ANOVA, GLM, was used to test the effect of planting date and soil treatment on mycorrhiza infection level. All statistical treatment of data was conducted using SPSS version 10.0 for Windows (SPSS, Inc. 1999).

RESULTS

Survival

All species on Dovre had high survival, ranging from 83 – 93 % at the end of the third growing season (Figure 5). Mortality for *Empetrum nigrum* ssp. *hermaphroditum* and *Vaccinium vitis-idaea* were highest during the first summer. Mortality in *Salix herbacea* increased towards the end of the experiment, while mortality in *Arctostaphylos uva-ursi* was low and stable (Figure 5). No significant difference in survival was found between species (Kruskal-Wallis, $p = 0.074$). No effect of soil type was observed ($p = 0.352$), but a significant effect of planting date ($p < 0.001$) was found. Mortality was higher for transplants of *E. nigrum* ssp. *hermaphroditum* ($p < 0.001$), *V. vitis-idaea* ($p = 0.014$) and *S. herbacea* ($p = 0.005$) planted in early summer (planting date 1) compared to transplants planted in late summer. No effect of planting date was found for *Arctostaphylos uva-ursi* ($p = 0.608$).

Clearly species-dependent survival was found for the transplants on Svalbard (Kruskal-Wallis test, $p < 0.001$). The pioneer species *Luzula arcuata* ssp. *confusa*, *Oxyria digyna* and *Papaver dahlianum* all had mean transplant survival above 78 %. *Saxifraga oppositifolia* and *Salix polaris* had medium survival of 26 – 50 %, while all individuals of *Cassiope tetragona* died during the experiment (Figure 6). In species with low and medium survival, mortality rates were highest during the first growing season, while mortality rates were more stable for species with high survival (Figure 6). There was no effect on survival related to planting date ($p = 0.682$) or soil type ($p = 0.149$).

Growth

Changes in plant size for the individual species during the experiment were expressed as the influence of registration time (repeated Factor) to the combined growth variable *bmcorr* (Table 4). Mean plant size increased for most species during the experiment, but transplants of *Oxyria digyna* and *Papaver dahlianum* showed a varying development (Figure 7).

Planting date showed a distinct effect on growth for *Empetrum nigrum* ssp. *hermaphroditum*, *Salix herbacea* and *Vaccinium vitis-idaea* (all $p < 0.001$), and limited effect for *L. arcuata* ssp. *confusa* ($p = 0.048$) and *P. dahlianum* ($p = 0.014$) (Table 4). In *P. dahlianum* the early-planted transplants were larger at the beginning of the experiment, but the transplants planted late became largest during the experiment. For all the other affected species transplants planted late were larger during the entire experiment (Figure 7). Soil type had a distinct effect on growth for *E. nigrum* ssp. *hermaphroditum* ($p < 0.001$), *O. digyna* ($p < 0.001$) and *P. dahlianum* ($p = 0.007$) (Table 4). For *P. dahlianum* this effect was also related to planting date (P x S interaction). A post hoc Tukey test showed that plants grown in natural soil were smaller than plants grown in other soil types. Growth in the other species showed no effect of soil type.

About 100 % of the transplants of *L. arcuata* ssp. *confusa, O. digyna* and *P. dahlianum* had abundant flowering and seed production during the first two growing seasons, while reproductive efforts were dramatically reduced for *O. digyna* and *P. dahlianum* the third season. Flowers or berries were observed in very few transplants of *A. uva-ursi, E. nigrum* ssp. *hermaphroditum, V. vitis-idaea* and *S. oppositifolia* (about 1% of the transplants at each registration time). No flowers or seeds were observed in *C. tetragona, S. herbacea* and *S. polaris*.

Mycorrhiza

All transplants from Dovre had mycorrhiza, present as ericoid in *Empetrum nigrum* ssp. *hermaphroditum* and *Vaccinium vitis-idaea* and as ectomycorrhiza in *Arctostaphylos uva-ursi* and *Salix herbacea* (type of mycorrhiza according to Miller 1982; Kohn & Stasovski 1990). All *S. polaris* transplants from Svalbard had ectomycorrhiza present. In the other Svalbard species no mycorrhiza was observed. Mycorrhiza frequencies were lower in *A. uva-ursi* and *S. polaris* than the other species (ANOVA; $F = 20.16$; $p<0.001$) (Figure 8), and there was no effect of planting date ($F = 0.024$; $p=0.879$) or soil type ($F = 0.65$; $p =0.528$) on mycorrhiza frequencies.

DISCUSSION

Transplant survival and growth

Species

High transplant survival was observed for 7 of 10 species after three growing seasons. For all these species the conditions in the experimental plots, respectively, resemble the conditions for the individual species natural occurrence. *Cassiope tetragona* and *Salix polaris* had low and medium survival, receptively, and in general poor growth. The experiment plot at Svalbard was dry and had very low organic content compared to the natural preferences of these two species. *S. polaris* is common throughout Svalbard and has a good capability for vegetative colonization, and *Salix* spp. have been successful in other restoration projects (Densmore et al. 1987; Houle & Babeux 1998; Hagen unpublished). *Cassiope tetragona* had weak rooting capacity in the greenhouse (Hagen 2002), and the roots were small and fragile at planting. Under natural conditions *C. tetragona* can spread laterally by weak adventiv roots (Oksanen & Virtanen 1997). Variable survival in *Saxifraga oppositifolia* was partly due to variable quality of transplants (cf. Kume 1999; Hagen 2002). Mortality were generally highest during the first year of the experiment, indicating that early survival is a critical stage for establishment, in conformity with the situation for naturally occurring seedlings in arctic and alpine vegetation (e.g., Bell & Bliss 1980; Chambers 1995; Bliss & Gold 1999).

Transplant size increased continually during the experiment for a majority of species, further indicating the importance of early survival to long-term establishment success. *Oxyria digyna* was the only species with a declined plant size at the last registration. *O. digyna* had very high seed production during the first and second growing season, making up a high proportion of total aboveground biomass, while seed production was low in the third growing season.

Planting date

Planting date had an effect on both survival and growth of *Empetrum nigrum* ssp. *hermaphroditum, Salix herbacea* and *Vaccinium vitis-idaea*, all planted on Dovre.

Transplants planted in early summer had higher mortality and were smaller during the entire experiment than transplants planted in late summer. Drought was a likely death cause during the first growing season on Dovre. Spring precipitation prior to the early planting, and the total summer precipitation in 1999 was below normal at Dovre (Figure 2). *Arctostaphylos uva-ursi* is a dry tolerant species with broad ecological amplitude. Neither survival or growth was affected by planting date, but lack of moisture is reported to be the most limiting factor to the establishment and growth of *A. uva-ursi* (Mukhina 1996). Also Svalbard transplants had high mortality during the first year, but not related to planting date. The early planting on Svalbard was carried out after a rainy period, providing wet and favorable conditions for the transplants during the first weeks in the plot, and also total summer precipitation was above normal in 1999 (Figure 2).

The real difference between the two planting dates was about three times as long for Dovre as for Svalbard, due to the different lengths of growing season in the two areas, and this is a likely explanation why differences between planting dates were more expressed on Dovre than on Svalbard. Larger mean plant size can be one explanation for the higher survival for late-planted transplants of *Vaccinium vitis-idaea*, and to a lesser extent for *Luzula arcuata* ssp. *confusa*, and is possibly related to the more favorable climatic conditions at the cultivation facilities compared to the experimental sites. However, in general, plant growth and phenology responses to increased temperature are not clear, and differ both between species and sites (e.g., Havström et al. 1993, Molau 1997).

Low reproductive efforts observed in alpine heath shrubs and willows can reflect that these species invest resources in growth during the first years (cf. Wookey et al. 1993). Species not producing offspring can also contribute to vegetation development through vegetative recolonization of bare ground, and thus be important in early stages of recovery. High seed production for several of the arctic transplants observed during the early part of this experiment can reflect their allocation of resources into reproductive efforts when favorable conditions are offered (Wookey et al. 1993, Mølgaard & Christensen 1997). After three growing seasons at the site the advantages obtained during greenhouse conditions seems to decline. Naturally occurring *Luzula arcuata* ssp.

confusa, *Oxyria digyna* and *Papaver dahlianum* next to the study site had high seed production (personal observations).

Soil type

Soil type did not influence transplant survival for any species. Moisture content is one principal factor affecting biological processes in dry tundra soil (Tedrow 1975; Oberbauer & Dawson 1992). Moisture availability seems to be directly involved in transplant survival, but the variation of soil types within the sites in this experiment was probably too small to reflect this.

Soil type had an effect on growth for *Empetrum nigrum* ssp. *hermaphroditum, Papaver dahlianum* and *Oxyria digyna,* as transplants growing in natural soil were smaller than those grown in other soil types. Nutrient supply in commercial soil (used in soil treatments C and R) was the most obvious reason for this result. The major nutrient admixture in commercial plant soil is nitrogen, phosphorus and potassium. These nutrients are limiting to plant growth in arctic and alpine ecosystems (e.g., Billings 1974; Shaver & Chapin 1980), and minor addition of nutrients is reported to increase vegetative growth in plants (Klokk & Rønning 1987; Wookey et al. 1993; Parson et al. 1994). Fertilizer is reported to increase biomass and branching in *E. nigrum* ssp. *hermaphroditum* and *Vaccinium vitis-idaea* (Shaver & Chapin 1980; Parson et al. 1994). No growth-stimulating effect from fertilizer is reported in *A. uva-ursi* (Nams et al. 1993; Turkington et al. 2002), and is supported by no effect of soil treatment for *A. uva-ursi* in the present study. In general, more response to nutrient supply is expected in species normally occurring in disturbed sites (Shaver & Chapin 1980), such as *O. digyna* and *P. dahlianum*. Within a limited time-scale the effect of nutrient supply is expected to terminate (Nadelhoffer et al. 1992; Jorgenson & Joyce 1994). This most likely was the situation in *O. digyna* and *P. dahlianum*, as differences in plant size between soil types decreased during the experiment, and were no longer significant at the last registration. For *E. nigrum* ssp. *hermaphroditum* a small difference between soil types was present during the entire experiment. Physical and microbiological attributes in the natural soil used in this experiment revealed no advantage for growth compared with commercial soil treatments.

Based on the results obtained in this experiment and the discussion above, it is possible to suggest that transplant survival was related to the species' natural habitat preferences, and that transplant growth can be related to nutrient supply. Both survival and growth were influenced by conditions related to planting date, such as summer precipitation and partly initial transplant size. Expected advantages of planting in early summer, such as a longer first growing season and moist soil from snow melting, were not confirmed.

Mycorrhiza inoculation

Transplants of species previously reported with mycorrhiza in literature (Miller 1982; Väre et al. 1992) had mycorrhiza present after three growing seasons. All species infected by mycorrhiza were propagated from cuttings (Table 2). Mycorrhiza enhances nutrient uptake (N, P, Fe) from mineral particles, and seem to be a key to success for alpine shrubs (Read & Hasselwandter 1981; Väre et al. 1992). As no effect of soil type on the presence or level of mycorrhiza was observed in this study, it is likely that mycorrhiza either was inoculated in all transplants by natural processes after planting, or was present in the cuttings during greenhouse propagation. Quick colonization of mycorrhiza following plant establishment is in agreement with other studies (Allen et al. 1987; Jumpponen et al. 2002). There is also a possibility, due to the creeping growth form of these shrubs, that small roots could have been present on the lateral branches used for cuttings, and so they inherited mycorrhiza from their mother plants. Mycorrhiza level reported in *Salix polaris* compared to the level in *S. herbacea* is supported by assumptions of decreasing mycorrhiza level with altitude (Read & Hasselwandter 1981). In addition to this the two *Salix* spp. were planted in sites with different soil and vegetation characteristics, as *S. polaris* was planted in a site with no organic matter, while *S. herbacea* was planted in a vegetated site with expected higher density and diversity of fungi. *Arctostaphylos uva-ursi* is ectomycorrhizal, as opposed to the other heath species in this experiment, and consequently the lower infection level recorded could be related to the counting-method. *Luzula arcuata* ssp. *confusa, Oxyria digyna*, *Papaver dahlianum* and *Saxifraga oppositifolia* did not have mycorrhiza in any treatments in this experiment, and all are reported as non-mycorrhizal on Svalbard (Väre et al. 1992). *S. oppositifolia* has been reported as mycorrhizal in other studies

(Harley & Harley 1987; Kohn & Stasovski 1990), and the occurrence of mycorrhiza in this species is probably related to its co-existence with other mycorrhizal plants (Väre et al. 1992).

The inoculation methods used in this experiment did not have any effect on the presence or level of mycorrhiza. Inoculation by native soil or collected root seems to be superfluous in restoration using these species in the tested soil.

Implications for practical restoration

Based on three years registration this experiment has shown that transplant individuals of several common and native species survive and grow in severely disturbed arctic and alpine sites. Transplants of the dry tolerant shrubs *Arctostaphylos uva-ursi, Empetrum nigrum* ssp. *hermaphroditum,* and *Vaccinium vitis-idaea* survived well and grew in the alpine site. These species naturally occur in heath vegetation, but are also able to establish and colonize bare soil. If the transplants survive and spread vegetatively they are likely to remain in the site during recovery. Transplants of *Luzula arcuata* ssp. *confusa*, *Oxyria digyna* and *Papaver dahlianum* survived and grew in the middle arctic site, and are abundant in disturbed sites in the area. Separation into pioneer and later successional species is not a functional way to group species in arctic and alpine vegetation (Svoboda & Henry 1987, Bliss & Peterson 1992, Urbanska 1997). These pioneer species also occur frequently in undisturbed vegetation next to the study site, and if they survive during the forthcoming growing seasons the transplants and their descendants will probably be a part of the recovered vegetation in this site in the future.

These results generate input concerning further improvement of the transplant method, and how it can be adapted for applied restoration efforts. This experiment has demonstrated that species habitat preferences must be complied with when selecting species for site-specific restoration. The observed effects of planting date and soil treatment indicate that increased transplant survival and growth can be obtained by planting in late summer, rather than in the spring. Additional water supply and extended cultivation in a greenhouse to increase initial planting size and to improve the advantages of late planting could be considered and further examined. The advantage of commercial plant soil can perhaps be further examined by specific testing of nutrient supply. Increased economic cost related to the method improvements must be balanced against expected improvement of restoration success.

Considering the improvements this method can be developed as a supplement to other revegetation methods for arctic and alpine disturbed sites. Economical prerequisites in transplant production probably limit the range of use to small sites with specific ecological, political or social demands for accelerated development of a native plant cover. Even when proper methods for restoration are used the recovery of severely disturbed sites in arctic and alpine vegetation has to be seen in a very long time perspective due to the naturally slow rates of vegetation change.

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Table 1: Characteristics of study areas and experimental sites. Vegetation zones are according to Moen (1999). Precipitation and temperature are presented as summer (May to September) mean (Norwegian Meteorological Institute, personal communication). Growing season is defined as number of days with an average temperature of ≥ 5°C (Moen 1999). Vegetation types are according to Rønning (1965) for Svalbard and Fremstad (1996) for Dovre.

	Svalbard	Dovre	
		"heath" site	"*Salix*" site
Geographical position	78ºN 16ºE	63°N 10°E	
Vegetation zone	Middle arctic	Low alpine	
Altitude	40 m	1000 m	
Summer precipitation	77 mm	248 mm	
Summer temperature	1.8°C	7.2°C	
Length of growing season	≈ 70 days	≈ 115 days	
Exposition	NV	SE	NE
Slope	20 %	0 %	10 %
Vegetation cover	< 10 %	< 10 %	≈85 %
Surrounding vegetation type	Dryas heath	Alpine ridge	Snow patch

Table 2: Species used in the experimental sites on Svalbard and on Dovre Mountain, including number of replicates for each specific treatment combination (two planting dates and three soil treatments), and total number of transplants. Source indicates whether the transplants are propagated from seeds or cuttings. Nomenclature follows Lid & Lid (1994).

Species	Site	Replicates	Total number of transplants	Source
Arctostaphylos uva-ursi	Dovre "heath"	8 *	360	cuttings
Cassiope tetragona	Svalbard	5 **	45	cuttings
Empetrum nigrum ssp. *hermaphroditum*	Dovre "heath"	9 *	405	cuttings
Luzula arcuata ssp. *confusa*	Svalbard	5	270	seeds
Oxyria digyna	Svalbard	6	324	seeds
Papaver dahlianum	Svalbard	5	270	seeds
Salix herbacea	Dovre "*Salix*"	7 *	315	cuttings
Salix polaris	Svalbard	6	324	cuttings
Saxifraga oppositifolia	Svalbard	5	270	cuttings
Vaccinium vitis-idaea	Dovre "heath"	6 *	270	cuttings

* only soil treatments C and N offered at early planting

** only planted early (Planting date 1) and with soil treatment N

Table 3: The combination of growth variables best corresponding to total biomass for the individual species (*bmcorr*), calculated by simple or multiple regression and expressed by R^2. Growth variables: *diameter* = projected width of the transplant in north-south direction, *rosettes* = number of rosettes/shoots, *leaves* = total number of leaves, *mainbra* = number of main branches, *secbra* = number of secondary branches, *longbra* = length of longest branch. In *Papaver dahlianum* no combined variable could express total biomass better than the measured growth variable *diameter*.

Combined variable (*bmcorr*)	R^2
$bmcorr_{\text{A.uva-ursi}} = secbra + 2mainbra + \ln longest$	0.747
$bmcorr_{\text{E.nigrum}} = longest \times (secbra + 2mainbra)$	0.451
$bmcorr_{\text{V.vitis-idaea}} = longest \times (secbra + 2mainbra)$	0.427
$bmcorr_{\text{S.herbacea}} = mainbra + secbra + \ln longest$	0.492
$bmcorr_{\text{L.arcuata}} = diameter \times \Pi$	0.562
$bmcorr_{\text{P.dahlianum}} = diameter$	0.359
$bmcorr_{\text{S.polaris}} = 2mainbra + secbra + \ln longest$	0.349
$bmcorr_{\text{O.digyna}} = diameter \times leaves$	0.480
$bmcorr_{\text{S.oppositifolia}} = longest \times (mainbra + secbra)$	0.883

Table 4: Repeated measures analysis of variance on the effects of registration time (within subject repeated Factor), planting date (P) and soil treatment (S) on the combined growth variable *bmcorr* tested individually for each species in the experiment. Asterisks behind F-ratios indicate p-values: ns ($p > 0.05$), * ($0.05 \geq p > 0.01$), ** ($0.01 \geq p > 0.001$), *** ($p \leq 0.001$).

a) Species planted on Dovre (*Salix herbacea* in the "*Salix*" site, other species in the "heath" site).

Source of	*A. uva-ursi*			*E. nigrum*			*S. herbacea*			*V. vitis-idaea*		
variation	df	MS	F	df	MS	F	df	MS	F	df	MS	F
Planting date (P)	1	0.05	0.16 ns	1	51.97 10^5	66.84 ***	1	71.32	42.96 ***	1	69.77 10^3	21.67 ***
Soil type (S)	2	4.55	1.50 ns	2	4.61 10^5	5.93 **	2	0.02	0.14 ns	2	0.53 10^3	0.17 ns
P x S	1	7.20	2.37 ns	1	0.12 10^5	0.15 ns	1	0.05	0.03 ns	1	0.04 10^3	0.01 ns
Error	35	3.04		43	0.78 10^5		30	1.66		28	3.22 10^3	
Factor	3	85.31	104.77 ***	3	19.57 10^5	107.70 ***	3	17.85	71.94 ***	3	38.67 10^3	28.45 ***
Factor x P	3	2.21	2.71 *	3	4.17 10^5	22.93 ***	3	10.05	40.49 ***	3	2.36 10^3	1.74 ns
Factor x S	6	1.12	1.37 ns	6	0.60 10^5	3.31 ***	6	0.37	1.49 ns	6	0.44 10^3	0.32 ns
Factor x P x S	3	1.52	1.86 ns	3	0.25 10^5	1.36 ns	3	0.14	0.56 ns	3	0.64 10^3	0.47 ns
Error	105	0.82		129	0.18 10^5		90	0.25		84	1.36 10^3	

b) Species planted on Svalbard

Source of variation	*L. arcuata* df	*L. arcuata* MS	*L. arcuata* F	*O. digyna* df	*O. digyna* MS	*O. digyna* F	*P. dahlianum* df	*P. dahlianum* MS	*P. dahlianum* F	*S. oppositifolia* df	*S. oppositifolia* MS	*S. oppositifolia* F
Planting date (P)	1	2844.73	4.37 *	1	$0.03\ 10^4$	0.12 ns	1	538.27	6.96 *	1	$3.53\ 10^5$	1.75 ns
Soil type (S)	2	188.41	0.29 ns	2	$43.42\ 10^4$	20.12 ***	2	466.77	6.03 **	2	$4.79\ 10^5$	2.37 ns
P x S	2	1156.65	1.78 ns	2	$5.66\ 10^4$	2.62 ns	2	496.23	6.07 **	2	$10.41\ 10^5$	5.15 *
Error	23	651.63		22	$2.16\ 10^4$		25	77.35		18	$2.02\ 10^5$	
Factor	3	8386.52	111.25 ***	3	$32.70\ 10^4$	27.23 ***	3	112.07	5.14 **	3	$1.53\ 10^5$	10.88 ***
Factor x P	3	384.71	5.24 **	3	$2.52\ 10^4$	2.10 ns	3	1169.10	53.59 ***	3	$0.31\ 10^5$	2.21 ns
Factor x S	6	330.54	4.50 **	6	$7.18\ 10^4$	5.98 ***	6	80.74	3.70 **	6	$0.16\ 10^5$	1.14 ns
Factor x P x S	6	125.30	1.71 ns	6	$1.42\ 10^4$	1.18 ns	6	234.34	10.74 ***	6	$0.60\ 10^5$	4.24 **
Error	69	73.41		66	$1.20\ 10^4$		75	21.82		54	$0.14\ 10^5$	

Figure legends

Figure 1: The study areas are located in Hjerkinn firing range on Dovre Mountain on the mainland of Norway, and near the settlement Longyearbyen on the Svalbard archipelago in the northern Barents Sea.

Figure 2: Monthly precipitation in the study areas during planting season 1999, indicated as departure from average mean (100%) for each area.

Figure 3: The experimental site "heath" on Dovre Mountain is situated along a road built about 1960, and natural recovery is virtually absent after 40 years. Transplants of the heath species *Arctostaphylos uva-ursi*, *Empetrum nigrum* ssp. *hermaphroditum*, and *Vaccinium vitis-idaea* were planted in this site.

Figure 4: A plot (0.5 m x 0.5 m) planted with 9 transplants of *Luzula arcuata* ssp. *confusa* in early summer (Planting date 1) and added commercial soil mixed with native roots (soil treatment R).

Figure 5: Survival (mean ± 1 SE) during three growing seasons for transplants planted in the study site on Dovre. Planting date 1 is early summer, planting time 2 is late summer. Survival is expressed as absolute number of surviving transplants within each plot at each registration time. Soil types are lumped due to no significant effect. Registration time *s* is early summer (spring), and *a* is late summer (autumn).

Figure 6: Survival (mean ± 1 SE) during three growing seasons for transplants planted in the study site on Svalbard. Survival is expressed as absolute number of surviving transplants within each plot at each registration time. Planting date and soil type are lumped for all species, due to no significant effects. Registration time *s* is early summer (spring), and *a* is late summer (autumn).

Figure 7: Plant size (mean ± 1 SE) for individual species during three growing seasons. Planting date 1 is early summer, planting date 2 is late summer. Soil treatments are lumped. Plant size is expressed by the calculated variable *bmcorr* for individual species (see explanation in the text and Table 3). Registration time *s* is early summer (spring), and *a* is late summer (autumn).

Figure 8: Mycorrhiza infection level (%) (mean ± 1 SE) at the end of the experiment. Transplants of *Salix polaris* were cultivated from cuttings collected on Svalbard, transplants from the other species were cultivated from cuttings collected on Dovre.

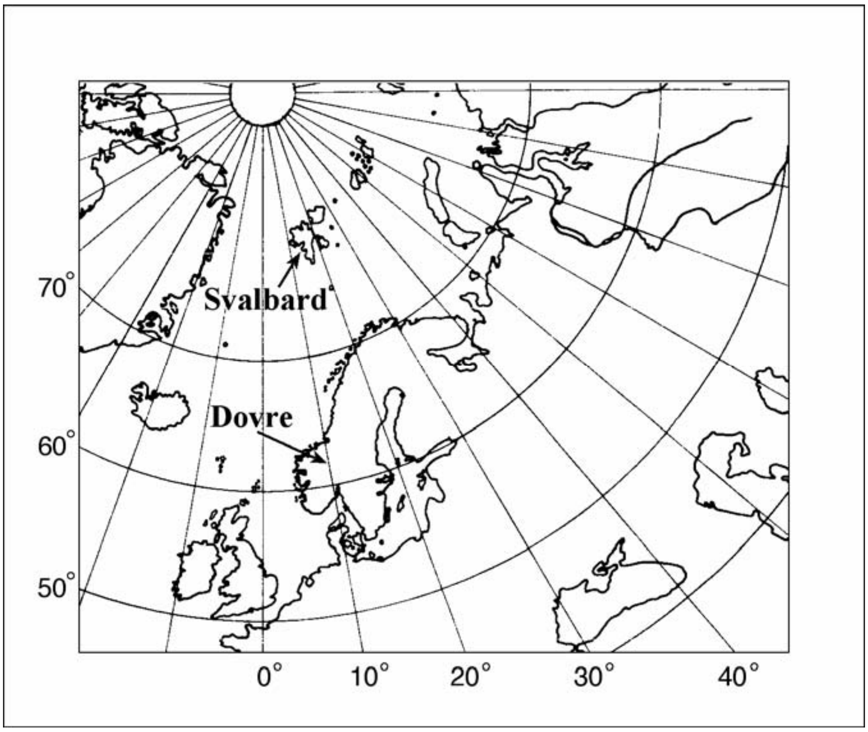
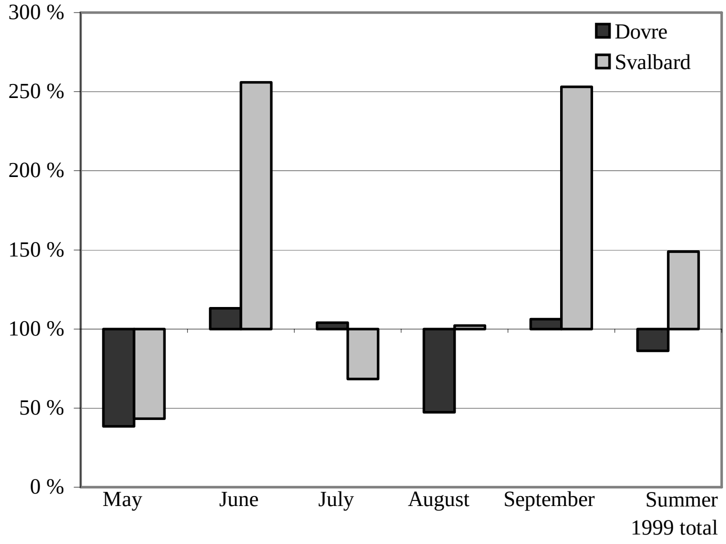


Figure 1



300 %
250 %
200 %
150 %
100 %
50 %
0 %
Dovre
Svalbard
May
June
July
August
September
Summer 1999 total

Figure 2

Figure 3

Figure 4

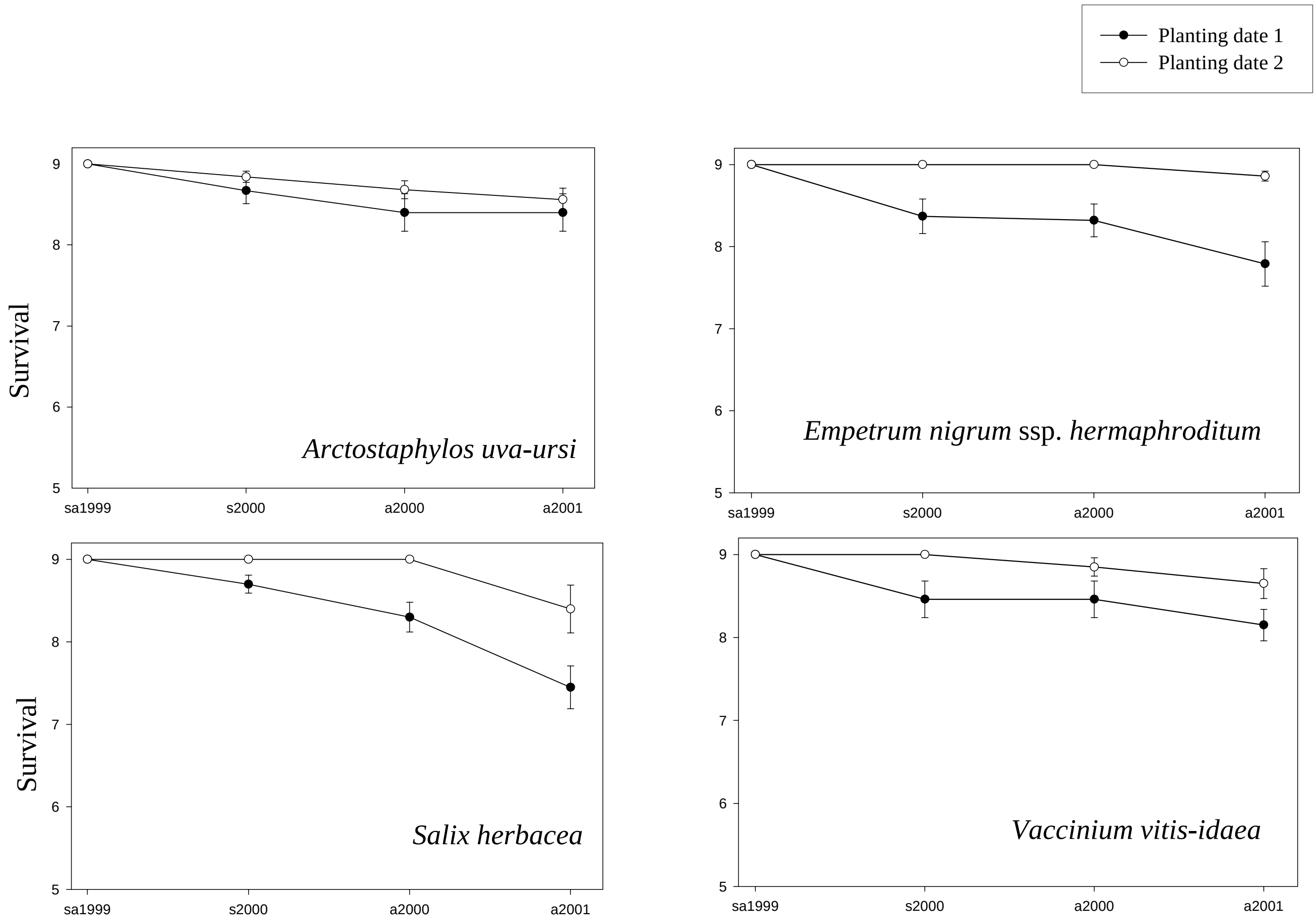
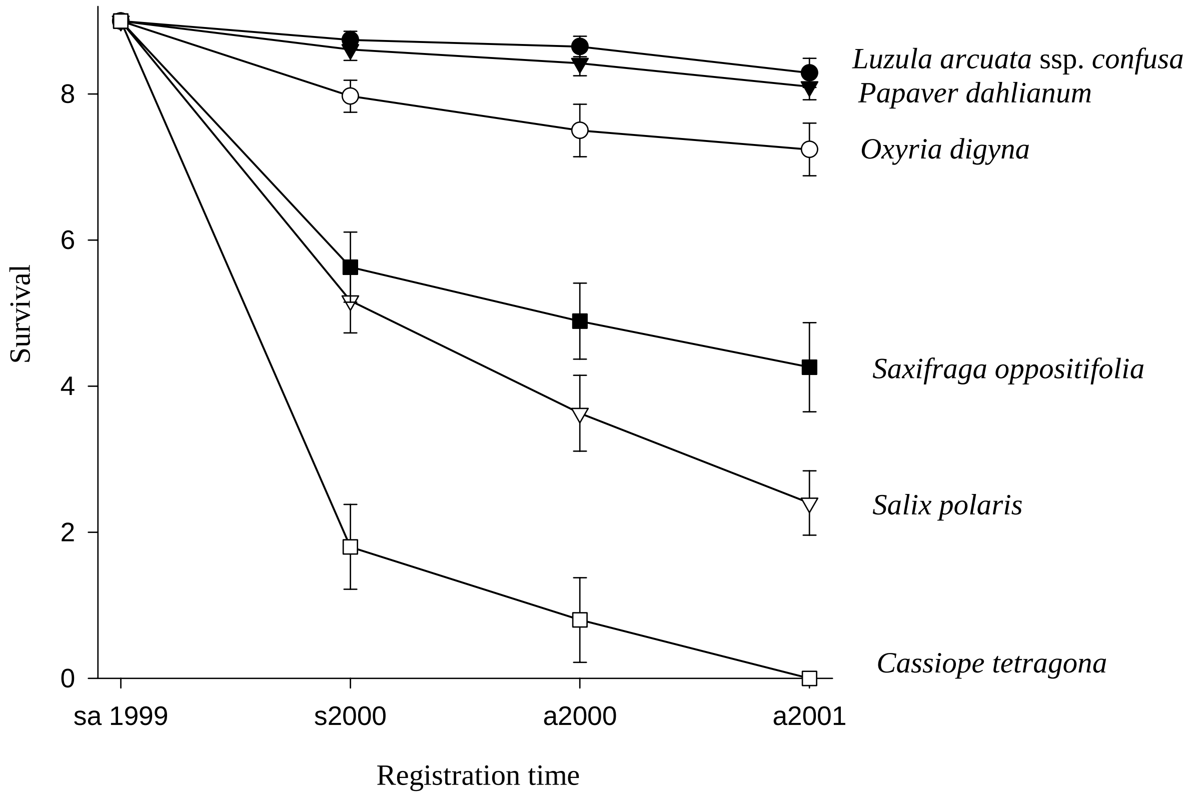
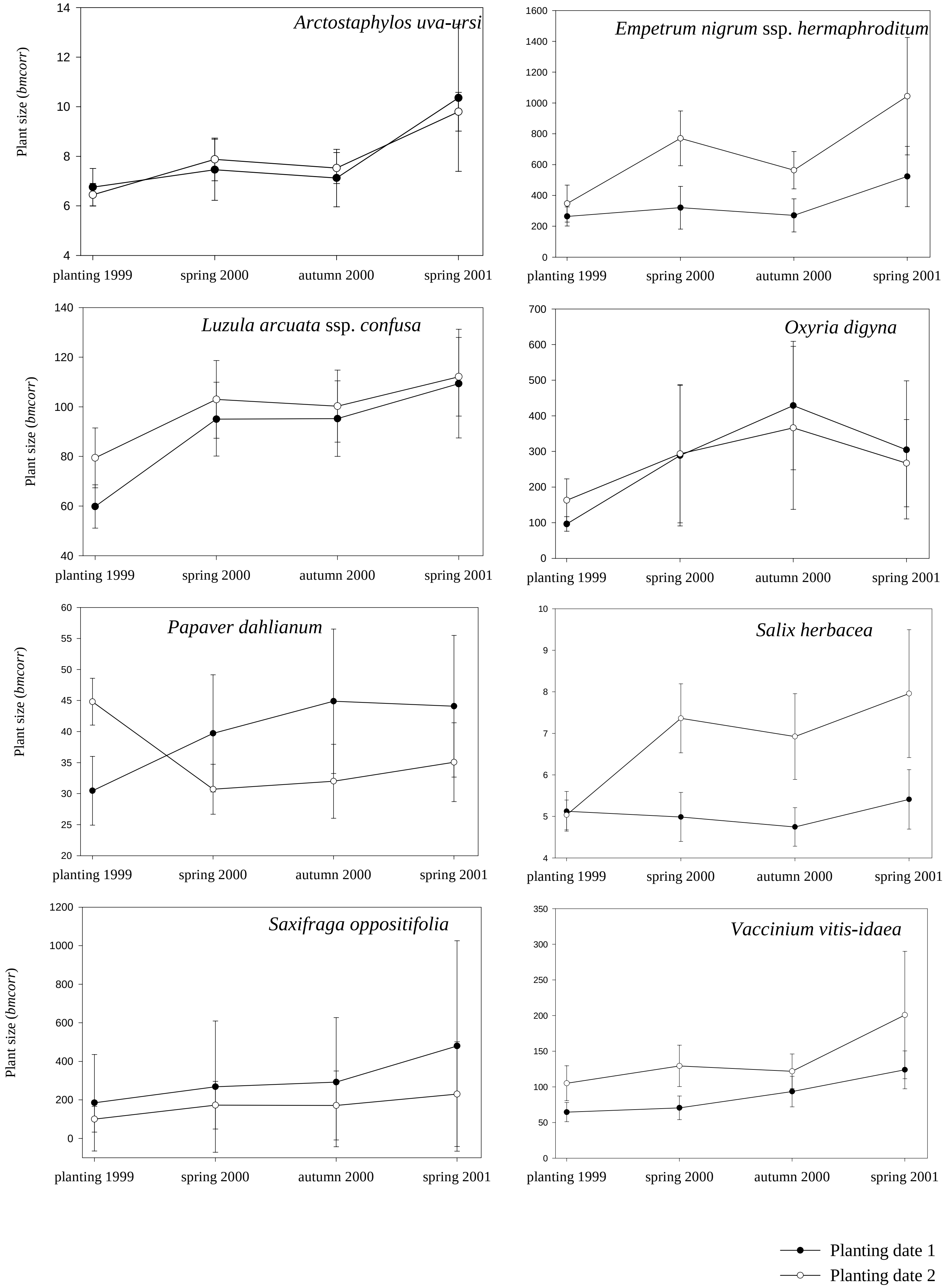

Planting date 1
Planting date 2
Survival
Arctostaphylos uva-ursi
Empetrum nigrum ssp. hermaphroditum
Salix herbacea
Vaccinium vitis-idaea
9
8
7
6
5
sa1999
s2000
a2000
a2001

Figure 5



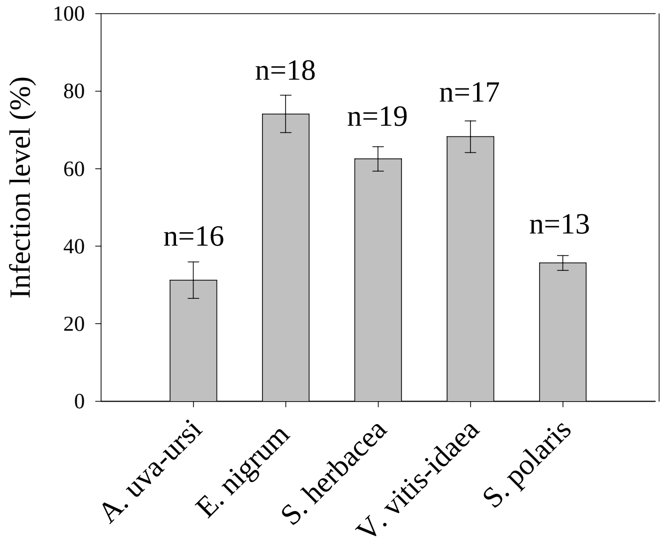
Luzula arcuata ssp. confusa
Papaver dahlianum
Oxyria digyna
Saxifraga oppositifolia
Salix polaris
Cassiope tetragona
Survival
0
2
4
6
8
sa 1999
s2000
a2000
a2001
Registration time

Figure 6



Arctostaphylos uva-ursi
Empetrum nigrum ssp. hermaphroditum
Luzula arcuata ssp. confusa
Oxyria digyna
Papaver dahlianum
Salix herbacea
Saxifraga oppositifolia
Vaccinium vitis-idaea
Plant size (bmcorr)
planting 1999
spring 2000
autumn 2000
spring 2001
Planting date 1
Planting date 2

Figure 7



100
80
60
40
20
0
Infection level (%)
n=16
n=18
n=19
n=17
n=13
A. uva-ursi
E. nigrum
S. herbacea
V. vitis-idaea
S. polaris

Figure 8

Paper IV is not included due to copyright

Paper V

Restoration by willow (*Salix* spp.) cuttings as a management strategy in Hjerkinn Firing Range, Dovre Mountain, Norway.

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ABSTRACT

Due to increased anthropogenic disturbances in alpine areas assisted recovery has been proposed as a management strategy in future landscape planning. Ecological knowledge, technological solutions and social considerations must be integrated to find good management solutions. Hjerkinn Firing Range on Dovre Mountain will be closed down, and there are political intructions to "*restore the area in a way that entails considerable profit for the nature*". The intention of this study has been to integrate scientific and applied approaches of restoration by using cuttings from native willows (*Salix* spp.) in planting experiments of various scales. The results showed that greenhouse propagation of common, native willows could fulfil the need for plant material in large-scale restoration. Planting of willows fulfilled several political, ecological and aesthetical goals that had been expressed for future management of the study area, like use of native species and to get immediate effect of restoration. Willow cuttings can be a useful restoration method at leeward sites with stable snow layer during winter, and with a particular need for immediate and visual results.

Key-words: alpine, development plan, landscape, restoration, *Salix* spp.

INTRODUCTION

Anthropogenic disturbances in alpine areas are increasing and span a wide range of scales, from small spots up to large landscapes (Walker and Walker, 1991; Reynolds and Tenhunen, 1996; Forbes et al., 2001). Slow recovery rates (e.g., Forbes, 1996; Harper and Kershaw, 1996) have raised the question of considering assisted recovery as a management strategy in future landscape planning. A broad range of ecological conditions in the disturbed sites are essential for the possible outcome of recovery, like original and adjacent vegetation cover, characteristics of the disturbance, moisture and temperature regime in the site, and presence of native seeds or soil seedbank (Walker and Walker, 1991; Urbanska, 1997; Forbes and Jefferies, 1999). Knowledge of these attributes must be the basis for selecting restoration methods, and to evaluate the ecological effects of an enterprise (Higgs, 1997). However, successful restoration requires an expanded approach including technological, social, political, economical, and aesthetical aspects (e.g., Diamond, 1987; Edwards et al., 1997; Hagen et al., 2002). These aspects are essential when scientific knowledge is transferred into practical restoration enterprises with a time frame, cost and scale that is relevant for the management of a specific area.

Native willow (*Salix* spp.) cuttings in restoration – a technical solution with ecological fidelity

The scientific approach of ecological restoration and the more applied approach of practical and technical rehabilitation (Harper, 1987; Jordan et al., 1987; Jackson et al., 1995; Bradshaw, 1997) have potential for mutual support. Application of ecological principles on the well-established technology of engineers, gardeners and contractors should be the basis when planning site-specific large-scale restoration enterprises (Bradshaw, 1987; Webb, 1997). The present study made use of this potential for mutual support in the development of a method using native willow cuttings in the restoration of an area.

Willows are known to be easy to propagate as cuttings (Chmelar, 1974; Ericsson, 1988; Hagen, 2002; Hartmann et al., 2002) and has been used in other restoration experiments in alpine and arctic areas (e.g., Miller et al., 1983; Densmore et al., 1987; Houle and Babeux, 1998). A cutting is a vegetative part separated from a mother-plant, which under certain environmental condition forms roots (Hartmann et al., 2002). Once a cutting has developed roots it is able to support itself with available water and soil minerals. By using a variety of species and treatment combinations it is possible to deduce appropriate methods for restoration of sites with different characteristics. Gravel roads and roadsides are typical disturbances where transplantation of willows can be a strategy (Jorgenson and Joyce, 1994).

Development Plan for future management of Hjerkinn Firing Range

The focus in this study is the application of practical large-scale restoration as a management strategy in Hjerkinn Firing Range on Dovre Mountain, Norway. In 1999 the Norwegian Parliament decided to close down the firing range during 2005-2008. The Parliament decision gave instruction concerning future management, including an enlargement of the neighbouring National Park and restoration of the firing range area. This work will be put in specific terms through a joint comprehensive Development Plan that combines the interests of The Norwegian Defence Estates Agency, the two involved counties, and environmental authorities (Anon., 2001). Several more or less consistent goals for restoration are indicated in this plan. The main focus is to *”restore the area in a way that entails considerable profit for the nature”*. A long time-scale for restoration is stressed and the main goal is to bring at least a part of the area back to an *”original state”*, but the need for some immediate results is also stated. Introduced species will be totally prohibited in the restoration. Hagen et al. (2002) examined local people and stakeholders’ preferences for restoration in Hjerkinn Firing Range. An explicit need for large-scale restoration in the area, and the importance of using native species when possible was stated. The immediate goal for restoration was defined by the participants as “*getting started*”, while the preferred long-term goal was to make the disturbed area an integrated part of surrounding vegetation.

Site-specific goals and success evaluation

Defining site or situation specific goals are essential to restoration projects (Densmore and Holmes, 1987; Jorgenson and Joyce, 1994; Slocombe, 1998). Goal formulation and restoration success must be evaluated at specific time-scales (Chambers, 1997; van Diggelen et al., 2001). Any defined goal in restoration is only one of many alternative solutions (Diamond, 1987; Bradshaw, 1997). Accordingly, goals will represent the management ideals of the actual participants in the goal-formulating process (Hagen et al., 2002), and can vary over time for one particular problem or situation (Magnusson, 1997). Ecological knowledge and experimental studies are essential for the formulation of realistic goals under prevalent environmental conditions. But political and management decisions prior to restoration provide guidelines for the actual enterprise, and obviously influence goal formulation (e.g., Maguire, 1995; Lackey, 1998; Slocombe, 1998). For instance, management authorities' prohibition against introduced species and the demand for some kind of immediate effect of restoration are examples of this (Anon., 2001).

The ecological effect of a restoration can be described as actual change in the site, and it is scientifically observable and predictable (Bradshaw, 1987). Evaluation of the environmental impact from an enterprise raises the question of whether this change matters to society i.e., evaluated against some value norm (Munn, 1979; Emmelin, 1996). Results regarded as successful from some specific ecological criteria, obtained in small-scale ecological experiments, are not necessarily evaluated as successful in landscape context. Both because there is a natural variation at the landscape level, which can be difficult to account for in small-scale experiments, and also because at the landscape level other values must be considered (Anderson, 1995; Makhzoumi and Pungetti, 1999; Hobbs, 2002).

Aims

This study will show how an integrated approach to restoration can be used in the management of an alpine area with severe anthropogenic disturbances. The integration of ecological and technological knowledge is used in the development of a method for large-scale restoration by willow cuttings.

The following questions are emphasised:

- What are the rooting capacity and the long-term prospects for survival and growth of fresh woody willow (*Salix* spp.) cuttings planted in the field?
- What are the prospects for survival and growth of greenhouse propagated *S. phylicifolia* planted in the field, and what are the effects of locality, peat soil treatment, and planting distance?
- What is the short-term progress for individuals of *S. phylicifolia* in large-scale plantings at disturbed sites?

The results of the experiments will be discussed in relation to aesthetical and social benefits of large-scale plantings in future management of the study area.

METHODS

Study area

Hjerkinn Firing Range is a 165 km^2 large military training area, situated in the southern part of the Dovre Mountain, Central Norway (63°N, 10°E) (Figure 1) at 1000 m a.s.l., in the low alpine vegetation region (Moen, 1999). Annual precipitation is 450 mm, of which 248 mm fall during May to September (Norwegian Meteorological Institute, personal communication). Mean summer temperature (May to September) is 7.2°C, and length of the growing season (number of days with an average temperature of ≥ 5°C) is 115. Coarse, calcium-poor glacial sediments dominate in the area, and vegetation is characterised by lichen and dwarf shrub heaths, *Salix* spp. meadows, and scattered bogs and fens (NIJOS, 1999). Dominating willow species are *Salix glauca*, *S. lapponum*, and *S. phylicifolia*. The vegetation layer is particularly thin and fragile at the top of ridges.

The Hjerkinn area has been used for summer farming, grazing, hunting etc. for centuries. The military activity has existed since 1923, and today 90 km of roads, more than 100 buildings, several target ranges, and other military installations fragment the area (Jacobsen and Skattum, 2002; Anon., 2003). The majority of disturbances are located in dry parts of the area, and the organic layer is removed, uncovering coarse gravel soil. Natural recovery following disturbances is slow, and 40-year old roadsides have hardly got any new vegetation. Hjerkinn Firing Range is surrounded by several protected areas, and a turnpike road through the military area improves the accessibility into large wilderness areas (Figure 1).

Fresh willow (*Salix* spp.) cuttings

In total 840 woody cuttings of *Salix glauca, S. lapponum* and *S. phylicifolia* (15 cm long, base diameter 0.3 to 1.5 cm) were collected in the firing range in May 1989. At each of three adjacent sites 280 fresh cuttings of each species were planted into groups of 40 immediately after cutting. Distance between cuttings were 20 cm. Site 1 and Site 2 had less than 5 % vegetation cover and coarse mineral soil, and Site 3 had about 15 % vegetation cover and mixed mineral soil. At the end of the first growing season cuttings were dug up for root recordings and gently planted back into the plant holes. After 11 growing seasons the number of living individuals, defined as “bearing green leaves”, were counted.

Greenhouse cultivation of *Salix phylicifolia* cuttings

Cuttings of *Salix phylicifolia* were used for greenhouse cultivation. The “fresh cutting experiment” showed that this species was easy to root, and successful greenhouse propagation and cultivation are documented from previous studies (e.g., Silvola and Ahlholm, 1993; Hytonen et al., 1995). The reddish top twigs made the species easy to characterise without leaves, and cuttings could be collected in winter without previous tagging. One-year old branch-tips of *S. phylicifolia* were collected in the firing range in December 1997, stored at 1°C in polyethylene bags for two months, and then divided into about 7 cm long cuttings. The cuttings were placed in organic peat soil at 21°C and 18 h daylight (procedures according to Hartmann et al., 1990, new edition 2002). During a six-week period 75 % of the cuttings developed roots. During March and April the cuttings had marked apical growth, and the top twigs were sheared twice to promote lateral branching (Figure 2). At the beginning of May 1998 greenhouse temperature was gradually lowered to 8°C and the plants were placed outdoors for hardening. At the end of June 3000 plants were transported to the study area by lorry. The cultivated willows were at that time in average 40 cm high with 2-4 branches, and had no catkins.

Experimental small-scale field planting of greenhouse-propagated *S. phylicifolia*

Three localities in the firing range were selected for small-scale experimental planting in June 1998: Ringvegen, Storranden, and Veslefallet. The localities were 30-40 year old roadsides with about 15 % vegetation cover, and dwarf shrub heath or willow shrubs dominated adjacent vegetation. All localities are covered with snow in the winter, but Ringvegen is more exposed than the two others. At each locality 120 cultivated willow plants were planted in four groups of 30 individuals. Two groups were planted sparse (2 m distance between all individuals) and two were planted dense (0.5 m distance). Each individual in one scarce and one dense group at each locality got 10 litre organic peat soil filled into the plant hole, while individuals in the other two groups were planted directly into the original soil.

In August 1998, 1999 and 2000 survival, and number and length of main and lateral branches were recorded. The majority of plants had the same number of main branches after three years as at planting time, a few plants had developed new main branches, and some had lost main branches by snow- or animal cracking. Length of main branches was almost totally dependent on snow depth. As a consequence of this the number of lateral branches was considered a better parameter for growth than number and length of main branches. At the end of the third growing season (2000) five individuals from each locality and treatment were collected randomly for biomass measurements, in total 60 plants.

Large-scale planting of greenhouse-propagated *S. phylicifolia*

Four disturbed sites in the central part of the firing range area were selected for large-scale plantings in July 1998: Langbakken, Bommen, Veslefall-bridge, and Haukberget (Table 1). Before planting all sites were covered with a 15-20 cm layer of organic peat soil. An excavator was used to dig peat soil from below water surface in a small swamp next to the sites (Figure 3). Total amount of peat soil needed was 200 m^3. In total 2640 individuals were planted into the organic soil in irregular rows, with 0.6 m distance. In August 1998 and 2000 willow survival in each site was roughly recorded, and the general situation in the site was described with respect to willow vitality, total recovery, and qualitative, aesthetical landscape evaluation.

Data analysis

Two-way ANOVA (general linear model, GLM) was used to test the differences in rooting ability between species and localities for fresh cuttings of *Salix glauca, S. lapponum*, and *S. phylicifolia.* Pearson chi-square statistics were used to test the effect of treatments to survival in field after three growing seasons for greenhouse propagated *S. phylicifolia* (Zar, 1996). A Kruskal-Wallis non-parametric test for several independent samples was used to test differences in number of lateral branches between localities and treatments for greenhouse propagated *S. phylicifolia* (Zar, 1996). Two-way ANOVA (general linear model, GLM) was used to test the effects of soil treatment and planting density to number of lateral branches for each locality separately (Zar, 1996). Only plants surviving during the entire experiment were included in statistical testing of lateral branching. Simple regression was used to outline the relationship between number of lateral branches and the destructive measurement of total biomass for *S. phylicifolia*. All statistical tests were performed using SPSS version 10.0 for Windows (SPSS, Inc., 1999).

Evaluation of large-scale plantings was done by registration of survival and vitality of *S. phylicifolia* during the experiment, and by qualitative descriptions of landscape and aesthetical values in the sites. *Immediate* effect was observed when the technical part of the restoration was finished. *Short-term* effect was observed within 2-3 years after the technical part was finished and natural recovery had started. *Long-term* effect can be evaluated after about 10 years (only for the fresh cutting experiment).

RESULTS

Fresh cutting experiment

Cuttings in Site 3 had higher rooting (%) than those planted in Site 1 and Site 2 (ANOVA; F = 38.52; $P < 0.001$). More than 90 % of *Salix phylicifolia* and *S. lapponum* cuttings developed roots during the first growing season in Site 3, while in Site 1 and Site 2 rooting did not exceed 60 % for any species (Figure 4). Cuttings of *S. phylicifolia* and *S. lapponum* had better rooting capasity than cuttings of *S. glauca* (ANOVA; F = 11.94; $P = 0.001$). No interaction between species and locality was observed. After 11 growing seasons the number of living plants was dramatically reduced. Site 1 had no surviving plants, Site 3 had 20 % surviving plants, but almost no new lateral branches. Site 2 was ruined by a human caused incident, and all plants were gone. Natural recovery had no visual progress during the 11 years.

Small-scale field planting

After three growing seasons 92 % of all greenhouse propagated *Salix phylicifolia* plants in the experimental plots had survived (Figure 5). The majority of death occurred just after planting, mainly due to herbivore jerking and browsing, while almost no death was recorded during the second and third growing season. Survival differed significantly between localities (chi-square (χ^2) statistics; $P < 0.001$). When testing each locality separately, peat soil treatment showed a negative effect on survival at Ringvegen ($P = 0.001$) but no effect in the other localities, while plant density had no effect at any locality.

Simple regression showed a close relationship between number of lateral branches and total biomass ($R^2 = 0.655$), and only results for number of lateral branches are presented here. Number of lateral branches per plant after three growing seasons differed between localities (Kruskal-Wallis; $P < 0.001$), with highest number of branches in Veslefallet and lowest number at Ringvegen (Figure 6). When testing each locality separately, peat soil treatment showed a negative effect to number of branches at Ringvegen, and there was a significant interaction between peat and density at Veslefallet (Table 2). Catkins were observed in the plots, but not quantified.

Large-scale plantings

In the large-scale plantings the aesthetical impression of a vegetated area was established immediately following planting, due to the size of the willow plants, the planting pattern, and the moderating effects on surface colour because of the peat soil (Figure 7). Plant survival was high at all sites during the experiment (Table 1). The majority of death occurred during the first month after planting, mainly due to sheep and muskox' trampling and jerking. Following these first months almost no mortality was observed. At Veslefall-bridge, and to some degree at Langbakken, tearing from snow and wind during winter reduced plant vitality at the most exposed positions (Table 1). In leeward sides of Veslefall-bridge and Langbakken and for the total plantings on Bommen and Haukberget tearing occurred only at outermost branch tips and this did not have a negativ effect on plant vitality. Additional vegetation recovery was mainly restricted to establishment of *Deschampsia cespitosa*, particularly at the site Bommen. Catkins were observed at all sites, and indicated that seed production had occurred or would occur in the near future.

DISCUSSION

The successful greenhouse cultivation and high survival and growth in the field for *Salix phylicifolia* gave good prospects for this method in large-scale restoration. The immediate aesthetical effect of the large-scale plantings further supports this impression. At the end of the experiment period most of the willows had creeping branches that are able to catch seeds or propagating units blowing near the ground. The willow plants will probably contribute further to recovery by creating safe sites for plant establishment (Urbanska, 1997), by influencing soil nutrient concentration and soil activity (Onipchenko et al., 2001), and by physical stabilisation of the environment (Whisenant, 2002). Transplanting willows is a recommended technique for rehabilitating gravel roads and to prevent erosion (Miller et al., 1983; Jorgenson and Joyce, 1994; Schichtl and Stern, 1996). Roads and roadsides are common types of disturbances in the study area, and in some of these sites planting of willows can be suggested for restoration.

Evaluation of the environmental impact from a restoration enterprise must include values and considerations of involved groups and stakeholders (Emmelin, 1996). The stakeholders' preferences for restoration in the Hjerkinn area (Hagen et al., 2002) were useful for evaluating the environmental impact of the large-scale plantings in the present study. The willow planting method can be evaluated as a success as the visual impression of the disturbance in the landscape was reduced. Plantings were located on easy accessible sites, contributing to fulfil the political and social needs for visible and immediate results – *"getting started"*.

Generating plant material for restoration

Fresh cuttings had high rooting capacity in the disturbed sites. However, the long-term evaluation of the fresh cuttings showed that this was not an useful method for restoration due to high long-term mortality and slow growth rates. Natural recovery was absent during this period, so the cuttings appearantly did not create safe sites for seeds or vegetative units. Water availability is perhaps the most critical factor for rooting and survival of cuttings (Hartmann et al., 2002). Dry and coarse mineral soil with poor waterholding capacity was an obvious reason for high mortality after 11 growing seasons, particularly in the driest site. Digging of cuttings at the end of the first growing season might have had some negative effect on long-term survival.

Greenhouse propagation and cultivation was a resource demanding technique to get appropriate native plant material for restoration. However, the good prospects of plant production makes this a much more promising method than using fresh cuttings. During the greenhouse cultivation period lasting from February to May, it was possible to produce new plants of *Salix phylicifolia* attaining the size of several years old individuals in the study area. The good rooting experiences for fresh *S. glauca* and *S. lapponum* showed that these species probably also could be successfully cultivated in the greenhouse.

Field survival and growth for greenhouse propagated *S. phylicifolia*

Field survival of *S. phylicifolia* was high in all localities of both small-scale and large-scale plantings during the three-year experiment, and this indicated good prospects for establishing a shrub layer during the coming years. Jerking and browsing by muskox and sheep immediately after planting occurred prior to ground fastening of roots, and the plants were detached from the ground. Later browsing did not detach plants, but seemed to increase lateral branching, as also shown by Tolvanen et al. (2001) and Bergmann (2002). This was a likely reason for the high number of lateral branches in the small-scale site Veslefallet at the end of the experiment. Fencing was not considered due to bad experiences of muskox being attracted to other fenced research sites in the area, but for the future some kind of protection from browsing animals should be considered during the first growing season, to prevent immediate jerking.

At the most exposed sites, the small-scale site Ringvegen and exposed sides of the large-scale sites Veslefall-bridge and Langbakken, insufficient snow-cover during winter and soil drainage during summer likely contributed to increased mortality and poor development of branches. The experiment showed that these sites were too exposed for the willows, and it seems like this method is suitable in leeward sites with a stable 20-30 cm thick snow layer during winter.

Peat soil treatment

In the small-scale experiment the peat soil had negative effect on overall survival and on development of lateral branches at Ringvegen. Adding peat soil was expected to have positive influence on the development of *S. phylicifolia*, as a slightly acid environment is reported to favour rooting and growth of cuttings (Hartmann et al., 2002). The peat had other physical characteristics than the original soil at the sites, and peat on top of the original soil created a barrier for water transport between soil layers with different capillary conductivity (Bradshaw and Chadwick, 1980). At Ringvegen this probably caused water deficiency and reduced growth. A possible long-term positive effect of peat soil can only be verified by further observations during subsequent growing seasons, and explicit soil water measurements. Animals partly caused the seemingly negative effect of peat on survival. Peat-treated individuals were grouped together in the research plot, and as browsing and jerking were likely to strike clustered this tended to affect neighbouring plants receiving the same soil treatment.

Total quantity of peat needed for the coverage of large-scale sites was huge, and the visual impression of the disturbed site was immediately moderated due to similar colours of peat and the surrounding vegetation. The necessary volume of organic soil needed to cover the sites must be obtained without causing new damages to the area. The best way to avoid such negative effects are through close contact between ecologists, contractors, and people with local knowledge about the area (Edwards et al., 1997; Higgs, 1997; Brussard et al., 1998). The main obstacle against top soil application is cost and availability, but also the necessity that underlying material is a part of the rooting medium, and the characteristics of the original soil can not be totally disregarded in the long term (Bradshaw and Chadwick, 1980).

Planting density

Planting density had no affect on survival, branching, or biomass at any of the small-scale localities in the time-scale of this experiment. At the end of the experiment there was no above- or below-ground contact between neighbouring individuals in the experiment plots. Effects of planting distance can perhaps be expected as individuals get larger and root distribution increases (Shaver, 1995; Onipchenco et al., 2001; Callaway et al., 2002). Practical experiences from other alpine willow-plantings indicate slow growth during the first 4-5 growing seasons, and then accelerated above-ground growth (Johan Sandberg, personal communication; Rytter, 2001). Size of disturbances and planting density are crucial to the economic costs of this method, as the actual number of willow plants is an essential part of total cost for a restoration enterprise.

Implications for future management

In the future management of Hjerkinn Firing Range planting of willows can be an applicable method in leeward sites with a particular need for immediate and visual results of restoration. Such needs can be ecologically, politically or socially motivated (Lackey, 1998; Forbes and Jefferies, 1999; Hagen et al., 2002). Alternative strategies for acceptable restoration level in the firing range are now discussed in an ongoing communicative process involving a broad range of interests (Faye-Schøll and Martinsen, 2002). Using willow cuttings is only one example of a restoration method that can be used in the future restoration process at Hjerkinn Firing Range. Application of topsoil is another method, also briefly discussed in this article. Like the willow example other methods can be developed based on ecological knowledge, experimental studies, technical experience, and value judgement and consideration from involved authorities, stakeholders and users. The actual costs of restoration can be the limiting factor for an enterprise. The literature on restoration ecology has very little focus on economy, but some examples exist (Edwards and Abivardi, 1997). Technical and applied restoration projects are traditionally the results of strict economic estimates, and this experience can be an important contribution to an integrated approach of restoration.

Mutual benefits from scientific and applied traditions of restoration were evident in this project. Engineers and contractors have some experiences from application of large-scale willow cultivation and plantings in alpine areas, but hardly any documentation exists. Ecological and physiological aspects of propagation and general knowledge about monitoring of plant individuals are common scientific topics. This study has shown that it is possible to create a link between these traditions, using restoration by willows as an example, and making this integrated knowledge available in a real management situation.

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Table 1: Site characteristics and development of large-scale *Salix phylicifolia* plantings during three growing seasons (1998-2000). Due to lack of detailed knowledge about the initial disturbance, and because upkeeping probably has occured at some of the sites, age of disturbance are only indications. Survival was roughly recorded at the end of the first and third growing season. Plants were defined as having "good vitality" if they produced new lateral branches in major parts of the individ, including the upper 15-20 cm.

Site	**Size**	**Disturbance type**	**Age of disturbance**	**# planted individuals**	**Survival (%) 1998**	**Survival (%) 2000**	**General situation for the site (2000)**	**Main death cause**
Langbakken	50 x 4 m^2	Along turnpike roadside	≈ 40 years	460	90	90	Good vitality for leeward growing willows, some tearing of exposed plants.	Muskox jerking
Bommen	20 x 10 m^2	Roadside by turnpike hut	≈ 40 years	500	100	98	Good vitality of willows. Grass establishment.	-
Veslefall-bridge	20 x 20 m^2	Enlarged crossroad, roadside	≈ 30 years	950	92	90	Tearing of most exposed willows, leeward plants of good vitality.	Muskox and sheep browsing and jerking, wind exposure
Haukberget	20 x 15 m^2	Gravel fill at launching ramp	≈ 10 years	730	98	98	Good vitality of willow plants. Some grass establishment.	-

Table 2. ANOVA (GLM) testing the effects of plant density and peat soil treatment to the development of lateral branches in *Salix phylicifolia* after three growing seasons in the field. Asterisks behind F-ratios indicate P-values: ns (P > 0.05), * (0.05 ≥ P > 0.01), ** (0.01 ≥ P > 0.001), *** (P ≤ 0.001).

Source of	***Storranden***			***Ringvegen***			***Veslefallet***		
variation	df	MS	F	df	MS	F	df	MS	F
Density	1	37.41	0.83 ^{ns}	1	480.29	29.68 ***	1	864.74	2.79 ^{ns}
Peat	1	31.01	0.69 ^{ns}	1	9.23	0.57 ^{ns}	1	1071.86	3.46 ^{ns}
Density x Peat	1	14.01	0.31 ^{ns}	1	10.09	0.62 ^{ns}	1	1568.22	5.06 *
Error	116	45.08		105	16.18		100	309.83	

Figure legends:

Figure 1: Hjerkinn Firing Range is situated on Dovre Mountain in Central Norway, at 1000 – 1400 m a.s.l. Roads and military installations fragment the area, and main disturbances are situated in western part of the firing range. The dark green area is Dovrefjell National Park. Since this map was made the national park has been extended, and now adjoins the firing range border in north, including Snøheim.

Figure 2: *Salix phylicifolia* propagated from cuttings and cultivated in the greenhouse during a three-month period. Top twigs were sheared twice during cultivation to promote lateral branching. The root ball is 10 cm x 10 cm.

Figure 3: An excavator was used to dig sufficient volume of peat soil for the large-scale plantings of *Salix phylicifolia*. The source for peat soil was a swamp next to the plantings. The digging caused no surface damage at the site, as water surface covered the depression.

Figure 4: Rooting (%) during one growing season for fresh hardwood *Salix* spp. cuttings planted in the field immediately after cutting. N = 80 for each species in Site 1 and Site 2, N = 120 for each species in Site 3.

Figure 5: Survival (%), after three growing seasons in the field, of greenhouse propagated *Salix phylicifolia* planted at three localities, two plant densities (d = dense, s = sparse), and two soil treatments (peat and no peat). N = 30 for each locality and treatment.

Figure 6. Number of lateral branches for each *Salix phylicifolia* (mean +/- 1 SE) after three growing seasons for each locality and treatment. Planting distance is indicated as s (sparse) and d (dense).

Figure 7. Large-scale planting of *Salix phylicifolia* at site Bommen.

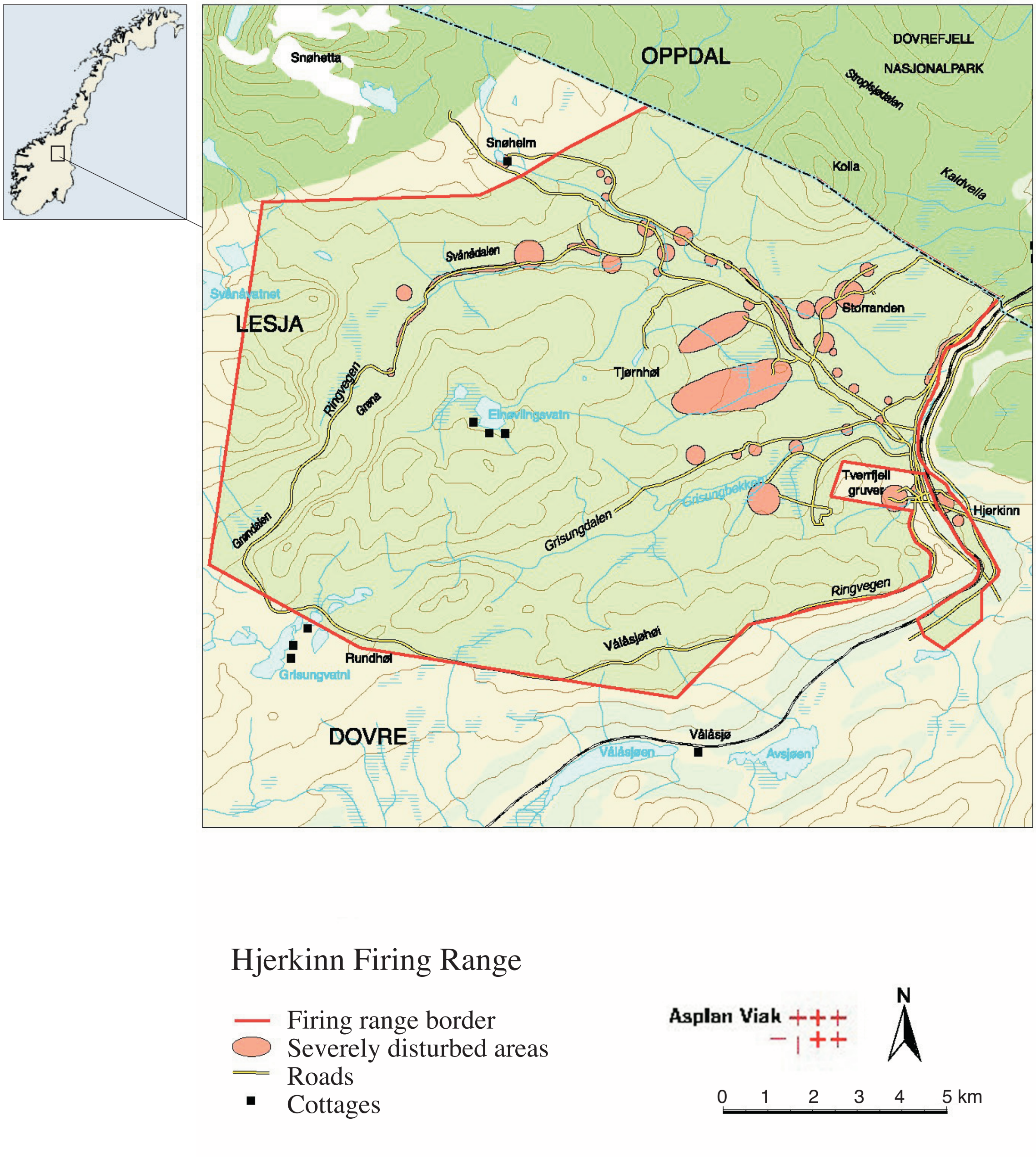

Snøhetta
OPPDAL
DOVREFJELL
NASJONALPARK
Snøheim
Kolla
Kaldvella
Svånådalen
LESJA
Storranden
Tjørnhøi
Ringvegen
Grøna
Tverrfjell
gruver
Hjerkinn
Grisungdalen
Grøndalen
Ringvegen
Vålåsjøhøi
Rundhøi
Grisungvatni
DOVRE
Vålåsjø
Vålåsjøen
Avsjøen
Hjerkinn Firing Range
Firing range border
Severely disturbed areas
Roads
Cottages
Asplan Viak
N
0 1 2 3 4 5 km

Figure 1

Figure 2

Figure 3

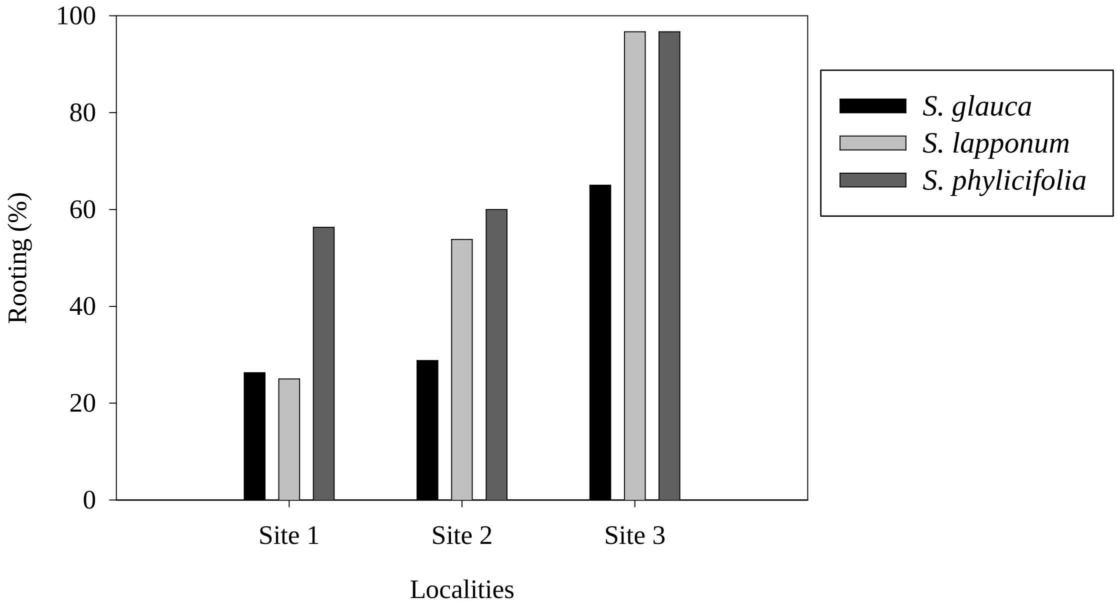

100
80
60
40
20
0
Rooting (%)
Site 1
Site 2
Site 3
Localities
S. glauca
S. lapponum
S. phylicifolia

Figure 4

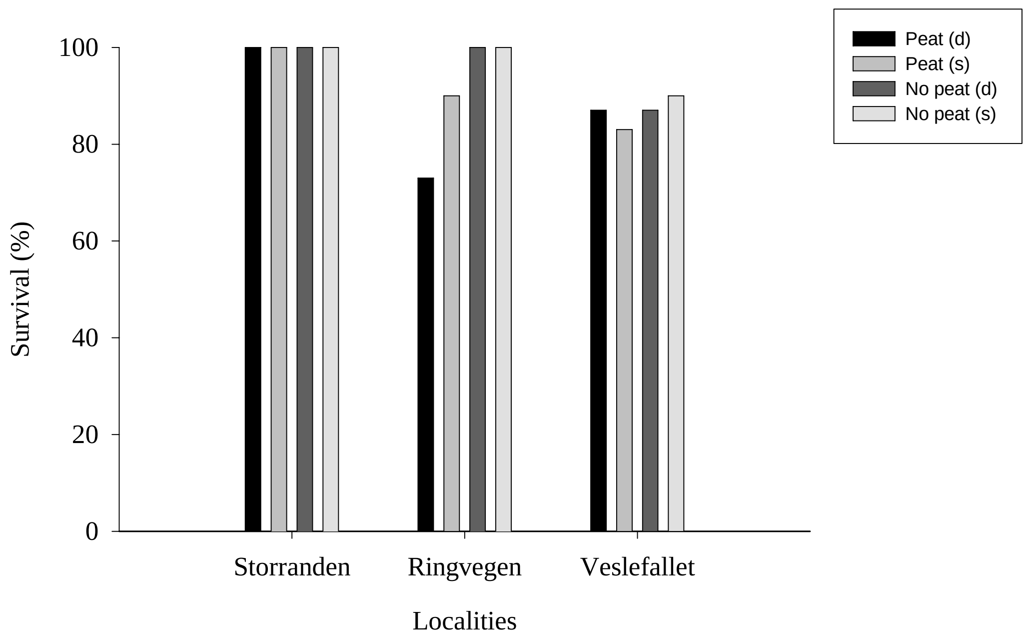
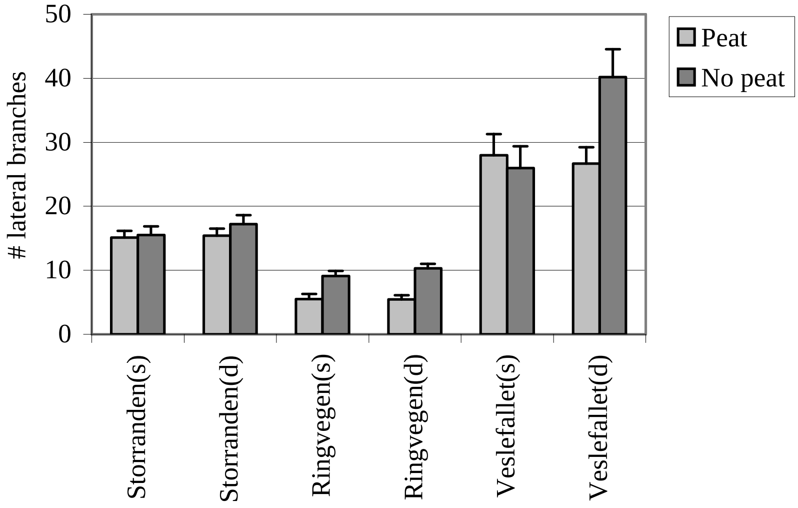

Peat (d)
Peat (s)
No peat (d)
No peat (s)
100
80
60
40
20
0
Survival (%)
Storranden
Ringvegen
Veslefallet
Localities

Figure 5



50
40
30
20
10
0
lateral branches
Peat
No peat
Storranden(s)
Storranden(d)
Ringvegen(s)
Ringvegen(d)
Veslefallet(s)
Veslefallet(d)

Figure 6.

Figure 7