

1075

NINA Report

Foreign Norway spruce (*Picea abies*) provenances in Norway and effects on biodiversity

Per Arild Aarrestad
Tor Myking
Odd Egil Stabbetorp
Mari Mette Tollefsrud



NINA Publications

NINA Report (NINA Rapport)

This is a electronic series beginning in 2005, which replaces the earlier series NINA commissioned reports and NINA project reports. This will be NINA's usual form of reporting completed research, monitoring or review work to clients. In addition, the series will include much of the institute's other reporting, for example from seminars and conferences, results of internal research and review work and literature studies, etc. NINA report may also be issued in a second language where appropriate.

NINA Special Report (NINA Temahefte)

As the name suggests, special reports deal with special subjects. Special reports are produced as required and the series ranges widely: from systematic identification keys to information on important problem areas in society. NINA special reports are usually given a popular scientific form with more weight on illustrations than a NINA report.

NINA Factsheet (NINA Fakta)

Factsheets have as their goal to make NINA's research results quickly and easily accessible to the general public. They are sent to the press, civil society organisations, nature management at all levels, politicians, and other special interests. Fact sheets give a short presentation of some of our most important research themes.

Other publishing

In addition to reporting in NINA's own series, the institute's employees publish a large proportion of their scientific results in international journals, popular science books and magazines.

Foreign Norway spruce (*Picea abies*) provenances in Norway and effects on biodiversity

Per Arild Aarrestad
Tor Myking
Odd Egil Stabbetorp
Mari Mette Tollefsrud

Aarrestad, P.A., Myking, T., Stabbetorp, O.E. & Tollefsrud, M.M.
2014. Foreign Norway spruce (*Picea abies*) provenances in Norway and effects on biodiversity. - NINA Report 1075. 39 pp.

Trondheim, October, 2014

ISSN: 1504-3312

ISBN: 978-82-426-2694-3

COPYRIGHT

© Norwegian Institute for Nature Research

The publication may be freely cited where the source is acknowledged

AVAILABILITY

Open

PUBLICATION TYPE

Digital document (pdf)

EDITION

Per Arild Aarrestad

QUALITY CONTROLLED BY

Signe Nybø

SIGNATURE OF RESPONSIBLE PERSON

Research director Signe Nybø (sign.)

CLIENT(S)/SUBSCRIBER(S)

The Ministry of Climate and Environment (KLD)

The Ministry of Agriculture and Food (LMD)

CLIENTS/SUBSCRIBER CONTACT PERSON(S)

Ernst Inge Dahl Espeland (KLD)

Ivar Ekanger (LMD)

COVER PICTURE

Picea abies. Photo: O.E. Stabbetorp

KEY WORDS

Norway spruce, provenance, afforestation, forestry, taxonomy, genetic variation, paleobotany, biodiversity, ecological traits, risk assessment

NØKKEWORD

Gran, proveniens, skogplanting, skogbruk, taksonomi, genetisk variasjon, paleobotanikk, biodiversitet, økologiske egenskaper, sårbarhetsanalyse

CONTACT DETAILS

NINA head office

Postboks 5685 Sluppen
NO-7485 Trondheim
Norway
Phone: +47 73 80 14 00

NINA Oslo

Gaustadalléen 21
NO-0349 Oslo
Norway
Phone: +47 73 80 14 00

NINA Tromsø

Framsenteret
NO-9296 Tromsø
Norway
Phone: +47 77 75 04 00

NINA Lillehammer

Fakkeltgården
NO-2624 Lillehammer
Norway
Phone: +47 73 80 14 00

www.nina.no

Abstract

Aarrestad, P.A., Myking, T., Stabbetorp, O.E. & Tollefsrud, M.M. 2014. Foreign Norway spruce (*Picea abies*) provenances in Norway and effects on biodiversity. - NINA Report 1075. 39 pp.

This literature review gives an overview of the distribution, taxonomy and genetic variations in Norway spruce (*Picea abies*) as background for evaluating whether native and foreign provenances of Norway spruce in Norway may have different effects on indigenous species and ecosystems according to current knowledge.

The modern range of Norway spruce in Europe is divided into a northern and a southern part. In the north, Norway spruce forms a large continuum covering almost the entire Fennoscandia, the Baltic States, Belarus, northern Poland and European Russia. In the southern range, the species mainly occurs along the mountain chains of central and south-eastern Europe. Norway spruce is a natural tree species, mainly in eastern and central parts of Norway, probably migrated from a large refugium on the East European Plain, following the retreat of the Scandinavian Ice Sheet. There is also evidence for migration from periglacial environments in northwestern Scandinavia. The genetic structure of Norway spruce is shaped by historical factors like glacial survival and processes during postglacial colonization and by present processes with large amount of gene flow over large distances. Since Norway spruce populations are strongly interconnected with gene flow, there are no sharp population boundaries in Europe.

Provenance in forestry refers to the particular place where trees are growing or the place of origin of seeds or trees. Norway spruce from different European countries, especially from Germany and Austria, has been used in afforestation in Norway for several decades. Such foreign provenances may differ in adapted ecological traits, such as phenology, frost hardiness, production and spread of seeds, resulting in different growth- and spread potential of the provenances. We know that afforestation with Norway spruce affects the indigenous biodiversity through altered light conditions, water balance and nutrient cycling. In addition, intraspecific diversity in plants may affect the composition of associated species in the forest ecosystem. Thus, one can speculate that any better growing provenances will affect the indigenous biodiversity most. However, searches in national and international databases, as well as personal enquiries at different forest and environmental research institutes in Europe, have not uncovered any literature or studies in support of differential effects on biodiversity of different provenances of Norway spruce. Research on this subject is probably non-existent.

Even if different provenances may affect the biodiversity differently, these effects are probably marginal compared to the effects of afforestation with Norway spruce itself when it is planted on habitats where there are not native spruce forest. In these areas density of planted trees, management of the plantation and the altered chemical composition of the soil are major determinants of altered biodiversity.

Per Arild Aarrestad. NINA, P.O. Box 5685 Sluppen, NO-7485 Trondheim, Norway.
E-mail: per.a.aarrestad@nina.no

Tor Myking. The Norwegian Forest and Landscape Institute, Fanaflaten 4, N-5244 Fana, Norway.
E-mail: mt@skogoglandskap.no

Odd Egil Stabbetorp. NINA, Gaustadalléen 21, NO-0349 Oslo, Norway.
E-mail: odd.stabbetorp@nina.no

Mari Mette Tollefsrud. The Norwegian Forest and Landscape Institute, P.O. Box 115, N-1431 Ås, Norway. E-mail: tom@skogoglandskap.no

Sammendrag

Aarrestad, P.A., Myking, T., Stabbetorp, O.E. & Tollefsrud, M.M. 2014. Foreign Norway spruce (*Picea abies*) provenances in Norway and effects on biodiversity. - NINA Rapport 1075. 39 s.

Rapporten gir en oversikt over granas (*Picea abies*) utbredelse, taksonomi og genetisk variasjon som en bakgrunn for å vurdere om planting av norske og utenlandske provenienser av gran kan ha ulike effekter på stedegent biologisk mangfold. Ifølge oppdraget skal en slik vurdering gis på bakgrunn av en sammenstilling av eksisterende kunnskap.

Granas utbredelse i Europa er delt i et nordlig og et sørlig område som utgjør to klart adskilte genetiske grupper, sannsynligvis som følge av isolasjon gjennom flere istider. I nord danner gran et sammenhengende område som dekker nesten hele Fennoskandia, Estland, Latvia, Litauen, Hviterussland, nordre deler av Polen og den europeiske delen av Russland. I sør opptre gran hovedsakelig langs fjellkjedene i sentrale og sørøstlige deler av Europa. I Norge er gran hovedsakelig utbredt i østlige og sentrale deler av landet, med spredte populasjoner i indre strøk av Vestlandet og i Øst-Finnmark. Både paleodata og genetiske data viser at grana vandret inn til Norge fra et stort Russisk istidsrefugium langs både nordlige og sørlige innvandringsveier. Samtidig tyder genetiske data på at grana også har overlevd siste istid i Skandinavia. Det finnes møtesoner i Skandinavia fra både et østlig og et vestlig refugium med genetiske subgrupper som følge av de ulike historiske prosessene. Videre bidrar genflyt over store avstander til genetisk homogenisering.

Proveniens (fra latin «provenir» – komme fra, opprinnelse) henviser til områdene der et treslag vokser eller stedsopprinnelsen til frø eller trær, og er ikke et taksonomisk begrep. Ulike provenienser av gran fra flere europeiske land, særlig fra Tyskland og Østerrike, har blitt benyttet i flere tiår til skogplanting i Norge. Slike utenlandske provenienser kan skille seg i adaptive økologiske egenskaper som fenologi, hardførhet mot frost og kulde, evne til frøproduksjon og frøspredning, noe som igjen kan føre til ulik vekst- og spredningspotensiale. Granplanting påvirker det stedegne biologiske mangfoldet betydelig gjennom redusert lystilgang, endret vannbalanse og næringsomsetning i jorda. Man kunne således anta at de proveniensene av gran som har best vekstegenskaper ville påvirke den stedegne biodiversiteten mest. Imidlertid har søk i internasjonale databaser, så vel som forespørsler til miljø- og skogforskningsinstitusjoner i Europa, ikke avdekket noe litteratur eller erfaringsbasert kunnskap som bekrefter dette. Forskning på temaet er trolig ikke-eksisterende.

Selv om ulike provenienser av gran skulle påvirke stedegent biologisk mangfold ulikt, vil slike forskjeller høyst sannsynlig være marginale, sammenlignet med effektene av selve granplantingen, der plantetetthet, skjøtsel av plantefeltene, endret jordkjemi og lysforhold er det viktigste påvirkningsfaktorene på biologisk mangfold.

Per Arild Aarrestad. NINA, Postboks 5685 Sluppen, 7485 Trondheim.
E-mail: per.a.aarrestad@nina.no

Tor Myking. Skog og landskap, Fanaflaten 4, 5244 Fana.
E-mail: mto@skogoglandskap.no

Odd Egil Stabbetorp. NINA, Gaustadalléen 21, NO-0349 Oslo, Norway.
E-mail: odd.stabbetorp@nina.no

Mari Mette Tollefsrud. Skog og landskap, Postboks 115, 1431 Ås.
E-mail: tom@skogoglandskap.no

Contents

Abstract	3
Sammendrag	4
Contents	5
Foreword	6
1 Introduction	7
2 Certification of forest reproductive material and the use of the term provenance in forestry	9
3 Taxonomy, distribution and genetic variation in Norway spruce	11
3.1 Taxonomy	11
3.2 Distribution	11
3.3 Genetic variation, postglacial history and migration	12
4 The use of Norway spruce in afforestation in Norway	16
4.1 General characteristics of seed sale in Norway 1952-2013	16
4.2 The use of Norwegian provenances from 1961-1995	17
4.3 Domestic sale of non-Norwegian provenances	18
5 Ecological traits of Norway spruce provenances	20
5.1 Budburst and growth cessation	20
5.2 Frost hardiness	21
5.3 Production and spread of seeds	21
6 Climate change mitigation by provenance transfer	22
7 Norway spruce afforestation on non-spruce habitats and its general impact on indigenous biodiversity	23
8 Different provenances - different ecological impacts? A risk assessment	25
8.1 Effects of different traits	25
8.2 Effects on genetic diversity in native Norway spruce forests	25
8.3 Effect of genetic diversity on associated biodiversity	26
8.4 Effects on indigenous species and habitats	27
8.5 Criteria for ecological risk assessment - the Norwegian Species information Center - used on Norway spruce provenances	28
9 Summary and conclusion	31
10 References	33

Foreword

The Ministry of Climate and Environment (KLD), and The Ministry of Agriculture and Food (LMD) have requested a risk assessment of effects on biodiversity of using foreign provenances of Norway spruce in afforestation in Norway and have financed this report. In this context, the Norwegian Institute for Nature Research (NINA) and the Norwegian Forest and Landscape Institute have been asked to compile existing national and international knowledge. The Norwegian Forest and Landscape Institute has been responsible for the background information on taxonomy, distribution and genetic variation of Norway spruce, the use of provenances in afforestation in Norway and present knowledge of ecological traits of different provenances. NINA has been responsible for the literature review on effects on biodiversity, and both institutions have together carried out the risk assessment based on current knowledge.

We thank Ragnar Johnskås (Norwegian Forest Seed Centre, Skogfrøverket) for provision of data on sale of Norway spruce seeds, and Senior researcher Harald Kvaalen (Norwegian Forest and Landscape Institute) for help with the figures and comments on the manuscript. We also thank Professor Christer Björkman (Swedish University of Agricultural Sciences), Professor Jørgen Bo Larsen and Senior researcher Hans Peter Ravn (University of Copenhagen) for their contribution in compiling relevant literature.

Trondheim 16.10. 2014

Per Arild Aarrestad
Senior researcher, project leader

1 Introduction

Norwegian forestry has a history of more than thousand years, but it was not until the late 19th century that Norway spruce (*Picea abies*) from outside Norway where introduced. Provenance in forestry refers to the particular place where trees are growing or the place of origin of seeds or trees (Callaham 1964), and several provenances have been imported to Norway from different parts of Europe. Norway spruce has always been the backbone of Norwegian forestry, and presently about 8 million m³ are harvested annually. The native range in Norway amounts to 2.83 million ha, whereas the cultivated range beyond the natural distribution is roughly estimated to approximate 150,000 ha (Jansson et al. 2013).

During the last decades there has been an international concern related to invasion of alien tree species and the risk for potential effects on indigenous ecosystems and biodiversity (Peterken 2001; Engelmark et al. 2001; Felton et al. 2010). The 1992 Convention of Biological Diversity (<http://www.cbd.int>) defines alien (foreign) species to include entities below species level (sub-species or lower taxon) recognizing that planting of non-local taxa may result in negative effects on biodiversity. In 2009, the Nature Diversity Act entered into force. Section 30 in the Act (<http://www.regjeringen.no/en/doc/laws/acts/nature-diversity-act.html?id=570549>) states that without legal authority under section 31 or a permit granted by the competent authority under this Act, no person must release organisms belonging to species or subspecies that do not occur naturally in Norway, including foreign tree species, into the environment.

Biological diversity is defined as “the variability among living organisms from all sources including diversity within species, between species and ecosystems” (Convention on Biological Diversity, United Nations 1992). According to the Nature Diversity Act, biological, geological and landscape diversity includes all diversity that is not largely a result of human influence. Biodiversity in a forest ecosystem is influenced by environmental factors such as climate and soil, and long term processes like evolution and changes in species geographical ranges. Population and community processes, as well as natural or human related disturbances, also influence the biodiversity in an ecosystem. Four components of biological diversity are particularly relevant for planted forests and their environmental impact (i) Genetic diversity, the genetic diversity within a population or a species. (ii) Species diversity, the frequency and diversity of different species in forest or community. (iii) Structural diversity, how forest plant communities are structured, e.g. in density and growth potential. Structural diversity can be important for e.g. lichens and animal species diversity. (iv) Functional diversity, variation in functional characteristics of trees and other plant species, i.e. shade tolerant versus light demanding species, deep rooted versus shallow rooted (Carnus et al. 2006). A useful approach for characterizing biodiversity is to identify measurable indicators that monitor change at different levels of organization, assessing the overall status of biodiversity (Noss 1990).

A regulation on the use of foreign tree species “Forskrift om utsetting av utenlandske treslag til skogbruksformål” (<http://www.lovdata.no/dokument/SF/forskrift/2012-05-25-460>) entered into force in 2012 in order to secure that afforestation using foreign tree species do not lead to undesirable effects on indigenous biodiversity. This regulation defines foreign tree species as species, subspecies or varieties of trees without present or historical natural distribution in Norway. The term provenance is however, not a taxonomic term, and neither is it a part of the definition in the regulation on use of foreign tree species. The discussion if provenances can include different taxonomical sub-levels, such as sub-species, variants or forms of a species has not been the task of this work.

The aim of this review is to evaluate whether native and foreign provenances of Norway spruce may have different effects on indigenous species and ecosystems. This, in turn, relates to the obligations of the Convention on Biodiversity on identifying and controlling spread of foreign organisms and the purpose of the Nature Diversity Act. The review is based on available national and international publications on the topic and personal contacts with relevant research communities. The study gives an overview of the taxonomy, distribution and genetic variations in Norway

spruce, quantitative traits, the use of Norway spruce in afforestation in Norway and general effects of afforestation on indigenous biodiversity as a background for the risk assessment.

2 Certification of forest reproductive material and the use of the term provenance in forestry

The establishment of forest plantations throughout the world demands increasing amounts of seeds and other plant reproductive material such as parts of plants and plants raised by seeds or parts of plants. Reproductive material have for a long time been transferred between countries, and at an early stage, the moving of reproductive material was accompanied by inadequate information about their source and history (Jones & Burley 1973). In order to cope with the origin and history of trade material, several national certification schemes were used (Matthews 1964). However, as the international trade increased it became important to create international acceptable systems for forest reproductive materials. From 1971 and onwards the Organization for Economical Cooperation and Development (OECD) developed a Forest Seed and Plant Scheme with rules and regulations for the certification of forest reproductive material in international trade ([http://www.oecd.org/tad/code/Brochure%20Forest%20%202014%20\(2\).pdf](http://www.oecd.org/tad/code/Brochure%20Forest%20%202014%20(2).pdf)). The F.A.O. Panel of Experts on Forest Gene Resources recommended that countries should model their own national seed certification schemes on that on OECD (FAO 1971). Norway became a member of the OECD forest seed and plant scheme in 1983, and the Norwegian regulation on use of forestry reproductive material from 1996 is harmonised with the OECD Scheme. This mean that when Norway is importing or exporting forest reproductive material, either an OECD certificate or a certificate similar to the OECD certificate must follow the plant reproductive material.

Based on the regulation on forest seeds and plants from 1996, the Ministry of Agriculture and Food established a national control committee which mandate is to have an overall control of the seed supply and ensure that the regulation is followed. One task of the control committee is to process application on use of imported plant material for forestry.

There are four categories recognised under which reproductive material can be certified:

1. *Source-identified* is the minimum standard permitted in which the location and altitude of the place(s) from which the reproductive material is collected must be recorded. Here minor or no phenotypic selection has taken place.
2. *Selected*. The basic material must be phenotypically selected at the population level.
3. *Qualified*. The basic material will be seed orchards, parents of families, clones or clonal mixtures, evaluation may not have been undertaken or completed.
4. *Tested*. The basic material will be seed orchards, parents of families, clones or clonal mixtures. The superiority of the materials must have been demonstrated by comparative testing or a genetic evaluation of the components of the basic material.

There are six types of basic material recognised in the OECD certification scheme from which reproductive material can be collected:

1. *Seed Source* (trees within an area from which seeds are collected).
2. *Stand* (a delineated population of trees possessing sufficient uniformity).
3. *Seed Orchard* (a plantation of selected individuals, which is isolated or managed to avoid, or reproduce pollination, from outside sources, and managed to produce frequent, abundant and easily harvested crops of seed).
4. *Parents of Family or Families* (trees used to obtain progeny by controlled or open pollination of one identified parent used as a female, with the pollen of one parent (full-sibling) or a number of identified or unidentified parents (half-siblings)).
5. *Clone* (group of individuals (ramets) derived originally from a single individual (ortet) by vegetative propagation (e.g. by cuttings, micropropagation, grafts, layers, etc.).
6. *Clonal mixture* (a mixture of initially identified clones in defined proportions).

The term provenance has partly been applied in forestry to deal with genetic variation within species, which is associated with geographical distribution and origin. Provenance research aims at defining the genetic and environmental components of phenotypic variability associated with geographical source, and the term has a biological meaning roughly equivalent to a local population (Callaham 1964). Information on provenances is important in assuring sources of seeds to give well-adapted, productive trees and in directing breeding of forest trees towards adaptation to particular localities. Several definitions of provenance have been published throughout the years. At early stages the provenance term was linked to the geographical source or place of origin from which a given seed or plant was collected (i.e. Empire Forestry Association 1953; Wright 1962, 1976; Ford Robertson 1971; Schmidt 1997). The term does however, not describe provenance as a taxonomic term, e.g. a morphologically separable unit below the species level.

The OECD separates the terms provenance and origin in their certification scheme. The term “provenance” is, according to OECD, defined as “The place in which any seed source or stand of tree is growing”. The Region of Provenance is defined as “For a species or sub-species, the Region of Provenance is the area or group of areas subject to sufficiently uniform ecological conditions in which stands showing similar phenotypic or genetic characters are found”. According to the OECD definition, seeds produced in Belarus by trees of Belarus of origin are obviously a Belarus provenance, but seeds produced in Norway by trees/seeds originating directly from Belarus are defined as a Norwegian provenance.

In the OECD certification scheme, the origin of the material is given. It must be stated whether the basic material is autochthonous/indigenous, non- autochthonous/non- indigenous or the origin is unknown. For an autochthonous seed source or stand, the origin is the place in which the trees are growing. For a non-autochthonous seed source or stand, the origin is the place from which the seed or plants were originally introduced. The origin of a seed source or stand may, however, be given as unknown in the scheme.

Since the Norwegian regulation on use of forestry reproductive material is harmonised with the OECD scheme, we have used the OECD definition of provenances in this work – which is the operational definition applied in European forestry.

3 Taxonomy, distribution and genetic variation in Norway spruce

3.1 Taxonomy

Taxonomically, Norway spruce (*Picea abies* L. Karst) belongs to the pine family (*Pinaceae*) and the genus *Picea*, which diverged from its sister clade 180 million years ago (Lockwood et al. 2013). The genus consists of about 34 species (Farjón 2001), of which two are confined to Europe (*P. abies* and *P. omorika*), 24 to Asia and eight to America. *Picea omorika* is today restricted to the Tatra Mountains in Serbia and is not a close relative to *P. abies* (Ran et al. 2006; Lockwood et al. 2013). Norway spruce is most closely related to Siberian spruce (Schmidt-Vogt 1974), but a consensus on their taxonomical classification has not been reached due to complex patterns of morphological variation. Some authors recognize them as two separate species (Pravdin 1975; Popov, 2003). Others consider them either as two closely related subspecies, *Picea abies* ssp. *abies* and ssp. *obovata* (Tutin et al. 1993), or two geographical races (Schmidt-Vogt 1974, 1977).

Phylogenetic analyses using molecular markers corroborated their close relationship (Ran et al., 2006). In a recent study it was further indicated that Norway spruce of northern Europe is more closely related to Siberian spruce than to Norway spruce of central- and south-eastern Europe (Lockwood et al. 2013). An extensive survey based on wide range sampling across northern Eurasia analyzed with mitochondrial and chloroplast markers, suggest on the other hand that Norway spruce and Siberian spruce are two well defined genetic units/species and that the genetic border between the taxa is situated east of the Ural Mountains, in the area of the Ob River (Tollefsrud 2008). This border also agrees well with morphological data on cone scale shapes (Popov 2003). Popov (2003) describes the most typical Siberian spruce forms of cone scales east of a borderline stretching from the Pechora River south-eastwards to the Ob River. West of this border, intermediate cone scale shapes prevail in a wide zone suggesting introgression.

Genetic and morphological data combined, suggest though that spruce east of the border along the Ob River constitutes a separate taxon/species (Tollefsrud et al. 2008). Results from multiple nuclear genetic markers analysed for an extensive population sample covering the total distribution range of Norway spruce and Siberian spruce moreover support the conclusion that Norway spruce and Siberian spruce are two separated taxa/species and that introgression occur along both sides of the Ural Mountains (Martin Lascoux and Yoshiaki Tsuda, pers. com., see <http://climate.nordgen.org/>, abstract by Tollefsrud et al. 2014).

3.2 Distribution

The modern range of Norway spruce in Europe is divided into a northern and a southern part (**Figure 1**). In the north, Norway spruce forms a large continuum covering almost the entire Fennoscandia, the Baltic States, Belarus, northern Poland and European Russia. In the southern range, the species mainly occurs along the mountain chains of central and south-eastern Europe. The two Norway spruce ranges come together in the middle Polish lowlands (the middle Polish disjunction according to Schmidt-Vogt (1974), see also Latałowa & van der Knaap (2006). The northern range of Norway spruce is in contact with Siberian spruce, which has a wide north Asian distribution (Schmidt-Vogt 1977), in the east. Their combined ranges cover a virtually continuous area across northern Eurasia, ranging from Norway in the west to the coast of the Sea of Okhotsk in the east.

In Norway, the main natural distribution of Norway spruce is in the eastern part of southern Norway, and in mid Norway from Sør-Trøndelag to Rana (**Figure 1**). In addition, there are numerous smaller occurrences in western Norway (Gløersen 1884), as well as a few populations in northern Norway (eastern Finnmark), close to the Russian border (Elven 1994). The alpine tree limit in southern Norway is at 1280 m asl (Hemsedal, Elven 1994). Beyond the natural distribution,

Norway spruce has been planted in the lowlands up to Finnmark, the northernmost county in Norway.

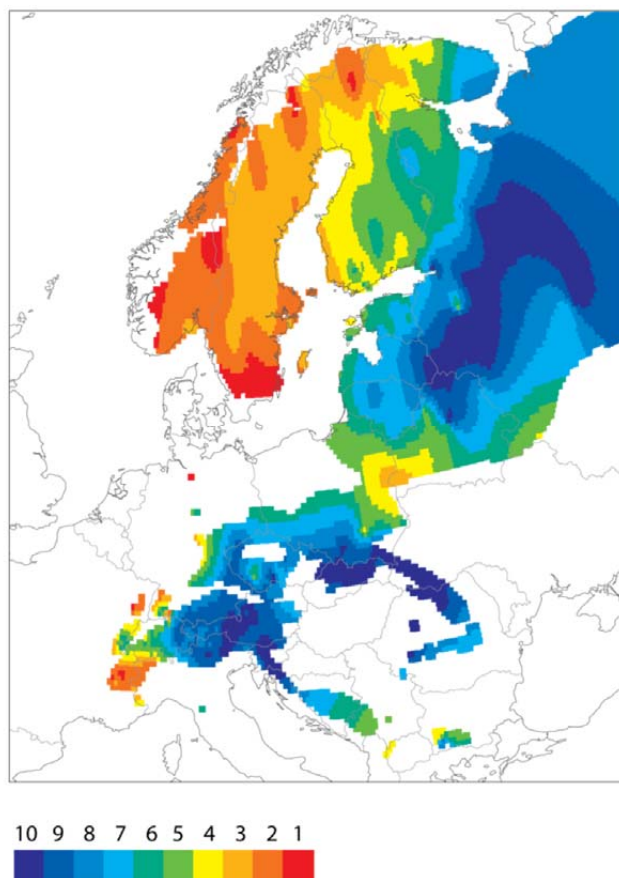


Figure 1. Map of modern distribution range of Norway spruce (the coloured area). The different colours relate to interpolated age of fossil *Picea abies* pollen (threshold larger than 2%), corresponding to time since forest development. Interpolated age is shown in time interval of 1000 years before present, according the colour code (map from Tollefsrud et al. 2008).

3.3 Genetic variation, postglacial history and migration

The glacial and postglacial history of Norway spruce has been intensively studied using both paleobotanical (e.g. Giesecke & Bennett 2004; Terhürne-Berson 2005; Latałowa & van der Knaap 2006) and genetic approaches based on both nuclear, chloroplast and mitochondrial data (e.g. Lagercrantz & Ryman 1990; Vendramin et al. 2000; Sperisen et al. 2001; Collignon et al. 2002; Heuertz et al. 2006; Tollefsrud et al. 2008, 2009; Parducci et al. 2012). Like in most conifers, mitochondrial and chloroplast DNA are maternally and paternally inherited, respectively. Nuclear DNA is inherited from both parents. Mitochondrial DNA is dispersed by seeds, whereas chloroplast and nuclear DNA is dispersed by both pollen and seeds. Mitochondrial and chloroplast DNA show highly structured genetic variation compared to nuclear DNA. Combined, the different types of markers will give information both on historical and present gene flow.

Both paleobotanical data and genetic studies agree that there were separated refugia for Norway spruce in the northern and the southern ranges. Both nuclear (Lagercrantz & Ryman 1990; Collignon et al. 2002; Heuertz et al. 2006), chloroplast (Vendramin et al. 2000) and mitochondrial (Sperisen 2001; Tollefsrud et al. 2008) DNA revealed two very distinct genetic lineages, suggesting long-term isolation over several ice ages. However, these lineages have not been related

to any taxonomical division, neither are they related to any clear morphological features. **Figure 2** show the two genetic lineages obtained from 28 different genetic variants detected in the mitochondrial DNA marker *nad1* (from Tollefsrud et al. 2008).

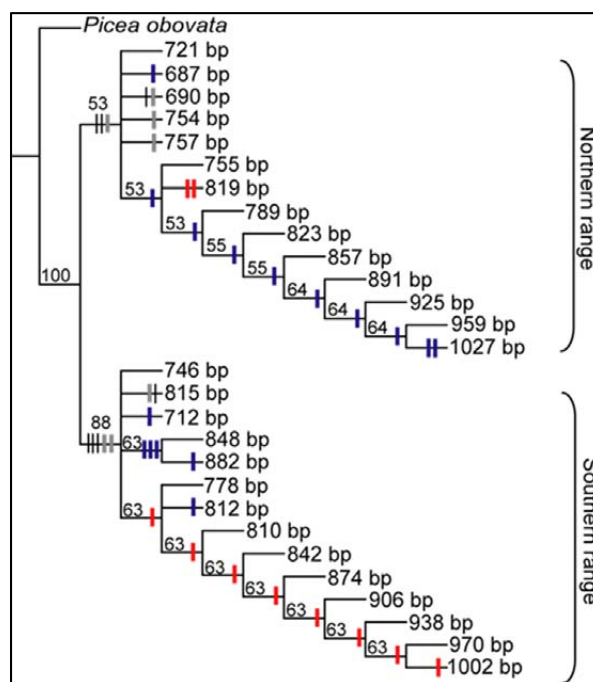


Figure 2. Phylogenetic tree inferred for 28 different genetic variants detected in the mitochondrial DNA marker *nad1*. Fourteen genetic variants are confined to the southern range and constitute a southern lineage, and 14 genetic variants are confined to the northern range and constitute the northern lineage. The numbers relate to size of the different genetic variants in base pairs. Numbers on the clades indicate the support for the clades (for more details see Figure 2 in Tollefsrud et al. 2008).

Meeting zones between the northern and the southern range is moreover demonstrated in a primeval forest in Poland (Dering et al. 2012), and in an ongoing detailed analysis on the genetic structures of Norway spruce. A postglacial meeting zone between the two ranges is depicted in the Baltics (<http://climate.nordgen.org/>, abstract by Tollefsrud et al. 2014). A meeting zone between the two ranges reaching from the Carpathians to the Baltics has also been proposed based on chloroplast markers (Vendramin et al. 2000).

Paleobotanical data combined with these genetic data indicates that the southern lineage survived in several isolated refugia, including the Carpathian Mountains, the Bohemian Massif, and the eastern Alps (Tollefsrud et al. 2008). In the north, both paleobotanical and genetic data indicate that Norway spruce expanded from a large refugium on the East European Plain, from where it colonized Fennoscandia following the retreat of the Scandinavian Ice Sheet (Giesecke & Bennett 2004; Latałowa & van der Knaap 2006; Tollefsrud et al. 2008; Valiranta et al. 2011).

Postglacial colonization followed two main migration routes from the Russian plain (**Figure 3**). One north-western route from Russia to Finland, following the mainland north of the Gulf of Bothnia and further to Norway and Sweden, and one south-western route over the Baltic states, crossing directly over the Baltic Sea to southern Scandinavia. The colonization of southern Scandinavia thus included long distance dispersal of seeds over large distances (Tollefsrud et al. 2008). A genetic connectivity between southern Scandinavia and the Baltics is also suggested by studies of nuclear microsatellites (Tollefsrud et al. 2009). There was probably also dispersal

events across the Baltic Sea, from southern Finland to mid-Scandinavia (Giesecke & Bennet 2004).

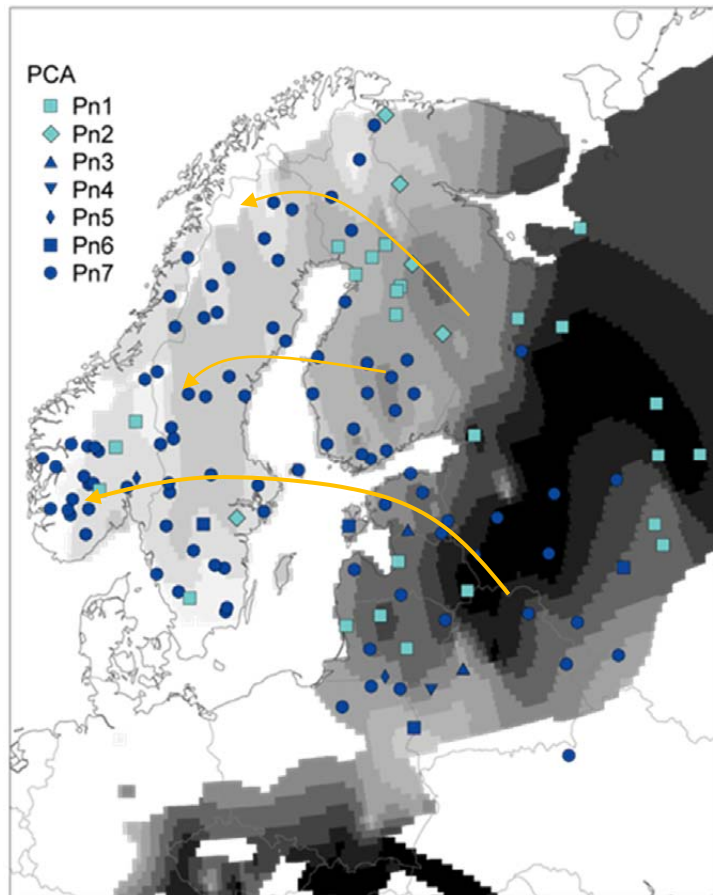


Figure 3. Combined map of genetic groups in the northern range and fossil pollen for the inference of Holocene expansion of *Picea abies*. Interpolated age as in Figure 1. The genetic groups are based on variation in the mitochondrial nad1 marker analysed with principal coordinate analysis combined with clustering. Arrows indicate migration routes (more details in Tollefsrud et al. 2008).

Based on modern and ancient DNA (Parducci et al. 2012) it has been suggested that Norway spruce also persisted locally in periglacial environments of north-western Scandinavia. This hypothesis is supported by large amount of old macrofossils in Scandinavia (Kullman 2008). Parducci et al. 2012 identified a genetic variant of the mitochondrial marker *mh05* endemic to Scandinavia (**Figure 4**), also found in ancient DNA in Trøndelag dating 10.300 and 6.500 years before present, strongly suggesting that this variant was already present in the region during the early Holocene. The hypothesis of glacial survival of both Norway spruce and Scots pine is strengthened by the findings of spruce and pine chloroplast DNA in lake sediments adjacent to the ice-free Andøya refugium at the Atlantic coast of north-western Norway as early as 22 000 and 17 700 years ago, respectively (Parducci et al. 2012).

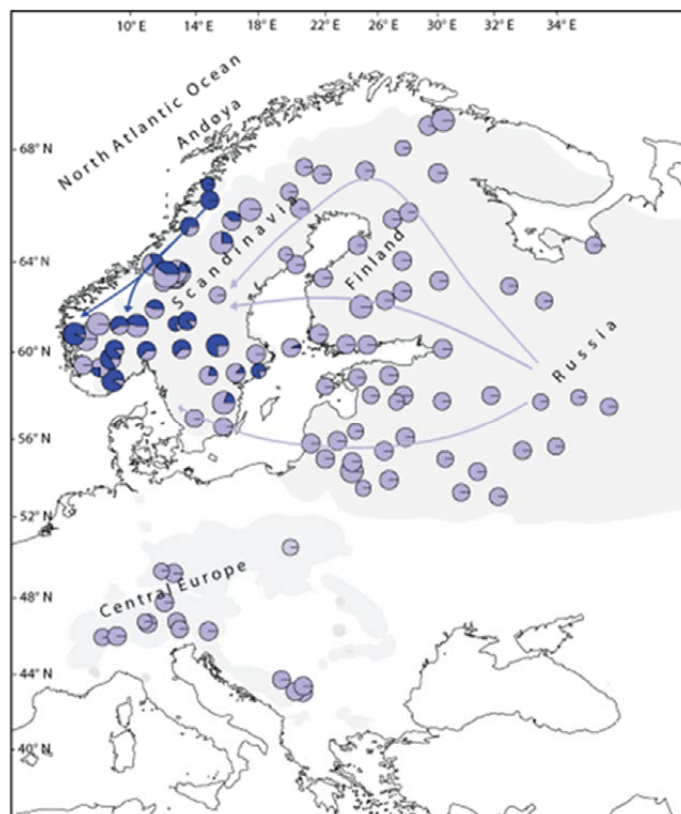


Figure 4. Geographical distribution of the two mitochondrial variants revealed in the mh05 marker in *Picea abies* populations. Arrows suggest putative migration routes. Map reconstructed after Parducci et al. (2012).

The presence of different genetic groups within the northern range related to historical events is supported by both latitudinal and longitudinal substructures shown at nuclear microsatellites. The power of the different genetic groups is, however, weak and difficult to interpret (Tollefsrud et al. 2009). Notably only 2.9 % of the variation is explained by among population genetic variation, suggesting that very high levels of gene flow among populations makes it difficult to reveal strong population structures. For instance, substructures in central Scandinavia may be explained both by glacial survival and by founder events and drift. High diversity in southern Scandinavia may be explained by both meeting zones between different refugia and pollen mediated gene flow from the southern range. Weak longitudinal patterns in the northern range were also revealed by Collignon et al. (2002) using another set of nuclear markers. A more detailed study is now undertaken to investigate the demographic history of Norway spruce (Martin Lascoux and Yoshiaki Tsuda, pers. com., see also <http://climate.nordgen.org/>, abstract by Tollefsrud et al. 2014).

The genetic structures in the Norway spruce mitochondrial genome are mainly shaped by historical factors like glacial survival and processes during postglacial colonization. Nuclear genetic structures, on the other hand, capture both the historical and the present processes, and show extensive gene flow over large distances. Most importantly, since Norway spruce populations are strongly interconnected with gene flow over large distances, there are no sharp population boundaries although we detect some latitudinal and longitudinal substructures over northern Europe. These substructures are largely correlated with adaptive phenotypic traits, and thus taken into account when breeding zones and regions of provenance are defined.

4 The use of Norway spruce in afforestation in Norway

4.1 General characteristics of seed sale in Norway 1952-2013

The Norwegian state has been strongly involved in forest seed supply from the 1930s, but harvesting and sale of forest seeds have been delegated to the Norwegian Forest Seed Centre (NFSC) from its establishment in 1946. The overall sale of seeds from NFSC to Norwegian nurseries has varied extensively from 1952 onwards. From the initial level of about 3000 kg/year the sale increased to about 12,000 kg/year in the early 1960s, after which it decreased steadily to the low present day level (**Figure 5**).

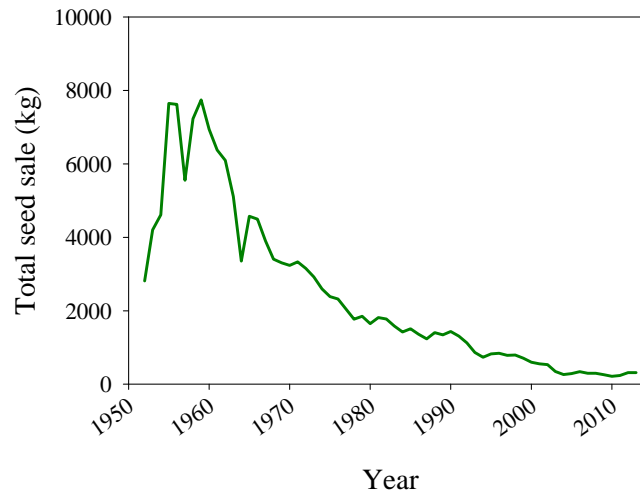


Figure 5. Sale of Norway spruce seed in Norway 1952-2013. Data from NFSC.

The high seed sales between 1950 and 1970 relate to the strong deficit of timber products following the Second World War, and a governmental emphasis on re-establishing forests to supply the markets. Between 1950 and 2010 the overall standing volume in Norwegian forests increased from about 370 mill m³ to 860 mill m³ (Granhus et al. 2012).

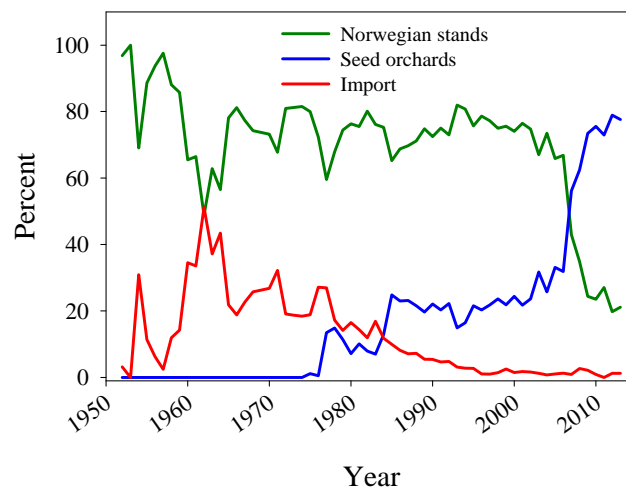


Figure 6. Proportion of seed from Norwegian stands, Norwegian seed orchards and import 1952-2013. Data from NFSC.

Figure 6 shows that the peak of sale between about 1950 and 1970 was partly due to extensive import of seed, due to the domestic deficit. However, both the proportion and absolute amount of imported seed decreased consistently from the 1960s onwards.

From the late 1970s seed orchard seed was released on the market, and after a lag phase the sale increased extensively and constitutes presently about 75% of the sale. This high proportion partly refers to a rather modest overall seed sale compared to 1950-1970. The proportion of imported seed has been marginal after the 1990s.

The accumulated seed sale after 1952 shows that stand seeds of Norway spruce dominates (**Figure 7**) and constitutes about 70%, whereas the proportion of imported seed and seed orchards seeds constitute about 18 and 12%, respectively.

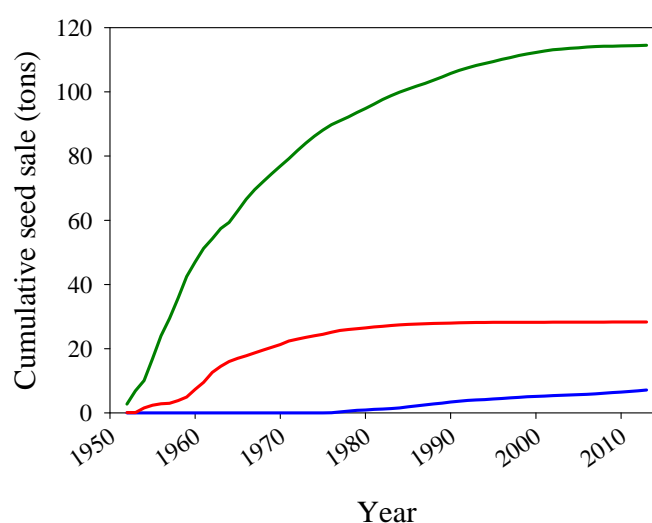


Figure 7. Cumulative sale of Norway spruce seed to the Norwegian market from Norwegian stands (green), import (red) and Norwegian seed orchards (blue).

The relative proportion of these seed sources in the forest changes continuously depending on where and when the different sources have been planted, and the actual logging in the different regions.

4.2 The use of Norwegian provenances from 1961-1995

To keep track of the different provenances the whole country is divided into seed harvesting zones (**Figure 8**), which are further subdivided into altitudinal zones (not shown). This exemplifies the practical application of the term provenance, and the fine geographical scale at which individual provenances can be defined. For the purpose of this report, we have combined seed harvesting zones and show seed sale from the main regions. Seed from eastern and mid Norway totally dominated the market from 1961-95 (**Figure 8**), simply because these are the main Norway spruce areas with the regular seed production. Smaller quantities were sold from southernmost Norway and in particular from northern Norway and coastal areas in western Norway. These figures correspond well with the sale before 1961-95.

The seed harvesting zones do not necessarily reflect where the provenances are actually used since local material may have poorer survival and development than provenances from e.g. adjacent seed harvesting zones, and since local seed production may be insufficient. For example, in western Norway where the natural distribution of Norway spruce is modest, provenances from eastern Norway and Germany have been, and still are widely used (A. Steffenrem

pers. com., see e.g. <http://www.skogfroverket.no/> for recommendation on the use of forest reproductive materials for the different regions). Thus, deployment of the different provenances is based on how well the material is climatically adapted to the site, shown by e.g. phenology, survival, vitality and growth in field trials, rather than origin of the provenances. **Table 1** gives a coarse summary of relevant provenances for different regions in Norway, including some foreign provenances. For climatic reasons, the number of provenances relevant for western Norway far exceeds the other regions.

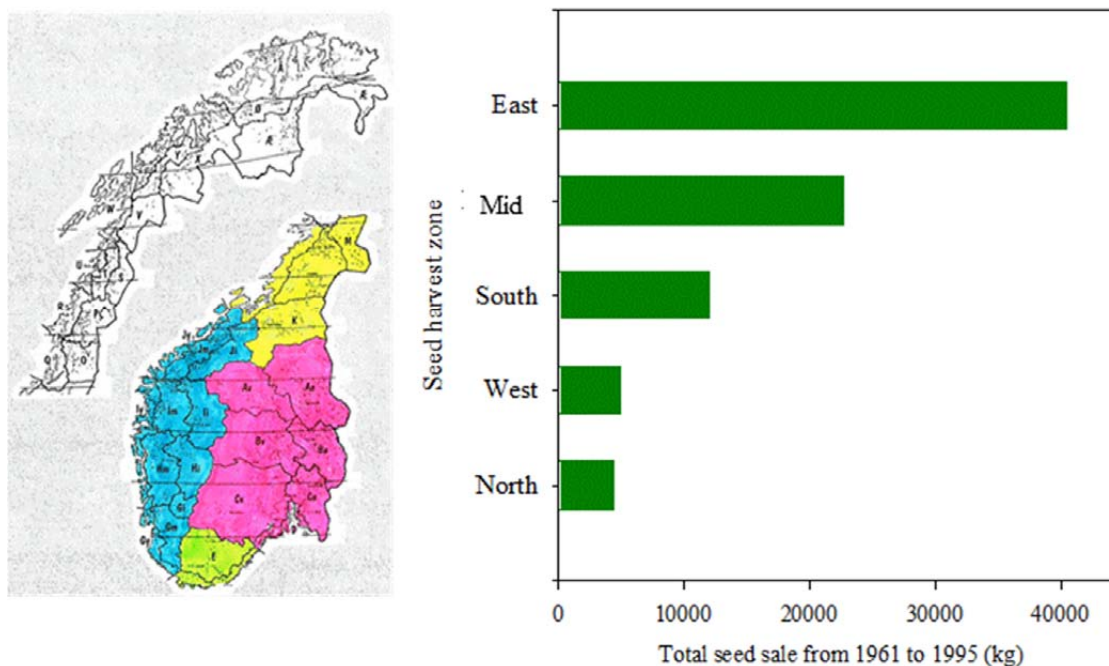


Figure 8. Sale of Norway spruce seeds from 1961 to 1995 from different regions. Data from NFSC.

4.3 Domestic sale of non-Norwegian provenances

The temporal trend and overall sale of imported seed are reflected in **Figures 6** and **7**, respectively. Imported seed constituted a substantial proportion between the 1950s and 1980s, but has been very modest the last 20 years.

German and Austrian provenances have been by far the most imported sources on the Norwegian market (**Figure 9**). In addition, provenances from the Czech Republic/Slovenia and Sweden have contributed, whereas seeds from Poland, Belarus, Denmark, Finland, Romania and Lithuania have been marginal. **Figure 9** also shows that the proportion of import from the southern genetic lineage dominates.

Table 1. Relevant Norwegian and non-Norwegian provenances recommended for use in different regions of Norway as based on field tests (Skrøppa et al. 2014). NFSC provides provenance recommendations at the municipality level (<http://asp.gitek.no/skogfroverket/pmws.dll/SFVFroLatSok>).

	Region		
	Eastern Norway	Western Norway	Mid- and northern Norway
Relevant provenances	Local/regional Provenances		
	Southern Sweden below 500 m asl	Eastern Norway	Eastern Norway (northern part)
	Baltic countries, Belarus	Baltic countries, Belarus	Rana (for use in Nordland and Troms)
		Harz (Germany), Denmark (German origin), Romania, Czech Republic	

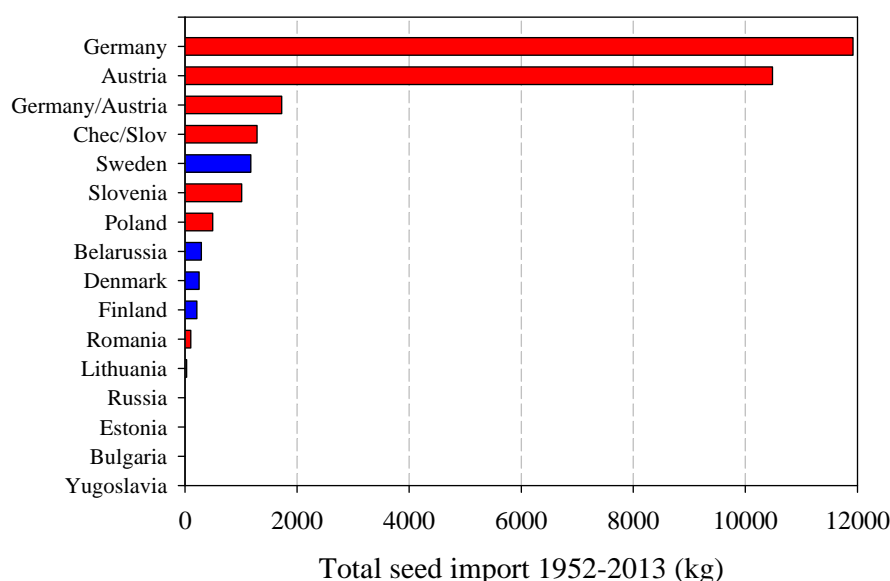


Figure 9. Total import of Norway spruce seed 1952-2013. Columns in red denote the southern genetic lineage, whereas columns in blue denote the northern genetic lineage to which Scandinavian Norway spruce belongs. Poland represent a meeting zone between the northern and the southern genetic lineages, and it is thus difficult to know which genetic lineage the material from Poland belongs to.

5 Ecological traits of Norway spruce provenances

In this context, ecological traits are confined to adaptive traits that are known to differ between provenances such as phenology, frost hardiness and growth potential. We first review differentiation in such traits between provenances, and in a later chapter undertake a risk assessment as to whether traits differentiation may affect biodiversity.

5.1 Budburst and growth cessation

Timing of phenological events, such as budburst in spring and growth cessation in autumn, is a critical component of climatic adaptation. Premature budburst and delayed growth cessation may both cause frost damages, or even dieback. On the other hand, very late budburst and early growth cessation and frost hardening will shorten the growing season and reduce the competitive ability of the trees. Thus, proper timing of the phenological events is a trade-off between survival and growth of the plants. Budburst occurs after accumulation of a specific heat sum, whereas cessation of growth is primarily controlled by day length.

The climate varies along geographical gradients, and the phenology of Norway spruce and other forest trees are significantly correlated with geographic and climatic variables. Generally onset and cessation of growth occur increasingly early with increasing latitude and altitude of origin (Jansson et al. 2013), i.e. early budburst is associated with cold climates.

Based on a number of reciprocal provenance trials it has been possible to compare growth rhythm of distant and adjacent provenances across Europe (**Table 2**). For example, budburst and growth cessation occur later in provenances from Poland than Norway if planted at the same site. But also within Norway the same latitudinal trend prevails, initiation of growth is earlier in southern Norway than in provenances from Trøndelag.

Table 2. The general pattern of regional variation in budburst and growth cessation in Norway spruce (Jansson et al. 2013). Extremely early cessation of growth occurs at high latitudes and altitudes. Although western European provenances terminate growth very late, growth cessation occurs increasingly early with increasing altitude, e.g. towards the Alps.

Budburst		Growth cessation		
Early	Late	Early	Intermediate	Late
Northern Scandinavia	Central Russia	Northern Scandinavia	Belarus	
Finland	North-eastern Poland	Finland	Southern and northern Poland	
High altitudes of central European Alps	Eastern Baltic area		East Carpathian Mountains	
Western Europe			High altitudes in western Europe	Western Europe

Due to the clinal variation in timing of budburst and growth cessation, transfer of provenances along environmental gradients affects adaptation. From a forestry point of view, this can be desirable, for instance by using east European provenances with late budburst that will be less prone to spring frost damages than local Norwegian provenances. Growth of Norway spruce is

better correlated to late growth cessation than to early initiation of growth in spring (Hannerz et al. 1999). Thus, by using southern provenances growth can be greatly enhanced compared to local provenances (Dietrichson 1977; Fottland & Skrøppa 1989; Skrøppa et al. 2005). South-eastern provenances from the East Carpathians and the Bihor Mountains in Romania appear to have the best growth potential (Jansson et al. 2013), but it is not known whether this applies to Norwegian conditions.

5.2 Frost hardiness

Dormancy develops gradually after growth cessation in early autumn, which implies that development of dormancy and frost hardiness critically depends on timing of growth cessation as a primary phenological event. Thus, frost hardiness shows a distinct seasonal pattern; susceptibility to freezing temperatures is high during the growing season whereas tolerance to frost is high during the dormant stage in winter. Development of frost hardiness takes place in three steps, 1) onset of dormancy, 2) first stage of hardening at about 0°C, 3) second stage of hardening during a gradual lowering of the temperature below 0°C (Levitt 1980). If growth cessation takes place too late, development of frost hardiness is delayed correspondingly and trees may suffer from early autumn frost (Jansson et al. 2013). The actual frost hardiness after onset of dormancy is an inverse function of temperature. Frost hardiness increases when temperature decreases, and is quickly lost in response to mild temperatures. Thus, rapid changes from mild conditions to extensive frost can cause frost damages even in midwinter when the trees are still dormant (Levitt 1980).

It should be emphasised that Norway spruce has extensive genetic variation within provenances. Actually, the variation in frost hardiness in progeny from 10 mother trees from the same stand corresponds to the difference between provenances separated by 3-4 latitude degrees (Skrøppa 1991; Johnsen & Østreg 1994).

As shown in **Figure 6** the proportion of imported seed was substantial between 1950 and 1980, and provenances from Germany and Austria dominated (**Figure 9**). These provenances were used both in eastern and western Norway. In eastern Norway (e.g. Vestfold and Hedmark) western continental provenances (from Germany and Austria) suffered from climatic damages, probably associated with delayed growth cessation and autumn frost (Skrøppa 1986; Magnesen 1992). Provenances from western Russia and northern Poland had less damages, whereas provenances from Finland, central Sweden and central Norway were least damaged (Skrøppa 1986). In western Norway, however, western continental provenances have grown and performed well, without climatically induced setbacks similar to eastern Norway (Skrøppa et al. 2014). This is probably due to milder autumns and less severe winters as compared to eastern Norway.

As shown above, phenological traits such as budburst, growth cessation and frost hardiness are strong determinants of adaptedness of trees. Given that the timing of these traits is well synchronized with the surrounding climate, the potential of climatic damages and mortality are greatly reduced. This conclusion holds true irrespective of the provenance being local or transferred. Moreover, Norway spruce displays an extensive phenotypic plasticity in phenological traits, which greatly contributes to adaptation and survival when climatic conditions are harsh.

5.3 Production and spread of seeds

The ability to produce seeds and spread is strongly related to temperature. Norway spruce usually starts producing seeds 20-40 years old. Two consecutive years with high summer temperatures are needed for good seed production, the first year to initiate development of flowering buds (correlated to July temperatures), the second year for flowering and seed maturation (Børset 1985). For this reason, good seed production occurs rarely, only every 6-8 years (<http://www.skogfroverket.no/Web/Informasjon/Artikler/Gode%20froar.htm>). It has not been possible to trace relevant literature on provenance differences in seed production and spread.

6 Climate change mitigation by provenance transfer

In Norway climate change has been predicted to imply increased precipitation, longer growing season, milder winters and warmer summers (Iversen et al. 2005). However, climate change is expected to vary between regions, and for south-eastern Norway the change by 2100 may include a rise in temperature of 2-3°C and a decrease in precipitation of 5-15 % (Iversen et al. 2005). In this region dieback symptoms observed in Norway spruce have already been related to warm and dry summers (Solberg 2004).

After dormancy release in midwinter budburst primarily takes place due to accumulation of heat in spring, which implies that onset of growth can be advanced with increasing temperatures (Schleip et al. 2008). Timing of growth cessation in Norway spruce, however, is controlled by daylength (Molmann et al. 2006), which is a very predictable and stable environmental cue. Although frost damages in Norway spruce in the 1980s were primarily associated with southern provenances with late bud set (Skrøppa 1986), the advancement of budburst over the last 50 years following increased spring temperatures (Schleip et al. 2008) indicate an increased risk of frost damages at the start of the growing season.

Recent climate scenarios predict that vegetation zones of southern Scandinavia will move northwards 272-645 km by 2100 (Hickler et al. 2012), and it has been suggested to track the changes by use of transferred forest reproductive material (Koskela et al. 2007). Presently deliberate use of forest reproductive material, including use of tested and characterised seed orchard material and provenances, represents a major component of adaptation to climate change in Norwegian forestry. Bred material combine survival and robustness with specific quality measures in a wide range of environmental conditions, while maintaining genetic variation (Edwardsen et al. 2010).

Norwegian seed orchards are presently based exclusively on Norwegian material, but this may change in the future. Increased use of seed orchard material and provenances that combine late budburst with intermediate timing of growth cessation may in the future be necessary. For example, provenances from Belarus (belonging to the north European genetic lineage, see **Figure 8**) have performed well both with respect to production and climatic adaptation in a wide range of environments in eastern and western Norway (T. Skrøppa, pers. com.). In western Norway Danish seed orchard material, originally based on German provenances, is also of interest, but remain to be tested. Considering the predicted climate change, forestry will benefit from having access to a diversity of provenances and seed orchard materials to avoid climate change related damages and to mitigate climate change by planting the best possible adapted forest reproductive material (Lindner et al. 2008).

7 Norway spruce afforestation on non-spruce habitats and its general impact on indigenous biodiversity

Afforestation with Norway spruce in non-spruce habitats affects the indigenous biodiversity through changes in ecosystem processes (Aarrestad et al. 2013). Introduction of spruce into deciduous forests changes the structure, growth form and biomass production of the forest (Hall-dorsson et al. 2007). A denser forest canopy reduces the solar radiation beneath the canopy and changes the microclimate, water balance and nutrient circulation within the forest. Along with a modified litter layer of different chemical composition and slower degradation rate, this contributes to a more acidic and nutrient-poor soil and a modified soil fauna (Mikola 1985; Frank 1994; Fjellberg et al. 2007; Spiecker 2003; Smolander et al. 2005).

Changes in soil properties into less nutrient-rich soils and an altered microclimate lead to changes in plant species composition on the forest floor and, in general, to a lower plant species diversity within the forest (Stabbetorp & Nygaard 2005; Barbier et al. 2008). Dense plantations nearly lead to extinction of the ground vegetation within the forests. In particular, the fungal flora, and thus the interaction between mycorrhizal fungi and higher plants, is affected (Brandrud & Bendiksen 2001, 2002; Gjerde et al. 2012; Bendiksen 2013). Indigenous epiphytes, which are dependent on deciduous bark, may also be negatively affected (Hilmo et al. 2009; Wannebo-Nilsen et al. 2010).

In open farmlands, spruce plantations will probably have the same effects on the biodiversity as described for tree species change in forests. Especially light-demanding plants will decline, and the risk of loss of vascular plant diversity may here even be higher than in the forest, since open areas that are considered for new afforestation, such as less managed meadows in culture landscapes (Haugland et al. 2013), still houses a high number of vascular plants and fungi (Aarrestad et al. 2013).

At the landscape level, planting of spruce will split up the natural variation in habitats, which may have effects on both vegetation and wildlife habitats by structural changes and modified interactions in the food chain at different trophic levels (Yoccoz et al. 2001; 2005). Introducing spruce in areas in Norway where spruce does not have its natural distribution, may increase the biodiversity at the landscape scale by changing homogeneous landscapes consisting of birch and pine forests to a more diverse landscape (Gjerde 1993; Gjerde & Sætersdal 1997; Hausner et al. 2002, 2003). However, there is also a risk that indigenous species diversity may be reduced (Pedersen et al. 2010 a,b; Gjerde et al. 2005). Gjerde et al. (2005) found that a high relatively amount of spruce plantations within the landscape negatively affected the biodiversity of birds. Thus, certain threshold values of spruce plantations may affect the species diversity on the landscape level.

The spread of Norway spruce from monoculture plantations into the surrounding landscape by seed dispersal may also be a threat to the indigenous biodiversity. The high shade tolerance of Norway spruce makes it very competitive to nearly all deciduous trees and the ground flora, and thus it has the possibility to change the dynamics of the habitats in the long run (Børset 1985; Tømmerås et al. 1996). Insect fauna that has Norway spruce as their main host and which feed on needles, flowers, cones and shoots, as well as species boring in the phloem or xylem of dead and dying wood, may spread to new areas (Nilssen 1976, 2010; Johansson et al. 1994). There are however few studies on the effects of dispersal of Norway spruce on indigenous biodiversity. Some biodiversity studies on *Picea sitchensis* reports negative effects on local biodiversity, effects that may also apply for the dispersal of *Picea abies* (Coote et al. 2008; Saure 2012; Sandvik 2012a; Saure et al. 2013).

In general, high diversity habitats are more affected than diversity poor habitats (Aarrestad et al. 2013). PEFC (Programme for the Endorsement of Forest Certification) is the World's largest

system for certification of sustainable forest management and products from sustainably managed forests (http://www.pefcnorge.org/side.cfm?ID_kanal=11). The Norwegian PEFC Forest Standard states that wooded ombrotrophic bogs on the west coast of Norway, rich broadleaved deciduous forests (except blueberry oak forest at low and medium site quality), swamp forests, calcareous forests, open heather and buffer zones along watercourses should not be exposed to tree species change, due to negative impact on indigenous biodiversity. A common report from the Norwegian Environment Agency, the Norwegian Agricultural Authority and the Norwegian Forest and Landscape Institute (Haugland et al. 2013), recommend that special consideration should be taken for planting Norwegian spruce in areas important for biodiversity. This includes the environmental management regimes *selected habitats* ("utvalgte naturtyper"), *red-listed habitats* (Lindgaard & Henriksen 2011), *culture landscape with high to medium priority*, *habitats with high value for biodiversity* and areas with species and habitats with red-listed species and those that are red-listed due to data deficiency (Kålås et al. 2010). Thus, there is a consensus that afforestation in certain areas is strongly negative for the indigenous biodiversity.

8 Different provenances - different ecological impacts? A risk assessment

8.1 Effects of different traits

As shown above, various adaptive traits show great variability across Europe. The aim of any forest establishment is to take advantage of well growing and well adapted forest reproductive material. However, will non-native provenances in a given environment differ in ecological effects from local provenances? This question has been addressed by means of search in international literature bases as well as personal enquiries for “grey” literature (reports etc.). We were not able to find any relevant scientific literature about the topic. Neither were we successful in finding grey literature, even though we contacted colleagues all over Europe in the intergovernmental EUFORGEN community (<http://www.euforgen.org/>) where presently 25 European countries are participating.

It can be argued that well growing and adaptable provenances may be more successful with respect to spread and colonisation, and as such, they might have greater ecological impact than less adaptable provenances. If introducing maladapted provenances, the overall viability and health of trees may be modest, leading to lower dispersal over the lifetime of trees than in the case of well-adapted provenances. We also know that non-local provenances in certain cases grow better and have less climatic damages than local provenances (Dietrichson 1977; Fottland & Skrøppa 1989; Skrøppa et al. 2005). However, provenance differences in ecological impact are difficult to quantify without well-designed long-term (decades) and high-resolution experiments.

The variation in adaptive (phenological) traits is not only about origin and provenances. It has been clearly shown that Norway spruce may adapt epigenetically to climate; trees produce offspring with notably later growth onset and later growth cessation under warm than cold summer temperatures (Kvaalen & Johnsen 2008, Skrøppa et al. 2010). This implies that offspring even from first-generation Norway spruce (e.g. from Germany) will have a growth rhythm more similar to local Norway spruce provenances. Thus, the effect of potential maladaptive phenology traits is reduced already in the second generation.

As a result of a warmer climate, the possibility exists that some introduced provenances may spread more than local provenances as a consequence of better growth and vitality. On the other hand, southern provenances of interest usually have later growth cessation than local provenances (**Table 2**). Therefore the period during which flowering buds can develop is delayed and may coincide with lower summer temperatures than what is the case in local provenances - leading to less flowering and seed production the following year. We have, however, no data or literature to support either scenario, suggesting that we should refrain from concluding on this matter.

8.2 Effects on genetic diversity in native Norway spruce forests

Norway spruce populations from the southern range and the northern range are genetically distinct due to separation over several ice ages (**Figure 2**). Planting of provenances from the southern range in Norway may therefore affect the molecular genetic composition of the native Norway spruce and per definition affect the biodiversity. Conversely, adding genetically differentiated spruce material may increase the genetic diversity and thus per definition the biodiversity of tree populations. In simulations, it has been shown that introgression mainly takes place from the local to the invasive species (Currat et al. 2008). This asymmetry is expected to lead to relatively limited “pollution” of the gene pool of the native species. Genes from the invading species will moreover introgress the local species only if they are under very strong positive selection (Currat et al. 2008).

Concerning adaptive traits, some studies show that planted trees originating from southern latitudes are more prone to frost damages on exposed sites in southern Scandinavia than trees of local provenances (Hannerz & Westin 2005), causing also a reduction in the timber quality of the spruce plantations (Skrøppa et al. 1993). This however, critically depends on the phenology of the material and how it matches the climate where it is used. As noted above, provenances from Belarus perform very well in a wide range of habitats in Scandinavia (see **Chapter 4**), and provenances from Germany that are exposed to climatic damages in eastern Norway grow well in western Norway. In addition, the epigenetic adjustment of the growth rhythm implies that introduced material becomes more similar to local material with respect to phenology after one generation (see **Chapter 7.1**). The effect of gene flow from one provenance to another may thus differ across the country depending on their frequency, how well they are adapted and if they are under positive selection.

In a project investigating the causes of spruce dieback, the origin of the trees (determined to northern- or central European origin) were investigated using molecular markers. In this project it was found that central European origin slightly increased the probability to have spruce dieback. There were, however, no clear correlation between spruce dieback and origin, rather was spruce dieback linked to how efficient the trees were in saving water during dry periods and soil type (Solberg et al. 2013).

Trees in general and conifers in particular, have high genetic diversity due to remarkable high gene flow and high outcrossing rates. Pollen flow over five to ten kilometers is not uncommon for trees (Petit & Hampe 2006). In Norway spruce, spruce from the southern range and the northern range met already during postglacial colonization about 6000 year ago and their ranges are now in contact (**Figure 1**). Populations are effectively connected by pollen flow over large distances (Vendramin et al. 2000; Tollefsrud et al. 2009), and the potential for long-distance dispersal of seeds is high (Piotti et al. 2009). Rare long-distance dispersal events of seeds in Norway spruce may range several hundred kilometers, such as post-glacial colonization of Scandinavia across the Baltic Sea (Giesecke & Bennet 2004; Tollefsrud et al. 2008). Still, extensive gene flow does not seem to compromise local adaptation in trees, as they are able to combine large genetic differentiation in adaptive traits with little differentiation at molecular markers (McKay & Latta 2002; Petit & Hampe 2006).

8.3 Effect of genetic diversity on associated biodiversity

Plant genes have been shown to affect associated species, and different communities of organisms (e.g. insects and microbes) have been shown to be associated with genetically distinct plants or animals forming community phenotypes (Whitham et al. 2006, 2012). Genotypic variation within foundation species can be particularly influential for dependent species because they create locally stable conditions for other species (Whitham et al. 2006).

Genotypes of individual trees may e.g. be associated with different arrays of phytochemical defenses, which in turn have different arthropod community phenotypes (Whitham et al. 2006). For example, intra specific variation in *Populus* species was found to be associated with a) different community phenotypes of terrestrial arthropods living in tree canopies, b) endophytic fungi inhabiting tree bark and c) aquatic macro-invertebrates. *Populus angustifolia*, *P. fremontii* and their hybrids were moreover associated with different arthropod communities (results on *Populus* reviewed in Whitham et al. 2006).

In the boreal forest, the diversity of ectomycorrhizal (ECM) species is much greater than that of their host trees and in a study of Norway spruce it was shown that the ECM community structure varied among clones. In a field study on eight Norway spruce clones, the diversity of ECM was higher in taller trees compared to smaller trees. As the size of their root system did not account for the variation observed, it was suggested that it was the genetic pedigree of the clones that was responsible for different ECM communities (Korkama et al. 2006). Endophytic fungi are especially important litter decomposers. In a study of clonal trial of Norway spruce, it was found

that different spruce clones did not differ in needle litter decomposition. The community of endophytic fungal decomposers varied however, among the slow- and fast-growing spruce clones *in vitro* (Korkama-Rajala et al. 2008). More examples are given in Whitham et al. (2012). These are all examples of different genotypes being associated with different community phenotypes (community phenotypes relate to the effects of genes at levels higher than the population; Whitham et al. 2006).

A growing body of evidence from community genetic studies suggest that ecosystem functions supported by plant species richness can also be provided by genetic diversity within plant species. In oak e.g., it was found that damage due to ectophagous herbivores increased with the genetic diversity in oak sapling populations because of higher levels of damage in mixtures than in monocultures for all families, rather than due to the presence of more susceptible oak genotypes in mixtures. Genetic diversity increased thus insect herbivory on oak saplings (Castagneyrol et al. 2012).

Individual plant genotype variation can thus play a major role in structuring local communities in associated species of e.g. invertebrate, fungi, arthropods and pathogens. How these results relate to different spruce provenances has, however to our knowledge not been investigated. Although most of the genetic variation within Norway spruce is found within populations, the use of different provenances will lead to an increase in genetic variability in general, and probably support an overall increase in associated biodiversity.

8.4 Effects on indigenous species and habitats

As described in **Chapter 7**, afforestation with Norway spruce may substantially affect biodiversity at the planting site. When it comes to differential effects on biodiversity of using contrasting provenances, nothing is known. Through searches in national and international databases as well as personal enquiries at different forest and environmental research institutes in Europe, we have not been able to detect *any studies* related to effects of *different provenances* of Norway spruce on indigenous biodiversity.

There have, however, been some studies on different provenances of *Picea alba*, *Quercus robur* and *Fagus sylvatica*. Provenance experiments with *Abies alba* in Vallumbrosa, North Italy, showed that the Calabrian fir, due to its vigorous growth, out-shaded the forest floor vegetation much more than the local fir (Bo Larson pers. comm.). Several Danish experiments comparing mid-European provenances with Calabrian fir, showed the same results (Larsen 1981). The Slovenian oak was not attacked by tortrix moths (*Tortrix viridana*), when introduced to North Germany, due to later flowering of the oak. Obviously, the local moths were closely synchronised with the local oak's phenology, and thus they had to adapt the Slovenian oak's phenology (Wachter 2011). Thus, use of different provenances of trees can give different impacts on biodiversity.

However, the possible different ecological impact of introduced versus local provenances is beyond any doubt of minor importance compared to the effects of afforestation itself (B. Larsen, pers. com.). What really matters is the density of the planted trees, the management of the plantations, the relatively acid spruce litter and in what kind of habitat the afforestation occurs. Dense spruce monocultures with minor thinning reduces the ground vegetation cover within the forests, while more open plantation, especially spruce-deciduous polycultures, maintain some of the original diversity (Frank et al. 1998; Wannebo-Nilsen et al. 2010; Felton et al. 2011; Gamfeldt et al. 2013).

8.5 Criteria for ecological risk assessment - the Norwegian Species information Center - used on Norway spruce provenances

The Norwegian Biodiversity Information Centre (NBIC) has a national responsibility for organizing the work on assessment of ecological impacts associated with species that are non-native to Norway (alien species), and to provide an overview of alien species found in Norway. In connection to the new blacklist in 2012 (Gederaas et al. 2012), NBIC developed a set of criteria based on quantitative measures to estimate the probability of establishment and spread (*the invasion potential axis*) and the effect on biodiversity (*the ecological effect-axis*). Thus, the ecological impact of the introduced species is evaluated using a combination of the two axes as shown in **Figure 10**, and the framework contains five impact categories:

1. No known impact (NK)
2. Low impact (LO)
3. Potential high impact (PH)
4. High impact (HI)
5. Severe impact (SE)

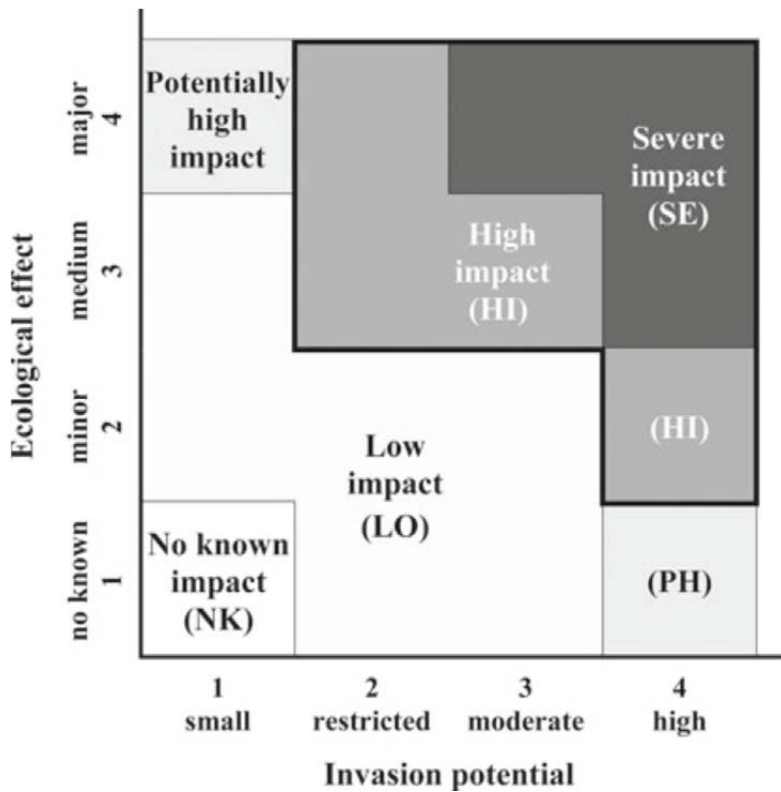


Figure 10. Ecological impact of introduced species as a combination of invasion ability (horizontal axis) and ecological effect of establishment of the species (vertical axis). From Sandvik (2012b).

The *invasion potential* is assessed from data on:

- A Expected population lifetime
- B Mean expansion rate
- B1 Expansion velocity
- B2 Increase in area of occupancy
- C Area of habitat type occupied

The *ecological effect* is assessed from data on:

- D Effects on native threatened or keystone species
- E Effects on other native species
- F Effects on threatened or rare habitat types
- G Effects on other habitat types
- H Transmission of genes (genetic introgression)
- I Transmission of parasites or pathogens

The method is developed for introduced species, and is mainly used for species that disperse naturally or unintentionally by humans. For detailed methods, see Sandvik (2012b). The ecological impact of introduced provenances of a native species (e.g. Norway spruce) may, in principle, be evaluated in the same way as for introduced species. However, the introduced provenances are conspecific with a native element in the ecosystem, and often their ecological function will be identical. Thus, in practice, risk assessment of introduced provenances of Norway spruce is not straightforward.

The ecological impact should be assessed in the spreading areas, and the offspring from introduced provenances will be morphologically inseparable from the native provenances. Thus, it will be much more complicated to obtain information on points A to C above (life expectancy, expansion rate, area occupied) on conspecific provenances than for introduced species. Certain provenances can be identified by means of molecular markers, which allow provision of data on relative invasion potentials (x-axis). This would give some indication, as a higher invasion potential of either provenance would imply higher impact, provided if the ecological effect (y-axis) is about the same. However, spreading areas consisting of offspring from both native and introduced provenances, as well as their hybrids, are likely to complicate assessment of ecological effect (y-axis) of the introduced provenance.

When different provenances are not possible to separate by means of genetic markers (e.g. different Scandinavian provenances) it may be possible to use spatially separated provenances, and study the invasion potential and ecological effect in the surrounding areas. In such cases, when effects of different provenances are studied in different environments, the scientific power is, however, greatly reduced. Accordingly, ranking ecological impact of different provenances may be very resource demanding, and/or scientifically inadequate. Transmission of parasites or pathogens (point I above) should however be investigated, especially for imported provenances.

Data concerning the invasion axes could be obtained from knowledge on where and to what extent different provenances are being used. This is registered today in the national register at the Norwegian Seed Centre. The historical records on where Norway spruce provenances from the southern range were planted in the 1950- and the 60ties, however, are scarce and unreliable. The expansion rate could probably be determined if careful investigations were performed using molecular markers, but probably only for provenances from the southern range since populations in the northern range are genetically very similar (see **Chapter 3**).

The invasive potential of an introduced provenance differs from that of introduced species in several aspects, and introduced and native Norway spruce provenances are interfertile. Thus, a

provenance will not only disperse as a distinct unit, but it may also increase the genetic variability of the native populations. However, such gene exchange is not regarded as an ecological effect (Transmission of genes, point H above) according to the evaluation scheme. Transmission of genes in this context refers to different species (Sandvik 2012b). As transmission of genes is not defined at the subspecies level, nor at the provenance level, the criterion on transmission of genes is not relevant for Norway spruce. In the European distribution of Norway spruce (*Picea abies*) no taxonomical sub-level has been singled out.

Thus, we see it very problematic to use the NBIC-criteria for risk assessment on foreign provenances of Norway spruce.

9 Summary and conclusion

Norway spruce (*Picea abies*) is a natural tree species in Norway, which migrated from a large refugium on the East European Plain, following the retreat of the Scandinavian Ice Sheet. However, there is also evidence for migration from periglacial environments in northwestern Scandinavia. The species is most related to Siberian spruce, which has a wide north Asian distribution. Some authors recognize them as two separate species. Others consider them, either as two closely related subspecies, *Picea abies* ssp. *abies* and ssp. *obovata* (Tutin et al. 1993), or two geographical races. Latest research suggest that they are two separated species with an introgression zone along both sides of the Ural Mountains (Martin Lascoux and Yoshiaki Tsuda, pers. com; Tollefsrud et al. 2014).

In Norway, the main natural distribution is in the eastern part of southern Norway, and in mid Norway from Sør-Trøndelag to Rana. In addition, there are numerous smaller occurrences in western Norway as well as a few populations in northern Norway, close to the Russian border.

The genetic structure of Norway spruce is mainly shaped by historical factors like glacial survival and processes during postglacial colonization. However, present processes with large amount of gene flow over large distances also contribute to the genetic variation. The modern range of Norway spruce in Europe is divided into a northern and a southern part. Since Norway spruce populations are strongly interconnected with gene flow over large distances there are no sharp population boundaries in Europe. Some latitudinal and longitudinal substructures are however evident over northern Europe. These substructures are largely correlated with adaptive phenotypic traits, and thus also taken into account when breeding zones and region of provenance are defined.

The term “provenance”, is defined by OECD as the area where the seeds are produced or a stand grows. The term thus not include the origin of the gene material. However, an OECD certificate/ or a similar certificate follow the plant material that is imported/exported, and here origin is given if it is known. It is thus possible to identify the origin of the forestry reproductive material in most cases. Foreign provenances from different parts of Europe have been used in afforestation in Norway for several decades. German and Austrian provenances have been by far the most imported sources. In addition, provenances from the Czech Republic/Slovenia and Sweden have been used, whereas contributions from Poland, Belarus, Denmark, Finland, Romania and Lithuania have been marginal.

Provenances may differ in ecological traits, such as phenology, frost hardiness, growth- and spread potential. Various adaptive traits show great variability across Europe. Budburst is earlier in proveniences from Northern Scandinavia, Finland, high altitudes of Central European Alps and Western Europe compared with provenances from Central Russia, North-eastern Poland and the Eastern Baltic area. Growth cessation is also earliest in Northern Scandinavia and Finland. Various provenances have been tested in Scandinavia in reciprocal field trials. The success of introduced provenances depends strongly on the climate of the planting site, and some provenances perform well in various regions of Norway (various East European provenances) whereas other provenances have a more limited application (Continental provenances). The ability to produce seeds is strongly related to temperature, but it has not been possible to trace any relevant literature on provenance differences in seed production and spread.

Afforestation with Norway spruce unquestionably affects the indigenous biodiversity through e.g. altered light conditions, water balance and nutrient cycling. Although it can be speculated that any better growing provenances will affect the indigenous biodiversity most, searches in national and international databases, as well as personal enquiries at different forest and environmental research institutes in Europe, have not uncovered any literature or studies in support of differential effects on biodiversity of different provenances of Norway spruce. However, it has been shown that intraspecific diversity in plants affect the composition of associated species (e.g. arthropods, microbes and fungi). Even if different provenances affects the biodiversity differently,

these effects are probably marginal compared to the effects of afforestation with Norway spruce itself, where the density of the planted trees, the management of the plantation and the altered chemical composition of the soil are major determinants of altered biodiversity. The literature review, however, has clearly shown that the basic knowledge on effects of different Norway spruce provenances on indigenous biodiversity is poor, and there is a probably need for further research on this topic.

Studies on ectomycorrhizal diversity e.g. would be very relevant for provenances differing in growth potential. One could argue, on the other hand, that it would be more important to investigate the differences in associated species following especially *imported* plant material compared to associated species in the Norwegian Norway spruce forest. Intensifying international trade of plant material has facilitated the introduction of species to new areas and export trade has been one of the recognized pathways for the spread of forest pathogens (Stenlid et al. 2011).

10 References

- Aarrestad, P.A., Bendiksen, E., Bjerke, J.W., Brandrud, T.E., Hofgaard, A., Rusch, G. & Stabbetorp, O.E. 2013. Effects of tree species shift, afforestation and nitrogen fertilization of forests on biodiversity. Status knowledge as basis for evaluation of actions in connection with climate policy. – NINA Report 959. 69 pp.
- Barbier, S., Gosselin, F., & Balandier, P. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved. A critical review for temperate and boreal forests. - *Forest Ecology and Management* 254: 1–15.
- Bendiksen, E. 2013. Registrering av biologisk mangfold i Rindal kommune (Møre og Romsdal) Supplerende naturtypekartlegging. – NINA Rapport 626, in prep.
- Brandrud, T.E. & Bendiksen, E. 2001. The *Cortinari* species of calciphilous *Tilia-Corylus* and *Quercus-Corylus* woodlands of Fennoscandia, outposts of the temperate *Fagus* and *Quercus-Carpinus* forest types of C Europe. – *Journal des J.E.C.* 3: 105-113.
- Brandrud, T.E. & Bendiksen, E. 2002. Artsdiversitet og populasjonsdynamikk hos slørsopper (*Cortinari*) knyttet til linde-hasselskoger på kalk – et truet element av mykorrhizasopper i Norge. - NINA-rapport, unpublished.
- Børset, O. 1985. Skogskjøtsel I. Skogøkologi. - Landbruksforlaget, Oslo.
- Callaham, R.Z. 1964. Provenance research: investigation of genetic diversity associated with geography. - In FAO/IUFRO meeting on forest genetics. *Unasylva* 18: chapter 4. (<http://www.fao.org/docrep/03650e/03650e05.htm>).
- Carnus, J.M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K. & Walters, B. 2006. Planted forests and biodiversity. - *Journal of Forestry* 104: 65-77.
- Castagneyrol B., Lagache L., Giffard B., Kremer A. & Jactel H. 2012. Genetic Diversity Increases Insect Herbivory on Oak Saplings. - *PLoS ONE* 7: 10.
- Coote, L., Smith, G.F., Kelly, D.L., O'Donoghue, S., Dowding, P., Iremonger, S. & Mitchell, F.J.G. 2008. Epiphytes of Sitka spruce (*Picea sitchensis*) plantations in Ireland and the effects of open spaces. - *Biodiversity Conservation* 17: 953–968.
- Collignon, A.M., Van de Sype, H. & Favre, J.M. 2002. Geographical variation in random amplified polymorphic DNA and quantitative traits in Norway spruce. - *Canadian Journal of Forest Research* 32: 266-282.
- Curat, M., Ruedi, M., Petit, R.J. & Excoffier, L. 2008. The hidden side of invasions: massive introgression by local genes. -*Evolution* 62: 1908-1920.
- Dering, M., Misiorny, A., Lewandowski, A. & Korczyk, A. 2012. Genetic and historical studies on the origin of Norway spruce in Bialowieza Primeval Forest in Poland. - *European Journal of Forest Research* 131: 381-387.
- Dietrichson, J. 1977. Proveniensenforsøk med gran i Danmark, Finland, Sverige og Norge. - Norsk institutt for skogforskning, Ås.
- Edvardsen, Ø.M., Steffenrem, A., Johnskås, O.R., Johnsen, Ø., Myking, T. & Kvaalen, H. 2010. Strategi for skogplanteforedlingen 2010-2040. - The Norwegian Forest Seed Station (Skogfrøverket).
- Elven, R. 1994. Lids Norske flora. - Det Norske samlaget, Oslo.
- Empire Forestry Association 1953. British Commonwealth forest terminology. Part 1. Silviculture, protection, mensuration and management, together with allied subjects. - Empire Forestry Association, London, 163 pp.
- Engelmark, O., Sjöberg, K., Andersson, B., Rosvall, O., Ågren, G.I., Baker, W.L., Barklund, P., Björkman, C., Despain, D., Elfving, B., Ennos, R.A., Karlman, M., Knecht, M.F., Knight, D.H., Ledgard, N.J., Lindelöw, Å., Nilsson, C., Peterkeni, G.F., Sörlin, S. & Sykes, M.T. 2001. Ecological effects and management aspects of an exotic tree species: the case of lodgepole pine in Sweden. - *Forest Ecology and Management* 141: 3-13.

- FAO 1971. Report of the second session of the FAO panel of experts on forest gene resources. – Rome, 68.pp.
- Farjón, A. 2001. World Checklist and Bibliography of Conifers, Second edition. - Royal Botanical Garden, Kew, England.
- Felton, A., Lindbladh, M., Brunet, J. & Fritz, Ö. 2010. Replacing coniferous monocultures with mixed-species production stands: An assessment of the potential benefits for forest biodiversity in northern Europe. - *Forest Ecology and Management* 260: 939-947.
- Felton, A., Andersson, E., Ventorp, D. & Lindbladh, M. 2011. A comparison of avian diversity in spruce monocultures and spruce–birch polycultures in southern Sweden. - *Silva Fennica* 45: 1143–1150.
- Fjellberg, A., Nygaard, P.H. & Stabbetorp, O.E. 2007. Structural changes in *Collembola* populations following replanting of birch forest with spruce in North Norway. - In: Halldorsson, G., Oddsdottir, E.S. & Eggertsson, O. (eds.), Effects of afforestation on ecosystems, landscape and rural development. -Proceedings of the AFFORNORD conference, Reykholt, Iceland, June 18-22, 2005. TemaNord 2007/508: 119-125.
- Ford Robertson, F.C. 1971 (ed.). Terminology of forest science, technology, practice and products. - Society of American Foresters: No. 1. Washington, D.C.
- Fottland, H. & Skrøppa, T. 1989. Proveniensenforsøket IUFRO 1964/1968 med gran (*Picea abies* (L.) Karst) i Norge. Variasjon i avgang og høydevekst. - *Meddelelser fra Norsk Institutt for Skogforskning* 43: 1-30.
- Frank, J. 1994. Use of broadleaved trees in conifers as a countermeasure to acidification: Effects on soil properties. - *Aktuelt fra Skogforsk* 14: 42–47.
- Frank, J., Stabbetorp, O., Frivold, L.H. & Eilertsen, O. 1998. Bjørkeinnblanding i barskog - effekter på jordforsuring, vegetasjonsutvikling og skogens vekst. - *Aktuelt fra skogforskningen* 2/98: 45-53.
- Gamfeldt, L., Snäll, T., Bagchi, R. Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G. Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J. & Bengtsson, J. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. - *Nature Communications* 4. Article number: 1340 doi: 10.1038/ncomms2328.
- Gederaas, L., Moen, T.L., Skjelseth, S. & Larsen, L.-K. (eds.). 2012. Alien species in Norway – with the Norwegian Black List 2012. - The Norwegian Biodiversity Information Centre, Norway.
- Giesecke, T. & Bennett, K.D. 2004. The Holocene spread of *Picea abies* (L.) Karst. in Fennoscandia and adjacent areas. - *Journal of Biogeography* 31: 1523-1548.
- Gjerde, I. 1993. Skogbruk og fauna på Vestlandet: Betydningen av treslagsskifte for forekomst og fordeling av skogshabitat. – Rapport fra Skogforsk 17/93: 1-21.
- Gjerde, I. & Sætersdal, M. 1997. Effects on avian diversity of introducing spruce (*Picea* spp.) plantations in the native pine (*Pinus sylvestris*) forests of western Norway. - *Biological Conservation* 79: 241-250.
- Gjerde, I., Sætersdal, M. & Nilsen, T. 2005. Abundance of two threatened woodpecker species in relation to the proportion of spruce plantations in native pine forests of western Norway. - *Biodiversity and Conservation* 14: 377-393.
- Gjerde, I., Blom, H.H., Lindblom, L., Sætersdal, M. & Schei, F.H. 2012. Community assembly in epiphytic lichens in early stages of colonization. - *Ecology* 93: 749-759.
- Gløersen, A.T. 1884. Vestlands-granen og dens innvandringsveie. - Forstforeningens Aarvog. Malinske Bogtrykkeri, Kristiania.
- Granhus, A., Hysten, G. & Ørnelund Nilsen, J.E. 2012. Statistikk over skogforhold og skogressurser i Norge, registrert i perioden 2005-2009. – Ressursoversikt fra Skog og Landskap 03-2012.
- Halldorsson, G., Oddsdottir, E.S. & Eggertsson, O. (eds.) 2007. Effects of afforestation on ecosystems, landscape and rural development. -Proceedings of the AFFORNORD conference, Reykholt, Iceland, June 18-22, 2005. TemaNord 2007/508.

- Hannerz, M., Sonesson, J. & Ekberg, I. 1999. Genetic correlations between growth and growth rhythm observed in a short-term test and performance in long-term field trials of Norway spruce. - Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 29: 768-778.
- Hannerz, M. & Westin, J. 2005. Autumn frost hardiness in Norway spruce plus tree progeny and trees of the local and transferred provenances in central Sweden. - Tree Physiology 25: 1181-1186.
- Haugland, H., Anfinnsen, B., Aasen, H., Løbersli, E., Selboe, O.-K., Terum, T., Lileng, J., Granhus, A., Søggaard, G. & Hanssen, K.H. 2013. Planting av skog på nye arealer som klimatiltak. Egnede arealer og miljøkriterier. – Miljødirektoratet Rapport M26-2013.
- Hausner, V.H., Yoccoz, N.G., Strann, K.B. & Ims, R.A. 2002: Changes in bird communities by planting non-native spruce in coastal birch forests of northern Norway. - Ecoscience 9: 470-481.
- Hausner, V.H., Yoccoz, N.G., & Ims R.A. 2003. Selecting indicator traits for monitoring land use impacts: birds in northern coastal birch forests. - Ecological Applications 13: 999-1012.
- Heuertz, M., De Paoli, E., Kallman, T., Larsson, H., Jurman, I., Morgante, M., Lascoux, M. & Gyllenstrand, N. 2006. Multilocus patterns of nucleotide diversity, linkage disequilibrium and demographic history of Norway spruce [*Picea abies* (L.) Karst]. - Genetics 174: 2095-2105.
- Hickler, T., Vohland, K., Feehan, J., Miller, P.A., Smith, B., Costa, L., Giesecke, T., Fronzek, S., Carter, T.R., Cramer, W., Kuhn, I. & Sykes, M.T. 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. - Global Ecology and Biogeography 21: 50-63.
- Hilmo, O., Holien, H., Hytteborn, H. & Ely-Aalstrup, H. 2009. Richness of epiphytic lichens in differently aged *Picea abies* plantations situated in the oceanic region of Central Norway. - Lichenologist 41: 97-108.
- Iversen, T., Benestad, R., Haugen, J.E., Kirkevåg, A., Sorteberg, A., Debernard, J., Grønås, S., Hanssen-Bauer, I., Kvamstø, N.G., Martinsen, E.A. & Engen-Skaugen, T. 2005. RegClim, Norges klima om 100 år. Usikkerhet og risiko (Climate in Norway in 100 years. Uncertainties and risks). – RegClim.
- Jansson, G., Danusevicius, D., Grotehusman, H., Kowalczyk, J., Krajmerova, D., Skrøppa, T. & Wolf, H. 2013. Norway spruce (*Picea abies* (L.) H Karst.). - In: Paques, L.E. (ed.), Forest tree breeding in Europe. Current state-of-the-art and perspectives, Springer, Dordrecht, pp. 123-176
- Johansson, L., Andersen, J. & Nilssen, A.C. 1994. Distribution of bark insects in "island" plantations of spruce (*Picea abies* (L.) Karst.) in Subarctic Norway. - Polar Biology 14: 107-116.
- Jones, N. & Burley, J. 1973. Seed certification, provenances nomenclature and genetic history in forestry. – Silvae Genetica 22: 53-58.
- Johnsen, Ø. & Østreg, G. 1994. Effects of plus tree selection and seed orchard environment on progenies of *Picea abies*. - Canadian Journal of Forestry 24: 32-38.
- Korkama T., Pakkanen A. & Pennanen T. 2006. Ectomycorrhizal community structure varies among Norway spruce (*Picea abies*) clones. - New Phytologist 171: 815-824.
- Korkama-Rajala T., Mueller M.M. & Pennanen T. 2008. Decomposition and fungi of needle litter from slow- and fast-growing Norway spruce (*Picea abies*) clones. - Microbial Ecology 56: 76-89.
- Koskela, J., Buck, A. & Teissier du Cros, E. (eds.). 2007. Climate change and forest genetic diversity. Implications for sustainable forest management in Europe. - Biodiversity International, Rome.
- Kullman, L. 2008. Early postglacial appearance of tree species in northern Scandinavia: review and perspective. - Quaternary Science Reviews 27: 2467-2472.
- Kvaalen, H. & Johnsen, Ø. 2008. Timing of bud set in *Picea abies* is regulated by a memory of temperature during zygotic and somatic embryogenesis. - New Phytologist 177: 49-59.
- Kålås, J.A., Viken, Å., Henriksen, S. & Skjelseth, S., red. 2010. Norsk rødliste for arter 2010. - Artsdatabanken, Norway.
- Lagercrantz, U. & Ryman, N. 1990. Genetic structure of Norway spruce (*Picea abies*): Concordance of morphological and allozymic variation. - Evolution 44: 38-53.

- Larsen, J.B. 1981. Waldbauliche und ertragskundliche Erfahrungen mit verschiedenen Provenienzen der Weißtanne (*Abies alba* Mill.) in Dänemark. - Forstwissenschaftl. Centralblatt 100: 275-286.
- Latałowa, M. & van der Knaap, W.O. 2006. Late Quaternary expansion of Norway spruce *Picea abies* (L.) Karst. in Europe according to pollen data. - Quaternary Science Reviews 25: 2780-2805.
- Levitt, J. 1980. Factors related to freezing tolerance. In: T.T. Kozłowski, T.T. (ed.), Physiological Ecology, Academic Press, Inc., Standford, California, pp. 160-227.
- Lindgaard, A. & Henriksen, S. (eds.) 2011. Norsk rødliste for naturtyper 2011. - Artsdatabanken, Trondheim.
- Lindner M., Garcia-Gonzalo J., Kolström M., Green T., Reguera R., Maroschek M., Seidl R., Lexer M.J., Netherer S., Schopf A., Kremer A., Delzon S., Barbati A., Marchetti M., Corona P. 2008. Impacts of Climate Change on European Forests and Options for Adaptation - In. Report to the European Commission Directorate-General for Agriculture and Rural Development http://ec.europa.eu/agriculture/analysis/external/euro_forests/full_report_en.pdf.
- Lockwood, J.D., Aleksić, J.M., Zou, J., Wang, J., Liu, J. & Renner, S.S. 2013. A new phylogeny for the genus *Picea* from plastid, mitochondrial, and nuclear sequences. - Molecular Phylogenetics and Evolution 69: 717-727.
- Magnesen, S. 1992. Treslagets og proveniensenes betydning for skogskader: En litteraturstudie fra en ca. 100-årig epoke i norsk skogbruk. - Research paper of Skogforsk 7:1-46.
- Matthews, J.D. 1964. Seed production and seed certification. - Unasylva18: 104-118.
- McKay, J.K. & Latta, R.G. 2002. Adaptive population divergence: markers, QTL and traits. - Trends in Ecology and Evolution 17: 285-291.
- Mikola, P. 1985. The effects of tree species on the biological properties of forest soil. - National Swedish Environment Protection Board. Report No. 3017, 27 pp.
- Molmann, J.A., Junttila, O., Johnsen, O. & Olsen, J.E. 2006. Effects of red, far-red and blue light in maintaining growth in latitudinal populations of Norway spruce (*Picea abies*). - Plant Cell and Environment 29: 166-172.
- Nilssen, A.C. 1976. Sprednings- og etableringsevne hos photofage barkskogsbiller belyst ved undersøkelser i granplantefelter i Nord-Norge. - Hovedfagsoppgave i terrestrisk økologi, Universitetet i Tromsø. 116 pp.
- Nilssen, A.C. 2010: Granplantefeltene i Lofoten og Vesterålen – ny ressurs også for insekter? - Ottar 281: 43-47.
- Noss, R.F. 1990. Indicators for monitoring biodiversity: A hierarchical approach. - Conservation Biology 4: 355-364.
- Parducci, L., Jørgensen, T., Tollefsrud, M.M., Elverland, E., Alm, T., Fontana, S.L., Bennett, K.D., Haile, J., Matetovici, I., Suyama, Y., Edwards, M.E., Andersen, K., Rasmussen, M., Boessenkool, S., Coissac, E., Brochmann, C., Taberlet, P., Houmark-Nielsen, M., Larsen, N.K., Orlando, L., Gilbert, M.T.P., Kjær, K.H., Alsos, I.G. & Willerslev, E. 2012. Glacial survival of boreal trees in northern Scandinavia. - Science 335: 1083-1086.
- Pedersen, Å.Ø., Ims, R.A., Yoccoz, N.G., Hausner, V.H., & Juell, K.H. 2010a. Scale-dependent responses of predators and prey to spruce plantations in sub-arctic birch forest in winter. - Ecoscience 17: 123-136.
- Pedersen, Å.Ø., Yoccoz, N.G., Ims, R.A. & Sigurdson, T. 2010b. Effects on non-native spruce plantations on small mammal communities in subarctic birch forest. - Journal of Forest Ecology and Management 260: 331-338.
- Peterken, G.F. 2001. Ecological effects of introduced tree species in Britain. - Forest Ecology and Management 141: 31-42.
- Petit, R.J. & Hampe, A. 2006. Some Evolutionary Consequences of Being a Tree. - Annual Review of Ecology Evolution and Systematics 37: 187-214.

- Piotti, A., Leonardi, S., Piovani, P., Scalfi, M., & Menozzi P. (2009) Spruce colonization at treeline: where do those seeds come from? - *Heredity* 103: 136-145.
- Popov, P.P. 2003. Structure and differentiation of spruce populations in eastern Europe and western Siberia. - *Russian Journal of Ecology* 34: 27-33.
- Pravdin, L.F. 1975. European spruce and Siberian spruce in the USSR (in Russian). - Izdatel'stro Nauka. Moskva. Cited in Schmidt-Vogt H (1977) *Die Fichte*. Verlag Paul Harvey, Hamburg and Berlin.
- Ran, J.-H., Wei, X.-X. & Wang, X.-Q. 2006. Molecular phylogeny and biogeography of *Picea* (*Pinaceae*): Implications for phylogeographical studies using cytoplasmic haplotypes. - *Molecular Phylogenetics and Evolution* 41: 405-419.
- Sandvik, H. 2012a. Kunnskapsstatus for spredning og effekter av fremmede bartrær på biologisk mangfold. - DN-utredning 8-2012.
- Sandvik, H. 2012b. Methods and set of criteria. - In: Gederaas, L., Moen, T.L., Skjelseth, S. & Larsen, L.-K. (eds.), *Alien species in Norway – with the Norwegian Black List 2012*, The Norwegian Biodiversity Information Centre, Norway: 57-64.
- Saure, H.I. 2012. Impact of native and introduced coniferous species on biodiversity in semi-natural coastal vegetation, western Norway. - PhD thesis, University of Bergen.
- Saure, H.I., Vandvik, V., Hassel, K. & Vetaas, O.R. 2013. Effects of invasion by introduced versus native conifers on coastal heathland vegetation. - *Journal of Vegetation Science* 24: 744–754.
- Schleip, C., Menzel, A. & Dose, V. 2008. Norway spruce (*Picea abies*): Bayesian analysis of the relationship between temperature and bud burst. - *Agricultural and Forest Meteorology* 148: 631-643.
- Schmidt, L. 1997. Tree Improvement Glossary. -Technical Note 46. Danida Forest Seed Centre.
- Schmidt-Vogt, H. 1974. Die systematische Stellung der gemeinen Fichte (*Picea abies* [L.] Karst.) und der sibirischen Fichte (*Picea obovata* Ledeb.) in der Gattung *Picea*. Ein Beitrag zur Einführung von Erkenntnissen auf dem Gebiet forstlicher Genökologie in die Systematik der Baumarten. - *Allgemeine Forst und Jagdzeitung* 145: 46-60.
- Schmidt-Vogt, H. 1977. *Die Fichte*. - Verlag Paul Parey, Hamburg and Berlin.
- Skrøppa, T. 1986. With the damage in the IUFRO 1964/68 provenance experiment with Norway spruce (*Picea abies* (L.) Karst.). - *Communications of the Norwegian Forest Research Institute* 39: 161-183.
- Skrøppa, T. 1991. Within-population variation in autumn frost hardiness and its relationship to bud-set and height growth in *Picea abies*. - *Scandinavian Journal of Forest Research* 6: 353-363.
- Skrøppa, T., Martinsen D.R. & Følstad A. 1993. Vekst og kvalitet til mellomeuropeiske granprovenienser plantet i Østfold (Growth and quality of Central-European Norway spruce provenances planted in Østfold) - *Reports from Skogforsk* 7:1-20
- Skrøppa, T., Kohmann, K., Johnsen, Ø. & Johnskås, R. 2005. Resultater med avkom fra Kaupanger granfrøplantasje. - *Rapport fra skogforskningen* 8: 1-18.
- Skrøppa, T., Tollefsrud, M.M., Sperisen, C. & Johnsen, Ø. 2010. Rapid change in adaptive performance from one generation to the next in *Picea abies* - Central European trees in a Nordic environment. - *Tree Genetics & Genomes* 6: 93-99.
- Skrøppa, T., Edvardsen, Ø.M., Steffenrem, A., Kvaalen, H. & Myking, T. 2014. Norsk perspektiv på nordisk samarbeid om skogfrøforsyningen. - *Rapport fra Skog og landskap*. In press.
- Smolander, A., Loponen, J., Suominen, K. & Kitunen, V. 2005. Organic matter characteristics and C and N transformations in the humus layer under two tree species, *Betula pendula* and *Picea abies*. - *Soil Biology & Biochemistry* 37: 1309-1318.
- Solberg, S. 2004. Summer drought: a driver for crown condition and mortality of Norway spruce in Norway. - *Forest Pathology* 34: 93-104.

- Solberg, S., Andreassen, K., Anton, C., Børja, I., Cermak, J., Dalsgård, L., Eklundh, L. M., Gessler, A., Godbold, D., Hentschel, R., Kayler, Z., Madsen, P., Nadezhdina, N., Rosner, S., Svetlik, J., Tollefsrud, M.M., Tveito, O.E. & Øyen, B.H. 2013. Sluttrapport fra grantørkeprosjektet. - Sluttrapport til Norsk Forskningsråd for prosjektet Sprucedieback.
- Sperisen, C., Büchler, U., Gugerli, F., Mátyás, G., Geburek, T. & Vendramin, G.G. 2001. Tandem repeats in plant mitochondrial genomes: application to the analysis of population differentiation in the conifer Norway spruce. - *Molecular Ecology* 10: 257-263.
- Spiecker, H. 2003. Silvicultural management in maintaining biodiversity and resistance of forests in Europe –temperate zone. - *Journal of Environmental Management* 67: 55–65.
- Stabbetorp, O.E. & Nygaard P.H. 2005. Økologiske effekter av fremmede treslag i kystområdene. – NINA Temahefte 33: 23-32.
- Stenlid J., Oliva J., Boberg J.B. & Hopkins A.J.M. 2011. Emerging Diseases in European Forest Ecosystems and Responses in Society. - *Forests* 2: 486-504.
- Terhürne-Berson, R. 2005. Changing distribution patterns of selected conifers in the Quaternary of Europe caused by climatic variations. – PhD-thesis, Rheinischen Friedrich-Wilhelms Universität Bonn, Bonn.
- Tollefsrud, M.M. 2008. Phylogeography, diversity and hybridization in Norway spruce inferred from molecular markers combined with pollen records. – PhD thesis, University of Oslo, Oslo.
- Tollefsrud, M.M., Kissling, R., Gugerli, F., Johnsen, Ø., Skrøppa, T., Cheddadi, R., van der Knaap, W.O., Latałowa, M., Terhürne-Berson, R., Litt, T., Geburek, T., Brochmann, C. & Sperisen, C. 2008. Genetic consequences of glacial survival and postglacial colonization in Norway spruce: combined analysis of mitochondrial DNA and fossil pollen. - *Molecular Ecology* 17: 4134-4150.
- Tollefsrud, M.M., Sønstebo, J.H., Brochmann, C., Johnsen, Ø., Skrøppa, T. & Vendramin, G.G. 2009. Combined analysis of nuclear and mitochondrial markers provide new insight into the genetic structure of North European *Picea abies*. - *Heredity* 102: 549-562.
- Tollefsrud, M. M., Tsuda, Y., Sønstebo, J.H., Latałowa, M., Laura, P., Källman, T., Chen, J., Semerikov, V., Skrøppa, T., Vendramin, G.G., Sperisen, C., Lascoux, M. 2014. The impact of glacial and postglacial history on the genetic structure of Norway spruce and Siberian spruce. Invited talk on the conference: Genetic Resources for Food and Agriculture in a Changing Climate, NordGen, Lillehammer, Norway. Abstract available at <http://climate.nordgen.org/>.
- Tømmerås, B.Å., Johnsen, Ø., Skrøppa, T., Hindar, K., Holten, J. & Tufto, J. 1996. Long-term environmental impacts of release of transgenic Norway spruce (*Picea abies*). - NINA.NIKU Project Report 003: 1-48.
- Tutin, T.G., Burges, N.A., Chater, A.O., Edmonds, J.R., Heywood, D.H., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. 1993. *Flora Europaea*, 2nd ed. - Cambridge University Press, Cambridge.
- Valiranta, M., Kaakinen, A., Kuhry, P., Kultti, S., Salonen, J.S. & Seppä, H. 2011. Scattered late-glacial and early Holocene tree populations as dispersal nuclei for forest development in north-eastern European Russia. - *Journal of Biogeography* 38: 922-932.
- Vendramin, G.G., Anzidei, M., Madaghiale, A., Sperisen, C. & Bucci, G. 2000. Chloroplast microsatellite analysis reveals the presence of population subdivision in Norway spruce (*Picea abies* K.). - *Genome* 43: 68-78.
- Wachter, Von Hubertus 2011. Die Stieleiche (*Quercus robur* L.) slawonischer Herkunft in Westfalen und am Niederrhein– Einführung, Anbau und Verhalten. - Verlag Kessel.
- Wannebo-Nilsen, K., Bjerke, J.W., Beck, P.S.A. & Tømmervik, H. 2010: Epiphytic macrolichens in spruce plantations and native birch forests along a coast-inland gradient in North Norway. - *Boreal Environment Research* 15: 43–57.
- Whitham T.G., Bailey J.K., Schweitzer J.A., Shuster S.M., Bangert R.K., Leroy C.J., Lonsdorf E.V., Allan G.J., DiFazio S.P., Potts B.M., Fischer D.G., Gehring C.A., Lindroth R.L., Marks J.C., Hart S.C., Wimp G.M. & Wooley S.C. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. - *Nature Reviews Genetics* 7: 510-523.

- Whitham T.G., Gehring C.A., Lamit L.J., Wojtowicz T., Evans L.M., Keith A.R., Smith D.S. 2012. Community specificity: life and afterlife effects of genes. - *Trends in Plant Science* 17: 271-281.
- Wright, J.W. 1962. Genetics of forests tree improvement. – FAO Forest and Forest Production Studies. No. 16, 399 pp.
- Wright, J. 1976. Introduction to Forest Genetics. - Department of Forestry Michigan State University. Academic Press. (AP) New York.
- Yoccoz, N.G., Ims. R., Hausner, V.H. & Sigurdson, T. 2001. Treslagsskifte i bjørkeskog. - NINA Temahefte 17.
- Yoccoz, N.G., Hausner, V.H. & Strann, K.-B. 2005. Landskapsendringer og treslagsskifte i nordnorske kystbjørkeskoger. - NINA temahefte 33.



The Norwegian Institute for Nature Research (NINA) is Norway's leading institution for applied ecological research.

NINA is responsible for long-term strategic research and commissioned applied research to facilitate the implementation of international conventions, decision-support systems and management tools, as well as to enhance public awareness and promote conflict resolution.

ISSN: 1504-3312
ISBN: 978-82-426-2694-3

Norwegian Institute for Nature Research

NINA head office

Postal address: P.O. Box 5685 Sluppen, NO-7485 Trondheim, NORWAY

Visiting address: Høgskoleringen 9, 7034 Trondheim

Phone: +47 73 80 14 00

E-mail: firmapost@nina.no

Organization Number: 9500 37 687

<http://www.nina.no>

Cooperation and expertise for a sustainable future