The status of tree breeding and its potential for improving biomass production

– A review of breeding activities and genetic gains in Scandinavia and Finland

PREFACE

Woody biomass must contribute more to meet fossil energy independence by 2050 as well as the EU 2020 renewable energy objectives, while at the same time securing sustainability and the provision of ecosystem services today and in the future.

A project financed by the Nordic Energy Research within the project "Wood based energy systems" was realized under the name "ENERWOODS" during year 2012 and 2015 with the main objective to strengthen the role of Nordic forestry as a significant contributor to the development of competitive, efficient and renewable energy systems.

One of the five main challenges linked to meet the project objectives was to increase forest productivity, where breeding is considered to be one of the most effective and environmentally friendly options to increase sustainable biomass production in our forests. Thus it was decided to give an insight of the forest tree breeding in Denmark, Finland, Norway and Sweden. In this publication we present the current status of breeding, the genetic and economic gain in yield of today and predictions about the situation in the year 2050.

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THE STATUS OF TREE BREEDING AND ITS POTENTIAL FOR IMPROVING BIOMASS PRODUCTION

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SUMMARY

There have been intense discussions about reducing fossil energy dependence for many years, indeed there is a vision to have a carbon-neutral energy system in Scandinavia by the year 2050. One way to address this ambition is to increase the use of woody biomass. This places a focus on forest tree breeding, since it is considered to be one of the most effective and environmentally friendly options to increase sustainable biomass production in our forests.

In this report we have summarised information about forest tree breeding in Denmark, Finland, Norway and Sweden, covering historic, current and future activities. It includes estimates of realised genetic gain in volume and dry matter production on a regional basis for regeneration materials of different improvement levels, which are available today and will be available in the year 2050. Genetic gains in economic terms are also discussed, and basic breeding and mass propagation principles are described. The report includes the most relevant commercial forest tree species in Scandinavia: Scots pine, Norway spruce, Sitka spruce, Douglas fir, grand fir, birch, poplars, alder, oak and beech.

Intensive and long-term breeding is carried out continuously in Sweden and Finland for Scots pine, Norway spruce and to some extent birch, while other species are worked with intermittently. In Norway the interest in breeding has, after a break of some years, now resumed, resulting in the initiation of a new breeding cycle for Norway spruce. The present resources put into breeding in Denmark are small, due to a major change in silvicultural management towards natural regeneration in the State Forests. However, as in all the other Scandinavian countries, there is great potential to increase growth through breeding.

Seed from seed orchards is, and will within coming decades, be the main way to supply the forestry with genetically improved plant material. The extra gain in yield that is obtained by using material from existing seed orchards varies among species, but in general it is, on average, 10–15% when compared to local unimproved material. In 2050 it is estimated that this gain will be 20–25% for many species, which is a substantial increase in productivity.

The time elapsed from establishment of a seed orchard to the first seed harvest for many species is quite long (10–20 years) and delays the realisation of the genetic improvement efforts. An alternative is to use plants obtained from the vegetative propagation of genetically well-performing seed sources or individuals, which makes it possible to capture the progress from breeding immediately. Utilisation of clones is also a way to reduce the consequences of limited amounts of seed from seed orchards, which for instance, is the case for Norway spruce in southern Sweden. For Norway spruce, using clonal material can immediately deliver a gain of around 25–35% in yield, and it is estimated that by 2050 this figure will have increased to 40%. It should be noted, however, that the use of clonal material may be limited by forest regulations.

Future climate change will probably alter the growing conditions in Scandinavia in a way that makes forestry with high productivity exotic species such as Douglas fir, grand fir, Sitka spruce and poplars more attractive. Using several species, instead of the few traditional ones, is a way to spread the risk of an unknown future. In Denmark, several exotic species have been an integrated part of forestry for more than 100 years. Limited breeding work has been performed for these species and the gain in yield is, for instance, estimated to amount to 40% for existing seed orchard material of Sitka spruce compared to unimproved material.

BACKGROUND

Wood biomass production must increase to meet the goal of fossil energy independence by 2050 as well as to deliver the EU 2020 renewable energy goals, while at the same time securing sustainability and the provision of ecosystem services now and in the future (IEA, 2013).

A project financed by Nordic Energy Research started in 2012 with the prime objective of strengthening the role of Nordic forestry as a significant contributor to the development of competitive, efficient and renewable energy systems.

Use of genetically improved material is one way to meet these objectives. Breeding is considered to be the most effective and environmentally friendly option to increase sustainable biomass production in our forests. Breeding offers significant advantages at little additional cost, since improved material is only slightly more expensive than unimproved material.

The effect of using genetically improved forest plant material is, at the stand level, similar to increasing the site index of the forest land. The forest grows faster, the harvests come earlier and the rotation time can be shortened while the effects on nature and the environment are small. Improved material is also more vital and has better overall quality and survival, of which the latter can be a great benefit in northern areas with harsh climate, providing opportunities to modify regeneration and silvicultural methods. For instance, higher survival gives the option to reduce the number of plants per ha. Choosing an appropriate regeneration material is of great importance since it will have silvicultural and economic consequences during the whole rotation period.

In this review, the current status of breeding, the genetic and economic gain in yield and predictions about the situation in the year 2050 are presented together with descriptions of basic breeding and mass propagation principles. We describe the situation in Denmark, Finland, Norway and Sweden, hereafter referred to as Scandinavia.

The most extensive long-term breeding programmes established in northern Europe are those for Norway spruce and Scots pine in Sweden, Finland and Norway. The aim of these programmes is to combine intensive breeding, gene conservation and preparedness for future climatic changes (Danell 1993, Westin & Haapanen 2013, Ruotsalainen & Persson 2013, Edvardsen et al. 2010).

BREEDING PRINCIPLES

Breeding normally includes

1) phenotypic plus-tree selection in forest stands based on visually assessed properties,
2) field testing of the plus-trees by their progeny or by vegetative propagation and finally
3) a selection of well-performing genotypes for commercial use by establishing seed orchards or using vegetative propagation (Figure 1).

The long-term breeding material for each species is divided into multiple breeding populations (see figure 2), where the breeding cycle is repeated generation by generation. The genetic gain in growth is estimated to be 10–15% per generation and is realized in operational forestry by mass propagation actions, in which the deployment of improved material across the country is optimised.

Intermittent breeding is an alternative for species of lower importance, where the main objective is maximum possible genetic gain over a short period of time in combination with sufficient genetic variation for commercial use. Less attention is paid to long-term management of genetic resources. However a variety of breeding goals can be addressed depending on species, specific challenges and aims.

Traditional breeding has focused on traits of important economic value for production of timber and pulp, such as growth, survival, stem quality and vitality. Vitality is a complex trait that encompasses climatic adaptation, pathogen resistance and robustness over a wide range of environments.

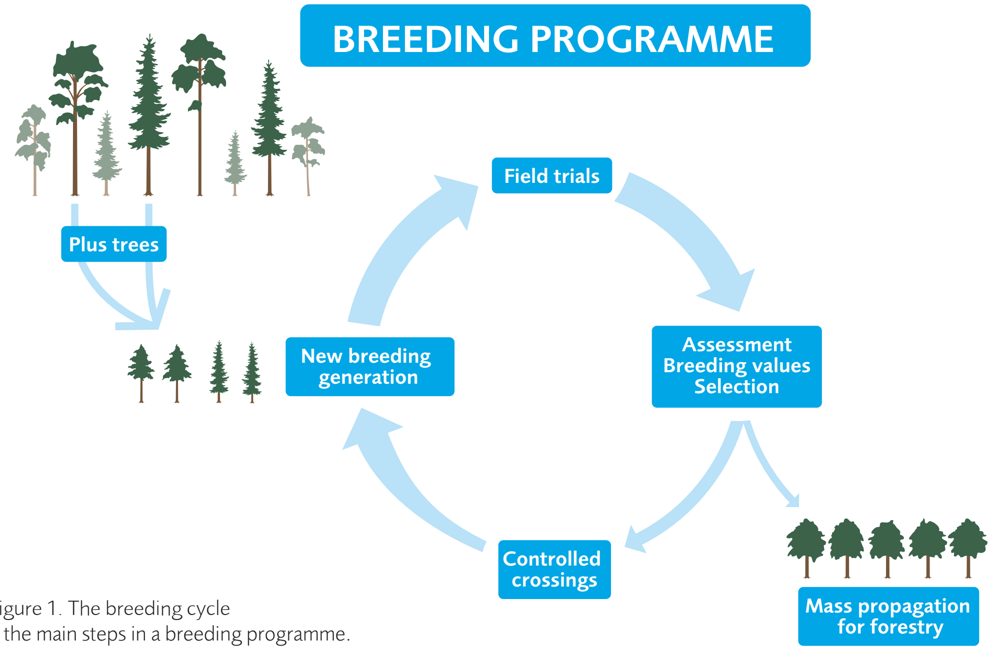


Figure 1. The breeding cycle
– the main steps in a breeding programme.

Climatic adaptation is essential throughout Scandinavia and particularly for introduced species such as poplars, Douglas fir, grand fir, Sitka spruce and lodgepole pine, which have not adapted naturally to the climate in Scandinavia. The identification of varieties with appropriate timings of bud-burst and growth cessation is crucial for good performance in the boreal regions (Hannerz 1998). This will be even more important in the face of climate change.

Resistance to different types of pathogens, such as root rot *(Heterobasidion sp.)* in spruce (Karlsson & Swedjemark 2006), *Gremminiella* on pine (Persson et al. 2010), stem canker on hybrid aspen (Copony & Barnes 1974) and ash dieback (Mckinney et al. 2011) are additional examples of essential selection traits. The growing interest in new species in northern Europe and the expectation of climatic warming in the near future will increase the importance of resistance breeding (Yanchuk & Allard 2009).

Wood property traits, such as wood density and lignin content can be of great importance when breeding is directed towards biomass production for energy supply. Wood traits are not always treated as long-term breeding traits since they are often refined through advances in industrial processing technology rather than being modified by breeding. However, they still have to be monitored in order to determine how they correlate with the selection traits and to avoid any unfavourable impact on future wood quality.

MOLECULAR AND BIOTECH METHODS IN BREEDING

PHOTO: ISTOCKPHOTO

Biotechnology is one of the most rapidly developing areas of science and includes new technologies that can be used in breeding. Some of these are described below.

Identification of genetic relationships by genetic markers is extensively used as a breeding tool, for purposes such as clonal verification. These methods have developed rapidly, becoming more simple, cheap and precise. In the near future, marker technology may be employed routinely for quantifying relatedness, reducing effective population sizes, and to gauge losses of gene diversity in operational breeding.

Selection based on data from genetic markers has substantial potential for increasing the cost-efficiency of breeding since it could reduce breeding rotation times, decrease costs by reducing the need for expensive field testing, and increase the intensity of selection. It has long been expected that molecular tools would enhance breeding progress, although in practice this has not happened as rapidly as was first hoped (Andersson & Lindgren 2011). Associations between phenotypic performance and genetic markers have been difficult to establish. The most important traits, such as yield, adaptability and wood quality, are complex and no major genes have been found for these traits. Many genes have effects on more than one character, and individual characters are often affected by small contributions from many genes. In addition, there are interactions between genes and the environment, i.e. genes that sometimes seem to be important may not be significant for all trees or in different environments. Marker-assisted selection (MAS), based on quantitative trait loci (QTL) analysis, has not been able to identify specific genes for complex traits in forest trees with the same effectiveness as was achieved in model systems (Neale & Kremer 2011). However, there is enormous on-going progress in the development of gene sequencing techniques. Thus, new techniques such as association mapping and genome-wide mapping seem to have great potential for establishing relationships between phenotypes and large numbers of gene markers (specifically, SNPs, i.e. single-nucleotide polymorphisms) (Meuwissen 2009). If such cost-effective markers are developed for population-wide applications, they could be applied in operational breeding in, perhaps, the next ten years, after being verified as appropriate in field tests.

Genetically modified organisms (GMOs) are generated by various genetic engineering methods that affect both genotypes and gene expression. GMO-crops have found relatively widespread use in commercial agriculture, largely due to their resistance to herbicides and insecticides. However, the development of GMO trees for forestry has been slow and modified genes seem to be a long way from finding applications in operational forest tree breeding in most countries. To be used in operational breeding, the stability of the gene expression must be verified in long-term field trials and negative side effects are not acceptable. The general public perceive GMOs negatively and the work required for licensing a GMO crop is time-consuming, expensive and unpredictable. GMOs are therefore not expected to have any significant impact on either operational breeding or commercial plant material in the near future.

PHOTO: ISTOCKPHOTO

BREEDING – CLIMATE CHANGE

There is a consensus among climate researchers that global warming is occurring and will continue for at least a few hundred years. For example, it has been estimated that the average temperature in Sweden will increase by 3–5°C between the years 1961 and 2100. This may increase the vegetation period by up to 40 days in northern Sweden and up to 100 days in the southern parts, resulting in an increase in growth of 20–40% (Brázdil et al. 2010, Jönsson & Bärring 2011). Simultaneously there will be greater risks of frost damage in spring and early summer in the southern regions and greater risk of damage due to pathogens and pests (Langvall 2011, Yanchuk & Allard 2009).

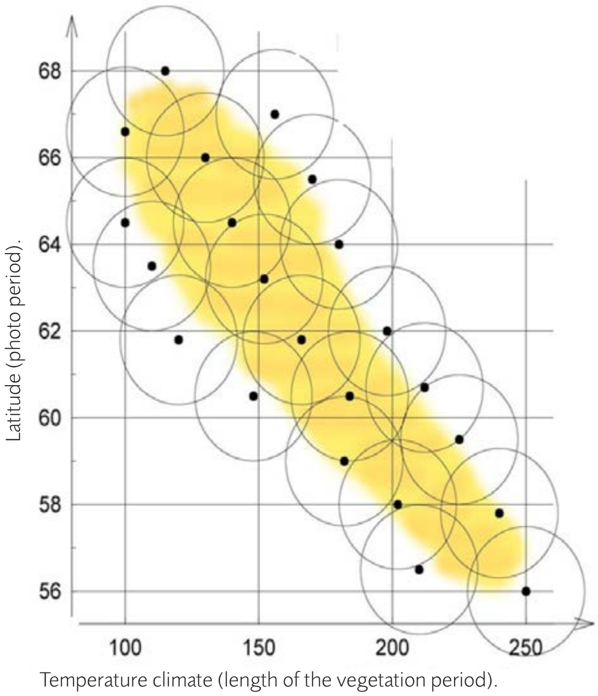


Figure 2. Distribution of breeding populations of Norway spruce across defined climatic gradients of light and temperature in Sweden.

In the long-run, trees will adapt to the changing climate by natural selection, but any adaptation occurs in response to the current conditions. Thus, adaptation lags behind, since it happens after the actual change in climate has occurred. Breeding, on the other hand, provides the opportunity to adapt trees to future climates in a faster and more efficient way. The Multiple Population Breeding Strategy (MPBS) for instance, is designed to provide preparedness for future climatic changes by dividing the breeding population into different sub-populations (Danell 1993), each of which is bred for different adaptation targets defined by temperature and photo period (Figure 2). On a long-term basis, each sub-population will gradually adapt to the climate profile for which it is designed. In the short-term it will be possible to use material from sub-populations adapted to more southerly climates in more northerly areas.

Another way to be prepared for an unknown future is to increase the plasticity and adaptability of existing populations. This is achieved by establishing field tests at several locations covering a wide range of climate conditions, and selecting trees that perform well at all locations. Genotypes performing well across a range of sites can be expected to be more robust, which is desirable when dealing with varied growth conditions and an uncertain future climate.

It will be essential for future research to respond to climatic change by placing greater emphasis on climatic adaptation and phenology, as well as resistance to pests and diseases. This is of greater concern for long rotation than short rotation species. For instance, planting fast growing species such as poplars gives the option to change species or genetic material after as little as 15–25 years of growth.

However, it is the climate of today which is crucial for the success of establishing plantations. Thus, choosing plant material today is a balance between the two objectives, namely high survival at the time of establishment and high yield in the future. The future production climate is actually considered, for instance, in the Swedish "Planter's guide" (at www.kunskapdirekt.se), in which recommendations for choosing forest material in Sweden are given to forest owners. A corresponding website is available for Denmark (www.plantevalg.dk).

In Norway spruce there are epigenetic mechanisms that have important implications for adaptation and phenotypic plasticity, since the performance of adaptive traits is influenced by temperatures during late embryogenesis and seed maturation (Johnsen et al. 2005, 2009). The influence of warmer temperatures during this phase produces progeny that are better adapted to a prolonged growing season without changes at the genetic level. Tree breeding programmes capable of utilising epigenetic effects together with genetic selection will be effective tools for breeding in the context of changes in climate.

In addition, future climate will probably change the growing conditions in a way that makes forestry involving exotic species more attractive, or possibly necessary (Rosvall 2011, Kjaer et al. 2014). Species currently adapted to conditions in more southerly regions may therefore be suitable for use in northern areas, leading to exploitation of such exotic species. The scope for breeding can be limited by regional climatological and ecological conditions and the biology of the species in question. However, many boreal species are distributed over large areas and normally there is considerable genetic variation that can be exploited by the breeder. Using several species instead of just the few traditional species is one way to spread the risk of an unknown future. High productivity exotic species of great interest include Sitka spruce, Douglas fir, grand fir and poplars. Several exotic species with the potential to grow in Scandinavia are already in field tests aimed at selecting the best performing genotypes for commercial use. However, there is a need for analysis of environmental consequences, political decisions and general acceptance by the environmental certification systems before commercial use on a broader scale. In Denmark, several exotic conifers and broadleaved species have been an integrated part of their forestry for more than 100 years.

SEED ORCHARDS

The gains from tree breeding are mainly delivered by mass production of seed in seed orchards (SO), consisting of selected genotypes tested for the targeted deployment area. These genotypes are multiplied by grafting and randomly distributed in an area of 1–20 ha. The number of copies per genotype is nowadays normally proportional to the breeding value (linear deployment), which optimises both genetic gain and genetic diversity (Rosvall & Mullin 2013). Other types of orchard designs are employed depending on the aim and species. For instance, seedling seed orchards are used when long-term survival of grafts is a problem, as for Douglas fir (Copes 1974, Hansen et al. 2005). Other examples are the use of rooted cuttings, as in Danish Sitka spruce orchards, or designs to produce hybrid seed as for larch.

The seed produced in SOs is normally open-pollinated, i.e. there is no control of the father's contribution. Pollen contamination from unimproved stands is common and reduces genetic gain. One way to reduce pollen contamination is to establish SOs in greenhouses, which is the strategy used for silver birch in Finland and Sweden (Koski & Rousi 2005, Rosvall 2011). Long distance movement of orchards, considering the origin of the parent material, to warmer climates or the use of greenhouse orchards can impose epigenetic effects. These effects may cause changes in the phenotypic performance of adaptive traits as the influence of a warmer climate in combination with southern latitudes implies delayed bud flush and growth cessation (Johnsen et al. 2005, 2009). This may cause hardiness problems, but could also be used for the adaptation to a warmer climate and prolonged growing seasons both in respect to frost risk in spring and productivity (Skrøppa et al. 2007).

SO material frequently has other advantages compared to unimproved material beside the genetic gain. The seed is generally heavier and germinates faster and more evenly, thus simplifying plant production. It also gives a more reliable and reproducible seed with a high genetic diversity since the selected materials in the seed orchards are of different

origins. Furthermore, as pointed out previously, tested SO material is probably better adapted (more robust) to a changing climate, since it consists of clones for which progeny have performed well at varying sites.

The genetic gain from a specific SO can be increased by genetic thinning – where parent clones with the lowest breeding values are removed – or by selective harvest – where seed is harvested only from the best parents. This option is normally used only when there is a surplus of SO seed production (Rosvall et al. 2001).

Production of improved seed is, for some species and regions, lower than the demand. This can be solved in the short-term at quite a low marginal cost by more intensive SO management and application of methods that promote flowering. Methods to limit seed-destroying insects should always be used (Almqvist et al. 2010).

The economic lifetime of SOs was recently calculated to be 40 years for spruce and 30 years for pine in Sweden (Almqvist et al. 2010). The establishment of SOs should therefore be a continuous process that follows the progress of breeding. For instance, new SOs of Norway spruce should be synchronised with the breeding populations over cycles of 20–25 years.

The possibilities for interaction between silviculture and breeding should be considered. For instance, there will always be a shortage of the best available genetic material. Thus, to optimise the economic return, highly improved material should in the first place be established on sites with the highest economic return rate, i.e. at the most fertile sites where the infrastructure is good and in combination with good site preparation.

VEGETATIVE PROPAGATION

Seed orchards are, and will within the coming decades, be the main source of genetically improved materials for plant production. The main drawbacks of the seed orchard concept are the long time until the trees start flowering and

contamination with unimproved pollen. These delay deployment and reduce genetic gain. Using vegetative propagation of superior clones or seed sources provides the opportunity to capture the progress from breeding early and is also a way to reduce the consequences of a shortage of seeds from SOs (Rosvall & Wennström 2008).

Rooted cuttings are the most inexpensive method of vegetative propagation for species such as poplars, Norway spruce and Sitka spruce. Bulk propagation of limited seed sources seems to be a promising vegetative propagation method for Norway spruce and has now been introduced commercially on a small scale in southern Sweden. Plants from seeds of elite families, i.e. controlled crossings between genetically superior parents, are multiplied by rooted cuttings with a limited number of copies per plant and mixed as a clonal bulk.

Tissue culture and somatic embryogenesis (SE) are other methods for producing large numbers of plants from a small initial quantity of material. SE is not yet fully developed for commercial use but seems to have a great potential in more efficient mass propagation than cuttings. (Högberg 2008).

PROVENANCES

An alternative to reforestation with genetically improved material is using stand seed sources of known provenance. A provenance is a population or group of individuals harvested in a defined geographic area. Local provenances, i.e. unimproved material originating close to the plantation area, are seldom the optimal choice. Using Norway spruce from north-eastern Europe in southern Sweden is an example which gives a gain in growth of around 8% compared to local Swedish seed sources (Rosvall et al. 2001). However, provenances are less genetically defined and not as homogeneous as seed orchard seeds, since a provenance can refer to an area covering several tens of km^2. Within the EU, there is strict regulation concerning the trade and use of different types of forest reproductive material ranging from well tested material, to large provenance areas (Anon. 1999).

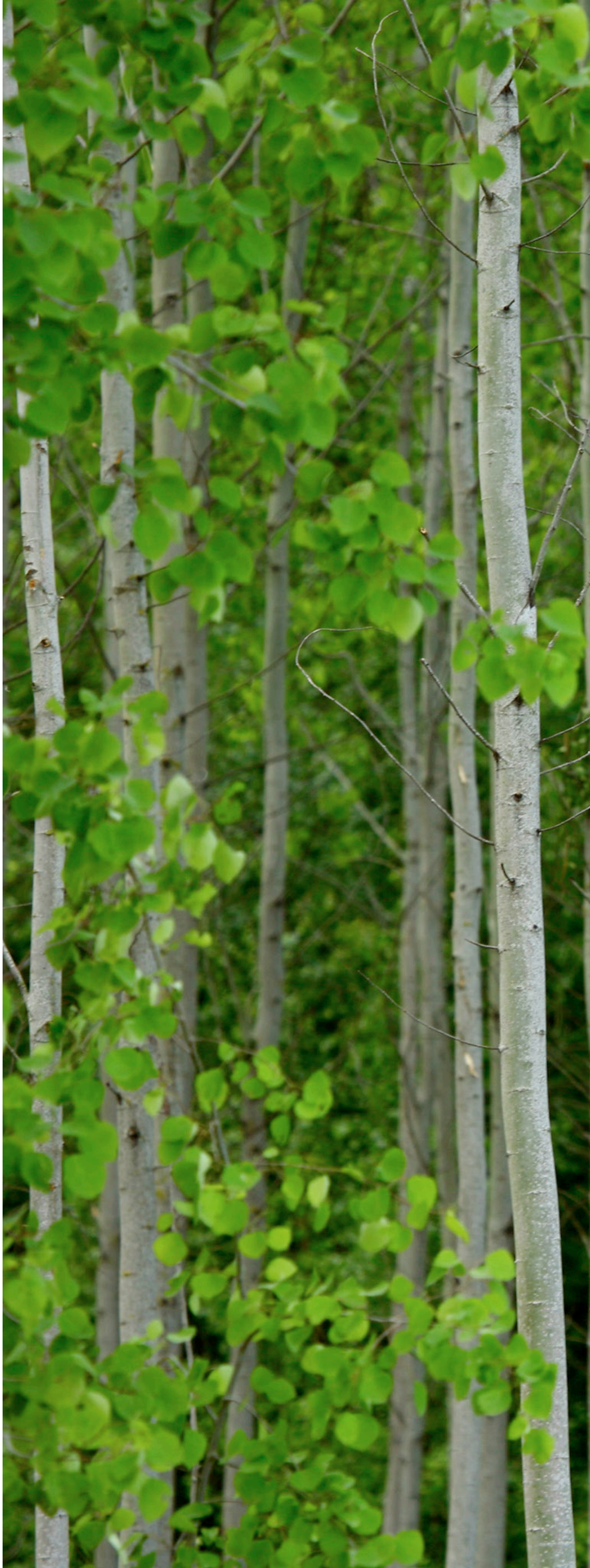
GENETIC DIVERSITY OF THE REGENERATION MATERIAL

Genetically improved material from seed orchards will most probably produce stands with genetic variation at least as high as in naturally regenerated stands (Lindgren 2010). From a landscape perspective, the genetic variation will be less for seed orchard material, especially when only a few orchards are used as the source for planting over vast areas. However, this decrease is considered to be small. The genetic diversity of vegetatively propagated material when using seed from many families (clonal bulk) is comparable with that from seed orchards (Sonesson et al. 2001, Rosvall & Lundström 2011).

LEGISLATION

There are different regulations, specific for each country, regulating the use of improved material, which have more or less impact on future growth potential. All regulations are within the general framework set by the European Union directive for Forest reproductive material (Anon. 1999). Nationally, for example, there may be restrictions on the minimum number of clones per stand when using vegetatively propagated material. Similarly, the scope for using non-native species may be restricted by national regulations or by forest certification organisations such as the FSC or PEFC. Such regulations are often modified over time and are difficult to foresee.

PHOTO: BJÖRN SVENSSON/SKOGENBILD



BREEDING STATUS

GENERAL

Breeding resources in the Scandinavian countries are focused on the commercially most important species i.e. Norway spruce *(Picea abies)* and Scots pine *(Pinus sylvestris)*. Other species having a more long-term breeding status are lodge-pole pine *(Pinus contorta)* in Sweden and silver birch *(Betula pendula)* in Sweden and Finland.

Minor and locally important species are included in short-term tree improvement programmes of less intensity, for example: Sitka spruce *(Picea sitchensis)*, grand fir *(Abies grandis)*, Douglas fir *(Pseudotsuga menziesii)*, larch *(Larix sibirica, L. decidua, L. kaempferi, L. eurolepis)*, alder *(Alnus glutinosa, A. incana)* aspen *(Populus tremula, P. tremuloides)*, poplars *(P. trichocarpa, P. maximowiczii)*, oak *(Quercus robur, Quercus petraea)*, beech *(Fagus sylvatica)*, ash *(Fraxinus excelsior)*, lime *(Tilia cordata)*, maple *(Acer platanoides)*, wild cherry *(Prunus avium)* and Lutz spruce *(Picea sitchensis x P. glauca)*.

The general breeding objectives for all species include high volume production and improved adaptation to various sites and climates and also, in most cases, high timber quality quality. The breeding objective traits and their relative importance depend on tree species and region. For instance, cold hardiness is the most important objective in the northern populations where conditions for forest production are considerably harsher than in the southern parts.

Note that the unit $m^3 ha^{-1}$ is henceforth used for yield and refers to the volume production of the stem if not otherwise specified.

INDIGENOUS CONIFERS

Norway spruce and Scots pine

SWEDEN

In Sweden, breeding of Norway spruce and Scots pine started in the 1940s and 1950s with phenotypic selection of plus-trees and establishment of seed orchards. The theoretical genetic gain for growth is estimated to be around 10% compared to unimproved material. Pollen contamination from unimproved trees reduces the gain to around 8%. These orchards still contribute a large part of the genetically improved plant production (Rosvall et al. 2001).

The breeding populations were expanded in the 1980s, with a large number of new plus-trees selected from young even-aged stands. For spruce, the selection was also perfor-med among seedlings in commercial forest nurseries, to be used in clonal tests. These new plus-trees, together with selection of the best progeny tested plus-trees from the previous selection, resulted in the second round of seed orchards. The genetic gain for growth in this case is estimated to be 10–15% in combination with increased survival and stem quality compared to unimproved stand seed sources.

Now, at the beginning of the 21st century, a third round of seed orchards is being established with the genetically best material (1.5 breeding generation material) based on results from genetic field tests. The predicted genetic gain for growth is estimated to be 20-25 %, along with increased survival, vitality, stem and branch quality (Rosvall et al. 2001). However, these orchards will not start to contribute to planting schemes until 2020 and will reach full produc-tivity around 2030 (Almquist et al. 2010). Meanwhile, the use of vegetative bulk propagation of Norway spruce selected families could provide a genetic gain in yield of 25-35%.

The drawback is a 50-100% higher cost for plants (Rosvall et al. 2001). Vegetative propagation of Scots pine is used for testing but will probably not be used for mass propagation (Högberg & Hajek 2011).

FINLAND

The founder material of breeding for all species in Finland comprises, in total, nearly 10 000 plus-trees, phenotypically selected in natural stands since the late 1940s. Almost 8000 of these are Norway spruce or Scots pine, Thousands of the plus-trees were grafted in the first generation of clonal seed orchards, which were established in the 1960s-1970s and cover 3300 hectares. Over the past decade, the collected crops of orchard seed have varied between 1500 and 6500 kg for Scots pine and between zero and 1500 kg for Norway spruce. Approximately 50% of around 160 million seedlings, currently produced annually by forest nurseries, originate from the first-generation orchards. Empirical results from field trials of Scots pine suggest that stem volume is 15% greater in seed orchard seed lots compared to stand seed lots at an age of 10-25 years and there is a slight improvement in branch characters (Westin & Haapanen 2013, Ruotsalainen & Persson 2013).

The first generation seed orchards are now being replaced by 1.5 generation elite seed orchards which include the 25-35 best progeny-tested plus-trees of each region. The first 1.5 generation orchards were established in 1997 and the replacement programme has now advanced more than half-way, amounting to 130 and 411 hectares of new seed orchards for Norway spruce and Scots pine, respectively. According to the state-financed forest seed procurement programme, some 900 hectares of elite seed orchards will be established by 2025. This target area is aimed at securing the supply of 1.5 generation seed for over 80% of the artificially regenerated area in Finland. So far, the new generation seed orchards have produced around 600 kg of seed, but the crops are rapidly increasing. The elite seed lots are estimated to yield genetic gains of approximately 25% in volume production.

In Finland, the seed crops from old Norway spruce seed orchards have fluctuated much due to poor flowering and extensive biological damage. This has resulted in serious shortages of orchard seed in some years. A research project on vegetative propagation of spruce based on somatic embryogenesis (SE) is now underway in close collaboration with commercial plant producers. Since the SE materials originate from controlled crosses between top-ranked plus-trees, the associated genetic gains are expected to exceed those of seed orchard material. So far no SE seedlings have been produced for commercial purposes.

DENMARK

Norway spruce breeding in Denmark started in the late 1960s and a breeding programme has been underway since the 1970s (Wellendorf 1988), but only limited activity has occurred since 2005.

Norway spruce is not a native species, although present in Danish forestry for more than 250 years (Larsen & Wellendorf 1997). Provenance research has been compulsory (e.g. Gøhrn 1966, Madsen 1989), and as such the breeding was founded on three subpopulations:

1) western European provenances;
2) domesticated, tested provenances; and
3) some sources of Romanian origin.

Seed orchards were established aimed at adaptation to varying site conditions based on

1) selections for fast growth and relatively short rotations in eastern Denmark and
2) slower growth in harsher western locations.

Breeding objectives include growth, vitality (adaptation, healthiness) and wood quality (density and spiral grain) using a nucleus strategy (Wellendorf et al. 1994, Wellendorf 1995).

An extensive rooted cutting propagation programme was developed during the late 1970s and 1980s. Despite good technical results and genetic gains, these cuttings were rarely used in forestry – mostly due to costs and conservatism.

General vitality problems started to occur in Norway spruce in the 1970s (Brandt 1976). During the late 1980s Ravensbeck (1991) documented provenance differences in severity of the so-called "red spruce damage" showing that east European sources were more prone to the syndrome. Today the forest industry benefits from the seed orchards established during the active period of the breeding programme, but due to political decisions relating to research and breeding funding, only limited activities have been going on since 2005. However, it is important to emphasise the potential for renewing a well-structured and documented programme to increase biomass production.

The genetic improvement of pines has been insignificant. Some limited activities have been undertaken to preserve and phenotypically select trees from superior provenances identified by provenance testing, for establishment of a few seed orchards.

NORWAY

The Norwegian seed orchard area for Norway spruce is presently 125 ha. This area can be divided into three rounds of selection and establishment: the first round includes 35 ha, the second 57 ha and the third 33 ha. The first round was established in the 1960s and 1970s and the second in the 1980s and 1990s, both based on phenotypic plus-tree selections in old natural stands. In total 7300 plus-trees have been selected and 3400 of these have been, or are being, progeny tested. The third round of seed orchards, based on 1.5 generation selections after progeny testing, started in the 1980s. This round will replace the older ones gradually, and second generation selections will, to an increasing extent, be introduced to increase genetic gain. The first harvest from about 30 ha of the third round seed orchards will be carried out in the near future.

Comparisons between stand seed checklots and the progeny from first and second round seed orchards show that genetic gain in volume production is about 10-15%. Based on genetic parameters and estimated breeding values, it is expected that genetic gain from the third round seed orchard seed will increase to around 20% for volume production together with a considerable improvement of stem form and branch characteristics. Seed orchards established with second generation selections are expected to have a genetic gain in volume production of 20-30%. Besides yield, stem quality traits are of great importance when selecting individuals for the new seed orchards and also for future advanced generation breeding programmes (Edvardsen et al. 2010).

Currently, there is no ongoing breeding programme for Scots pine in Norway. Previous activities have, based on phenotypic plus-tree selections from stands, resulted in the creation of 9.5 ha of first generation seed orchards in central Norway.

NON-NATIVE CONIFERS

Douglas fir

Douglas fir *(Pseudotsuga menziesii)* exhibits substantial genetic variation across several traits between and within provenances and stands. Sensitivity to frost during establishment is the most significant problem in northern Europe. Hansen (2007) showed that there are significant differences among seed sources in terms of frost damage sustained during artificial freezing tests.

Some breeding work on this species has been conducted in Denmark, where plant material derived from coastal provenances has been used (Hansen et al. 2005). Several seed orchards established with phenotypically selected plus-tree clones are in use in Denmark and could also be used in southern Sweden (Karlsson 2007).

A small tree breeding project was recently initiated in southern Sweden, including progeny tests of plus-trees selected in southern Scandinavia (Karlsson et al. 2010) aimed at the establishment of seed orchards.

Graft incompatibility is a serious problem in seed orchards. Early incompatibility results in the loss of grafts during the first years after grafting but can persist and become more severe after several years (Copes 1974).

The establishment of seedling seed orchards is one way to overcome this problem. Such seedlings should originate from tested and genetically well-defined seed sources. The best option would be full-sib families after controlled crosses between tested parent clones, and the plantation should be designed in a way that allows roughing between and within seed sources (Hansen et al. 2005).

Preliminary results from Danish yield trials comparing a set of tree species (Nielsen et al. 2014, Nord-Larsen pers. comm.) clearly indicate that the growth potential of Douglas fir exceeds that of Norway spruce and resembles Sitka spruce on medium to fertile soils.

Hansen et al. (2005) estimated a gain in volume production of approximately 30% at age 10 based on a breeding seed orchard concept, although emphasis was on yield as well as stem form. A conservative estimate is 10% gain in volume by extrapolating one-site results at age 10 to full rotation yield based on general use of the genetically improved seed material (Hansen et al. 2013).

Grand fir

Denmark is responsible for most of the genetic research on grand fir *(Abies grandis)* in northern Europe. However, this species deserves more attention due to its high potential for genetic improvement. To exploit this, it will be necessary to address the problem of high seedling mortality after planting.

Danish provenance experiments have been used to draft recommendations for reforestation material. The first generation grand fir stands established in Denmark have, to some extent, formed a landrace, i.e. an adaptation to the Danish climate, from which seed are available for commercial use (www.plantevalg.dk).

A series of three provenance trials (Madsen & Jørgensen 1986, Kromann 2003, Kroman & Hansen 2004, Hansen, J.K. unpublished 2015) resulted in recommendations for seed sources from the northern part of Washington State, especially the Olympic Peninsula or western Cascades and Vancouver Island in British Columbia. Danish domesticated stands exhibiting good performance are recommended as well. So far, no grafted seed orchards exist, but based on selections of superior trees in provenance trials, new seed orchards were grafted in spring 2014 (Hansen, J.K. unpublished 2015).

Preliminary results from Danish yield trials comparing a set of tree species (Nielsen et al. 2014, Nord-Larsen pers. Comm.) demonstrate the superior growth potential of grand fir and indicate an average biomass production of 15–18 tons dry matter per year at an age around 40 years (Nielsen et al. 2014). The production is still expected to increase as indicated by the shape of the growth curves. Jørgensen and Bergstedt (1998) found a mean stem volume growth at age 33 of about 20 m^3 ha^{-1} $year^{-1}$ (Hansen, J.K. unpublished 2015). Results from trials in protected fjord sites in Norway indicate yields of up to 30 m^3 ha^{-1} year-1 (Øyen et al. 2008, Øyen 2001).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Larch

Larch is mainly used in Sweden and Denmark today and it is primarily *Larix eurolepis*, i.e. the hybrid between L. *decidua* and L. *kaempferi*, that is of interest. The hybrid has exhibited higher growth than the parent species and also a high resistance to larch canker *(Lachnellula willkommii)*. In Finland and in the northern parts of Sweden and Norway the hardier L. *sibirica (succaczewii)* is preferred (Paques et al. 2013).

In Norway (Øyen et al. 2012) and Finland (Matti Haapanen pers. comm.), limited resources have been invested in larch breeding. There are two *Larix sibirica* seed

orchards in Norway and six in Finland, mainly including phenotypically selected material originating from the area around Arkhangelsk.

In Sweden and Denmark, basic larch breeding work, such as provenance testing, plus-tree selection, progeny testing and selection for establishment of seed orchards, has been carried out on a very small scale (Westin et al. 2015, Roulund 2007, Kiellander & Lindgren 1978, Keiding & Olsen 1965). Knowledge about larch is mainly based on research performed primarily during the 1950s and 1960s. Seed orchards are available for L. *eurolepis* and L. *kaempferi* in Sweden and Denmark and also for L. *sibirica* in northern Sweden.

Westin et al. (2015) have analysed prerequisites for operational larch breeding in Sweden. Results show large differences among provenances and plus-tree progeny of L. *decidua*, L. *kaempferi* and their hybrid (L. × *eurolepis*) (Pâques & Rozenberg 1995, Stener 2007a), indicating high breeding potential. In combination with an increasing interest by forest owners in planting larch, this will result in new resources for improvement activities.

Due to lack of relevant trials, it is difficult to estimate the genetic gain of the larch breeding carried out so far. However, new yield studies for *L. eurolepis* indicate an annual mean growth between 12.1 and 17.4 m^3 ha^{-1} $year^{-1}$ (Ekö et. al. 2015). The best hybrid seed orchards are probably in the upper end of this interval.

Seed orchards seem to be the basic option for plant production but seed production, so far, is quite limited and much lower than the demand. Thus, future resources must also focus on mass propagation and some progress has been reported for somatic embryogenesis recent years (Paques et al. 2013).

Lodgepole pine

Lodgepole pine *(Pinus contorta)* is by far the most planted non-native tree species in Swedish forests. Since its use peaked in the late 1980s, the annual planting area has decreased significantly. Now the species is increasing again but is legally restricted to the north of Sweden where it covers about 600 000 ha.

Unimproved plant material in Swedish forests has been estimated to be 30–40% superior to that of unimproved Scots pine regardless of site fertility, and its wood density is around 3% less than for Scots pine (Elfving & Norgren 1993, Elfving et al. 2001, Persson 2008). The reason for the better growth performance is mainly due to a high tolerance to low temperatures and less damage by moose, by snow blight *(Phacidium infestans)* and by twist rust *(Melampsora pinitorqua)*. On the other hand, lodgepole pine is more prone to damage by wind and snow than Scots pine (Elfving et al. 2001).

Significant breeding activities in Sweden began at the end of the 1970s with the initiation of a seed orchard programme. The programme included

1) plus-tree selection in Canada,
2) genetic testing of open-pollinated families in field tests in Sweden and
3) establishment of six seedling seed orchards for genetic roughing (Rosvall et al. 2001, Ericsson 1994).

The second round of seed orchards is now being established by grafts from selections in the progeny tests. High gain is attained by combining progeny tested old plus-trees (backward selection) with phenotypically tested young plus-trees (forward selection, within-family). The gain is estimated to be 23% compared with unimproved material. Rooted cuttings could provide plant material with 25–35% gain. In 15 years, after evaluation and selection in currently newly established clone tests, it is estimated that new seed orchards will deliver a 32–36% genetic gain in volume.

In Norway, lodgepole pine was also identified as an important species in the sub-alpine areas during the 1970s and 1980s, although focus suddenly changed in the 1990s towards natural regeneration of Scots pine. Provenance and progeny testing and establishment of a seedling seed orchard have been accomplished. Norwegian results confirm the superiority in growth compared to Scots pine and show, on average, 40% higher production (Magnesen 2001). Breeding in Norway will be focused on seedling seed orchards that have been roughed on the basis of individual tree performance in the orchard and family performance in parallel trials.

Activities in Finland are still being conducted at the provenance research level (Ruotsalainen & Velling 1993).

In Denmark, lodgepole pine is used for sites with very harsh conditions, where it exhibits quite good productivity. However it is considered an invasive species due to its abundant natural regeneration on sandy sites (Naturstyrelsen, 2014a).

Sitka spruce

Sitka spruce *(Picea sitchensis)* is mainly used in Denmark, south-western Sweden and Norway where its production exceeds that of Norway spruce.

The Danish Sitka spruce breeding programme is, besides that in Great Britain, the most ambitious in northern Europe and has demonstrated a considerable potential for improvements in biomass production. Hansen and Roulund (2011) predicted that the improved plant material of today will produce 30–50% more dry matter than unimproved material, resulting in an average production exceeding 20 tons dry matter of aboveground biomass ha^{-1} $year^{-1}$ during a 40-year rotation. In addition, Denmark is well prepared for the production of improved seed (Anon. 2006), not only for domestic use but also for use in southern Sweden.

In Sweden, there is a limited breeding programme based on phenotypic plus-tree selections in improved materials. Sitka spruce is well suited to the southern parts of Sweden, as indicated by substantial genetic variation in several traits and a superiority of 30% in volume production compared to unimproved sources of *Picea abies*. Seed orchards are being established (Karlsson 2007).

Data from southern Norway indicate yields of 14–26 m^3 ha^{-1} $year^{-1}$ for rotations of 80 years (Øyen 2005). There are two Sitka spruce seed orchards in Norway but no on-going breeding activities.

Sitka spruce is rather easy to propagate by rooted cuttings, which facilitates mass propagation of controlled crossings among selected parent trees. (Lee 2006). Some attempts were made in Denmark to produce rooted cuttings

from selected families (clonal bulks), but the commercial interest was low (Erik D. Kjær 2014, pers. comm.). In Sweden, rooted cuttings are produced when suitable seed sources are available (Johan Henriksson pers com).

Lutz spruce

The species hybrid between *Picea glauca* and *P. sitchensis* called Lutz spruce grows naturally in the western parts of British Columbia and Alaska, where the continental white spruce meets the coastal Sitka spruce populations. Lutz spruce is more frost hardy and has finer branching characteristics than Sitka spruce and has produced extremely high yields in northern latitudes in Norway. Artificial hybrid crossings and progeny tests have been performed in Norway and results show that genetic gain can be achieved by further breeding (Øyen et al. 2012, Steffenrem & Skaret 2015). A seedling seed orchard is now established based on this material, and there are also plans for clonal seed orchards based on second generation selections from the progeny trials.

INDIGENOUS BROADLEAVED SPECIES

Birch

The most intensive breeding programme for birch is in Finland (Koski & Rousi 2005) and has been in progress on a continuous basis since the 1960s. The main focus is on *Betula pendula*, for which breeding is carried out in the southern part of Finland. *B. pubescens* has also been on the breeding agenda but it is no longer a subject of active breeding. There are two breeding zones for *B. pendula*, each comprising a breeding population of 160 trees (Haapanen & Mikola 2008). Mass production of improved birch seed is carried out in greenhouse seed orchards. Genetic gain in growth has been estimated to be around 30%, along with improvements in stem quality relative to unimproved plant materials (Hagquist & Hahl 1998).

Long-term breeding of silver birch is also carried out in Sweden. A Swedish indoor seed orchard at Skogforsk Ekebo has been estimated to deliver a 15% genetic gain in growth and better stem quality than unimproved material (Rosvall et al. 2001).

Extensive activities have been undertaken in Denmark and during 2007–2009 breeding seed orchards of both *B. pubescens* and *B. pendula* were established.

Vegetatively propagated plants for commercial use are an alternative to seedlings, and were used in Finland for a short period in the 1990s. However, this project was terminated due to high propagation costs.

Other birch species have also been tested in field trials. Results from 20-year-old trials in southern Sweden, including *B. pendula, B. papyrifera, B. pubescens, B. lutea* and their hybrids, indicate that *B. pendula* is the best choice in the long-run (Högberg 1986).

Alder

Genetic improvements in alder have been limited, but activities have so far resulted in the establishment of seed orchards for black alder *(Alnus glutinosa)* in all Scandinavian countries.

Recent studies of black alder have shown considerable selection effects (Stener 2007b, Alfas Pliura, Lithuania, pers. comm.). For instance, growth was increased by 18% when selecting the best 10% fraction of a 125 plus-tree population, which is similar to the gain estimates for silver birch (Stener & Jansson 2005).

Grey alder *(A. incana)* is probably a better option for biomass production due to its fast initial growth and good ability to regenerate by root suckers. It is highly likely that grey alder has a similar breeding potential to black alder. A grey alder project including selection of plus-trees and establishment of progeny tests was initiated in Sweden in 2013, aimed at intensive cultivation for bioenergy production.

The hybrid between *A. glutinosa* and *A. rubra* may be an interesting future alternative. Results from two nine year old trials in southern Sweden demonstrated a 50% higher growth compared to *A. glutinosa* (Stener 2007b). However, very little is known about this hybrid and commercial material is not yet available. Vegetative propagation of the best clones within the best families is a possible option.

"Noble" broadleaved species

The breeding work with noble species such as oak *(Quercus robur, Quercus petraea)*, beech *(Fagus sylvatica)*, ash *(Fraxinus excelsior)*, lime *(Tilia cordata)*, maple *(Acer platanoides)* and wild cherry *(Prunus avium)* has been rather limited, and consists mainly of phenotypic plus-tree selections for establishment of grafted seed orchards (Sweden) or seedling seed orchards (Denmark) (Jensen 2000).

These species are managed for long rotations, with the aim of producing valuable timber trees. The long rotation times, high establishment costs, and relatively low yields suggest that they should not be planted with the primary purpose of biomass production.

NON-NATIVE BROADLEAVED SPECIES

Poplars

Species within the genus *Populus* are among the highest yielding trees that are adapted to temperate climates, especially when considering the rotation time, while some of the conifers may, over a longer time span, be equal or superior. With the exception of *P. tremula*, poplars are introduced species in Scandinavia, i.e. they are not naturally adapted to the local climate. The challenge, therefore, is to find clones that are climatically adapted and also exhibit

high biomass production with acceptable stem quality and tolerance to abiotic and biotic stresses. Greatest interest is placed on hybrids between *P. tremula* and *P. tremuloides* and single species or hybrids of *P. trichocarpa* and *P. maximowiczii*.

The improvement of hybrid aspen *(P. tremula × P. tremuloides)* has been performed discontinuously in Scandinavia but most work originates in Sweden and Finland (Stener & Karlsson 2004, Yu 2001). In southern Sweden and Finland clonal tests of phenotypically selected plus-trees of hybrid aspen were established in the 1980s and 1990s, from which the best clones were selected for plant production. Growth is estimated to be 20–25 m^3 ha^{-1} $year^{-1}$, equivalent to 8–10 tons of dry matter per ha and year on fertile soils during a 20–25 year rotation time in southern Sweden (Rytter & Stener 2014).

Improvement of other poplars *(P. trichocarpa, P. maximowiczii)* has been very limited in Scandinavia and mainly consists of testing clones selected in other European improvement programmes. Most work has been carried out in southern Sweden, where tests of 140 clones of different species and hybrids were established in 1991 (Stener, 2010). The 12 best clones were selected for mass propagation for use on mild, fertile sites in southern Sweden. Growth is estimated to be slightly better than that of hybrid aspen.

In a recent Danish study, 36 clones were tested, most of them used in Europe, indicating superiority for hybrids between *P. maximowiczii* and *P. trichocarpa* and selections within *P. trichocarpa*. The hybrid OP42 produced around 9 tons of dry matter per year after 13 years, equivalent to 26 m^3 ha^{-1} $year^{-1}$ (Nielsen et al. 2014).

Other broadleaved species

Sycamore *(Acer pseudoplatanus)* was introduced from continental Europe and, due to its rather high yield and ability for self-regeneration, is interesting for forestry. However, the latter characteristic also makes it controversial from an environmental point of view. It occurs in limited amounts in southern Sweden and in Denmark. Seedling seed orchards of Sycamore have been established in Denmark aiming to improve growth and external stem quality, mainly stem straightness. Apart from this, there are no plans for improvement activities.

Red oak *(Quercus borealis)* is a North American species which is used to a very limited extent in Scandinavia. It is characterised by a growth rate comparable with *Q. robur*, it is quite hardy and has moderate site requirements, thus presents an interesting option. Limited breeding activities, such as plus-tree selection, have started in Sweden.

POTENTIAL INCREASES IN GROWTH THROUGH BREEDING

GENERAL

Estimates of genetic gain and commercial availability of different types of material for years 2014 and 2050 are presented in Table 1 for different species and regions of the Scandinavian countries.

The total number of used plants (in millions) of each species and within each region are presented as relative figures (%) for different breeding levels (unimproved, provenances, seed orchards and vegetative propagation). Estimates of mean annual yield (volume in m^3 ha^{-1} and dry matter in ton ha^{-1}) at the specified rotation time, are shown for the unimproved material. That level is the basis on which the relative genetic gain is calculated. The yield in volume and dry matter production refers to the stem biomass, except for broad-leaved species in Denmark where, traditionally, both stem and branches are included.

The annual dry matter yield (ton ha^{-1}) was estimated by multiplying volume yield by the basic density in Table 2 from Rytter et al. (2014).

The reference yield is estimated based on current knowledge, which may be limited for many species and for some species refers to only a few field trials. Since the estimates may have been performed differently in each country, it is important to read the comments relating to each country in the following sections.

Genetic gain for yield in Table 1 refers to realised gain after reduction for unimproved pollen contamination in seed orchards. Furthermore, ”genetic gain” is used in a broad sense and comprises all differences between materials that can be explained by the genetic source. Seed orchards are the most common delivery system of genetic gain from selection from breeding based on additive genetic variation. However, characteristics typical of seed orchards such as reduced inbreeding and localisation in warmer environments (Skrøppa et al. 2007, Johnsen et al. 2009) often also have positive effects on growth and will then be confounded with the pure effects of selection.

Most of the estimates of genetic gain were derived from measurements in rather young field trials. Reliable estimates of genetic gain require that relevant materials are compared in designed field trials replicated in a number of environments over a substantial part of a rotation. Most field trials are still too young to provide verification of the development of genetic gains in stand-level yield for a full rotation.

MAJOR RESULT – ALL COUNTRIES

The number of plants of Norway spruce and Scots pine used annually amounts to around 350, 170 and 30 millions in Sweden, Finland and Norway respectively and corresponds to 94-99 % of the total number of plants used (including all species). Denmark is in this respect a small country where a total of around 10 million plants are used annually, of which roughly 50% is oak and beech.

Seed from seed orchards is, and will within the next decades, be the dominant way to supply forestry with genetically improved plant material. Figure 3 illustrates the percentage of the total number of plants of Norway spruce and Scots pine used that originate from seed orchards as well as the realised genetic gain. The extra gain in yield obtained by using material from existing seed orchards is currently, on average, 10–15% when compared to local unimproved material. In 2050 it is estimated that this gain will be 20–25% and together with increased use of improved plants, this will result in a substantial increase in productivity.

An alternative to seed orchards of Norway spruce is to use plants produced by vegetative propagation of genetically well-performing individuals, which makes it possible to capture the progress from breeding immediately. Using clones of Norway spruce could immediately provide a gain of 25–35% in yield, which, it has been estimated, will increase to 40% by 2050.

Some species are more productive than Scots pine and Norway spruce if used in Scandinavia (Table 1). However, their contribution to the overall regional increase in production is and will be small in relative terms, when compared to the two main species, due to their limited use in Scandinavian forestry.

Table 1. Plant deployment for different species, countries and regions for material of varying breeding levels (unimproved, provenances, seed orchards and vegetative, i.e. clonal material) and estimations of average realized genetic gain (%) based on current knowledge for years 2014 and 2050. Genetic gain (%) is related to the annual mean volume and dry matter (DM) production of stems (m^3 ha^{-1} and DM ton ha^{-1}) for unimproved material for which mean rotation periods are presented as well. The columns of "utilisation of the no of plants used" adds up to 100% for the four types of material within each period. See sections "Comments to data in table 1" and Appendix 1-2 for detailed information. Note that yield in m^3 ha^{-1} $year^{-1}$ normally only includes the stem volume, except for broad-leaved species in Denmark, where branches are included as well .

Species / Country		Region	Today (Year 2014)											Year 2050							
			No of pl.	Unimproved (reference level)				Provenances		Seed orchards		Vegetative propagation		No of pl.	Unimproved	Provenances		Seed orchards		Vegetative propagation	
			Total plants used, millions per year	Yield, m^3 ha^{-1} $year^{-1}$	Yield, DM ton ha^{-1} $year^{-1}$	Rotation time, years	Utilisation, % of the total no of plants used	Genetic gain, %	Utilisation, % of the total no of plants used	Genetic gain, %	Utilisation, % of the total no of plants used	Genetic gain, %	Utilisation, % of the total no of plants used	Total plants used, millions per year	Utilisation, % of the total no of plants used	Genetic gain, %	Utilisation, % of the total no of plants used	Genetic gain, %	Utilisation, % of the total no of plants used	Genetic gain, %	Utilisation, % of the total no of plants used
Sweden																					
Scots pine	Pinus sylvestris	North	97	3.3	1.37	100	2%	2	8%	12	90%			110				23	100%		
		Central	26	4.9	2.03	80				10	100%			40				21	100%		
		South	15	5.3	2.22	70				10	100%			15				21	100%		
Norway spruce	Picea abies	North	50	3.4	1.29	90		8	10%	9	90%			50				21	95%	40	5%
		Central	45	7.6	2.90	70		8	20%	9	80%			45				17	95%	40	5%
		South	120	10.0	3.82	55	2%	8	33%	12	64%	25	1%	120				21	95%	40	5%
Sitka spruce	Picea sitchensis	South	2.0	12.5	4.63	50				40	100%			5				50	100%		
Grand fir	Abies grandis	South	0.1	21.0	6.41	60	100%							3		25	70%	30	30%		
Douglas fir	Pseudotsuga menziesii	South	0.1	15.0	6.15	80				8	100%			5				15	100%		
Sibirian larch	Larix.sibirica	North	2.0	4.0	1.88	80				10	100%			5				20	100%		
Sibirian larch	Larix.sibirica	Central	0.5	5.9	2.81	70				10	100%			2				20	100%		
Hybrid larch	Larix eurolepis	South	2.0	12.0	4.93	40				30	100%			5				40	100%		
Lodgepole pine	Pinus contorta	North	13	4.6	1.70	80				10	100%			20				25	100%		
		Central	3.0	6.9	2.55	60				10	100%			5				25	100%		
		South																			
Silver birch	Betula pendula	North	0.1	3.0	1.45	80								1				15	100%		
		Central	0.5	7.0	3.38	60				25	100%			2				35	100%		
		South	0.9	8.0	3.86	50				15	100%			3				30	100%		
Black alder	Alnus glutinosa	South	0.1	9.0	3.33	35				10	100%			1				20	100%		
Poplar sp	Poplars sp.	North		12.0	3.96	35								0.5						35	100%
		Central		16.0	5.28	25								1						50	100%
		South	0.7	16.0	5.28	25						45	100%	3						70	100%
Oak	Quercus robur	Central	0.1	3.9	2.24	150	100%							1	100%						
		South	0.2	5.2	2.99	130	90%			10	10%			2	80%			15	20%		
Beech	Fagus sylvatica	South	0.1	6.3	3.59	120	70%			10	30%			2	80%			15	20%		
Finland																					
Scots pine	Pinus sylvestris	North	27	2.0	0.83	100	80%			15	20%			27	55%			25	45%		
		South	23	5.0	2.08	70	25%			15	75%			33	30%			25	70%		
Norway spruce	Picea abies	North	20	3.0	1.14	100	90%			10	10%			16	20%			20	80%	30	
		South	100	7.0	2.66	70	40%	5	10%	10	50%			140	5%			20	70%	35	25%
Silver birch	Betula pendula	North	0.6	3.0	1.45	80	30%			10	70%			1.6	20%			20	80%		
		South	3.7	7.0	3.38	60	5%			25	95%			14	5%			35	85%	50	10%
Hybrid aspen	P. tremula x P.tremuloides	South	0.1	16.0	5.28	30						40	100%	5						70	100%
Norway																					
Scots pine	Pinus sylvestris	North	0.1	1.5	0.62	140	100%							0.05	100%						
		Central	0.1	2.3	0.95	130	50%			10	50%			0.1	50%			10	50%		
		West	0.2	3.3	1.37	130	100%							0.2	100%						
		South	0.4	3.5	1.45	120	100%							0.5	100%						
Norway spruce	Picea abies	North	1.3	4.0	1.52	110	80%			15	20%			1	5%			20	95%		
		Central	5.0	4.4	1.67	105	80%			15	20%			5	5%			20	95%		
		West	1.7	8.5	3.23	85		30	100%					5				20	100%		
		South	22	5.2	1.98	100	10%			13	90%			30	5%			20	95%		
Sitka spruce	Picea sitchensis	North	0.01	12.0	4.44	70	100%														
		Central	0.01	14.0	5.18	60	100%							0.1	50%	5	50%				
		West	0.04	18.0	6.66	60	100%							0.5	25%	5	25%	15	50%		
Lutz spruce	P glauca x P sitchensis	North	0.05	9.0	3.33	80	100%							0.5				20	100%		
Denmark																					
Scots pine	Pinus sylvestris	All	1.2	7.0	2.91	70	5%			<2	95%			1.2				<2	100%		
Norway spruce	Picea abies	All	0.8	18.0	6.84	50		8	10%	8	90%			0.8				10	100%		
Sitka spruce	Picea sitchensis	All	0.6	17.0	6.29	45		30	20%	40	80%			0.6				40	100%		
Grand fir	Abies grandis	All	0.02	21.0	6.41	50		20	100%					0.02		25	70%	30	30%		
Douglas fir	Pseudotsuga menziesii	All	0.7	17.0	6.97	80		8	75%	8	25%			0.7		8	75%	10	25%		
Larch	Larix ssp.	All	1.2	13.0	5.34	50	5%	10		60	95%			1.2				80	100%		
Poplars	Poplars sp.	All	0.4	16.0	5.28	25						55	100%	0.4						70	100%
Oak	Quercus robur/petraea	All	2.6	6.0	3.45	120	40%	10	60%					2.6	40%			16	60%		
Beech	Fagus sylvatica	All	2.5	10.0	5.70	110	90%	6	10%					2.5	50%	9	50%				

Table 2. Basic density of dry matter (DM) stem wood including bark for different species in northern Europe. From Rytter et al. (2014) and Thomas Nord-Larsen (pers. comm.).

Tree species	Basic density (kg DM m^{-3})	References
Norway spruce	380	Hakkila 1979, Moltesen 1988, Lundgren & Persson 2002
Scots pine	415	Hakkila 1979, Moltesen 1988
Siberian larch	476	Pâcques 2004
Hybrid larch	411	Chauret & Zhang 2002
Birch	483	Hakkila 1979
Poplars, hybrid aspen	330	Stener, 2010
Oak	575	Sveriges Skogsvårdsförbund 1994, Moltesen 1988
Black alder	370	Sveriges Skogsvårdsförbund 1986
Grand fir	305	Danish unpubl. preliminary data (Thomas Nord-Larsen)
Beech	570	Sveriges Skogsvårdsförbund 1994, Moltesen 1988
Sitka spruce	370	Moltesen 1988
Douglas fir	410	Moltesen 1988
Lodgepole pine	370	Moltesen 1988

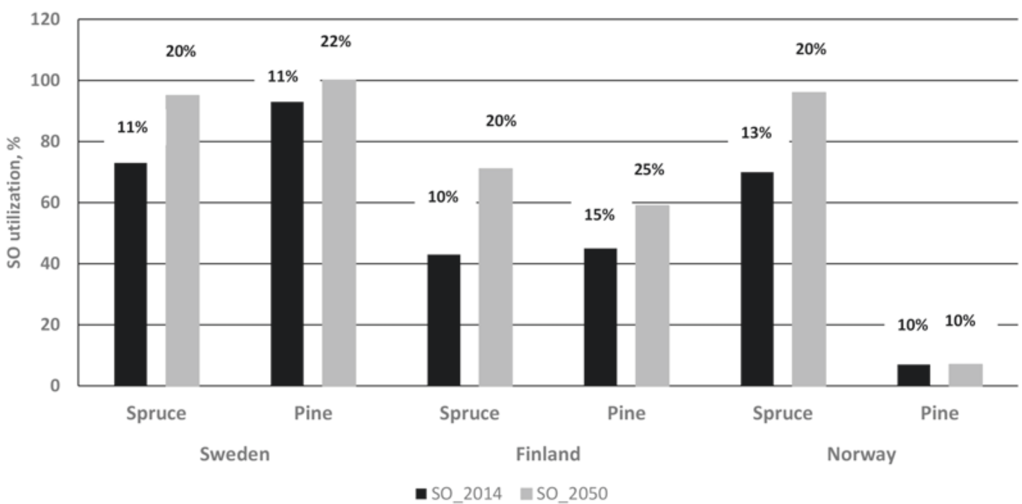

Figure 3. Proportion of plants used per year originating from seed orchards (SO) in 2014 (black bars) and 2050 (grey bars) for Norway spruce and Scots pine in three countries. The percentage value above each bar represents the estimated realised genetic gain for volume production.

Table 3. Number (millions) of plants sold for reforestation for different species and the distribution (%) of their origin in 2013 (Anon, 2014). "SO" = Seed Orchard. "Other conifers" mainly comprises hybrid larch and Sitka spruce.

	Norway spruce	Scots pine	Lodgepole pine	Other conifers	Birch	Other broad leaved	Total
Plants sold, millions	216	138	16	7	1.4	2.5	381
Origin, %							
Swedish stands	12	8	10	5	0	6	10
Foreign stands	13	0	0	9	4	54	8
Swedish SO	69	91	90	31	46	10	77
Foreign SO	5	0	0	47	29	7	4
No information	0	0	0	8	22	23	0
Total	**100**	**100**	**100**	**100**	**100**	**100**	**100**

SWEDEN

General

In recent years, 380 million plants have been planted in Swedish forests. The major part consists of Norway spruce and Scots pine and the proportion of broadleaved species and other conifers besides lodgepole pine is small (Table 3).

The high growth potential of improved material has led to an increased demand for improved seed over time. Today around 90% of the Scots pine plants and nearly 70% of the Norway spruce plants originate from Swedish seed orchards.

Seed orchards will be the main source for the production of genetically improved material for a long time ahead. However, the supply of improved seed is limited. Analysis of seed supply has shown that there is a shortage of spruce in the southern parts of Sweden (Almqvist et al. 2010). The situation will improve over time when new seed orchards start producing seeds, but the supply will not meet the demand of spruce seed until around 2030. This unbalance is handled by extending the utilisation time of older seed orchards with less genetic gain. For Scots pine there is currently a shortage of improved seed in the very north, which will be taken care of around 2020, while other regions are in balance or have a surplus. However, for both species, new seed orchards have to be established in the near future to avoid a shortage in the 2040s and later. Thus, seed orchard establishment should be carried out along with progress in breeding.

The shortage of Norway spruce seed can, in the short term, be solved, at quite a low marginal cost, by more intensive management and using methods that promote flowering and limit seed-destroying insects in the seed orchards. Importing surplus seed from seed orchards in north-eastern Europe (the Baltic countries, Poland, Belarus) is another alternative to overcome the lack of seed. A more efficient option is to increase the use of vegetative propagation (bulked cuttings), since the genetic gain will be higher (see section ”Vegetative propagation”).

According to the latest National forest growth and yield forecast (Anon. 2008), the increase in yield through using improved material is estimated to be 7–8% during the period 2060–2100. This scenario was based on estimates involving a shortage of improved material the next 30 years (see above). If this deficit could be covered, the increase in yield by breeding would be 10%, i.e. around 11 million m^3 (Rosvall & Lundström 2011). If vegetatively propagated Norway spruce plants were gradually used on 5% of the annual regeneration area, which today is the maximum utilisation permitted by the Swedish forest regulations, then growth would increase by an additional 1%. If vegetatively propagated spruce was used more widely, eliminating the 15–20 year period until the genetic gain from new seed orchards can be realised, another 1%, i.e. a total 12% yield increase would be possible.

These figures are more easily understood when compared to other yield-increasing actions. Planting lodgepole pine instead of Scots pine, on the permitted maximum 14 000 ha per year, would give an increase of 1% and traditional forest fertilisation a 1–4% increase, depending on intensity. However, fertilisation requires annual investments of hundreds of millions of SEK while the surplus cost for genetically improved plants is negligible, at least for seed orchard material.

Comments on the data in table 1

Plant utilisation

Based on rough estimates, the number of utilised plants from different types of material across the whole of Sweden (Table 2) for the different species and regions is presented in Table 1, where North = ”Norrland”, Central = ”Svealand” and South = ”Götaland”.

Calculations of the future plant utilisation of spruce and pine were mainly based on estimates by Rosvall & Wennström (2008). Estimates relating to the future are, of course, difficult but increased planting has been the general trend since 1996 in Swedish forestry, while natural regeneration has decreased and sowing has increased (Anon. 2014). Shorter rotation times as a result of using material with higher genetic gain indicates an increasing demand for plants in the future. On the other hand, there is also increasing interest in continuous cover forestry management, in which natural regeneration is used. This, in combination with improved site preparation, may lead to a reduction in the number of planted seedlings per ha.

Predicting demand for species other than spruce and pine is even more difficult. It is highly likely that the increasing interest in intensive biomass production and modified management due to climate change will favour species such as Sitka spruce, hybrid larch, grand fir and poplars. Even so, the main biomass increase from breeding will be achieved from spruce and pine due to their large proportions of the total forested area.

Yield and genetic gain

The genetic gain in yield in this report was, in general, based on Rosvall et al. (2001), where genetic gain from present and future seed orchards and clonal mixes is presented. The genetic gain is related to a reference level which is defined as the yield for unimproved stand material. Knowledge of yield in Swedish conditions over a total rotation time is quite poor for many of the species. In addition, the exotic conifer and poplar species are not domestic, making a reference level hard to define, especially since the basic material used for yield studies are quite limited and often includes provenances or clones that are not climatically well adapted. However, in order to present the results in a consistent way, we have estimated a reference level for all species in the best possible way.

It is important to stress that the estimates of a reference yield for Scots pine and Norway spruce are made at regional level, while the yield for the other species often refers to a rather limited number of successful stands and survey plots with restricted geographic distribution. In Appendix 1, there is detailed information relating to the estimates in table 1.

FINLAND

Comments on the data in table 1

Plant utilisation

The number of plants sold today is based on the official statistics published on the internet by the Finnish Food Authority (Evira, www.evira.fi). The corresponding figures for 2050 are based on projections of future reforestation areas as presented in the revision of the current seed orchard programme (Anon. 2011). The figures relating to the present relative proportions of seed orchard versus non-improved plants were derived from the figures published in the Finnish Statistical Yearbooks of Forestry (Anon. 2012) and by Evira (www.evira.fi) using approximate averages over a number of years. Professional guesses were used to compensate for the lack of available statistics. For instance, the figures for "South" and "North" should be taken as approximations as there are generally no separate statistics for such loosely defined regions.

Yield and Genetic gain

The estimates of genetic gain are based on results from realised genetic gain trials and progeny trials (mostly Scots pine and Silver birch) measured for height and diameter growth traits at age 10–30 years. Some estimates have been published (Hagqvist & Hahl 1998, Ruotsalainen & Nikkanen 1998), whereas others are based on unpublished data. The estimates derived from realised gain trials usually comprise commercial orchard seed lots (mixtures of open-pollinated families of phenotypically selected parents) which means that the reduction in genetic gain due to pollen contamination has already been taken into account in the estimates.

DENMARK

General

Danish forestry has a long tradition of introducing and testing exotic plant material, especially conifers. The native forest contains a variety of broadleaved species, whilst the main commercial species are beech *(Fagus sylvatica)* and oak *(Quercus robur* and *Q. petraea*), and until recently ash *(Fraxinus excelsior)*, which has declined due to ash dieback.

The State Tree Improvement Station, now the Danish Nature Agency, initiated an improvement programme in the late 1980s aimed at supplying 75% percent of the Danish demand for forest seed of conifers and 50% of broadleaved tree species, with the best possible seed. This has resulted in a total of more than 200 ha of seed stands and seed orchards (Anon. 2000). In addition, private forest owners and seed companies also supply seed from approved Danish stands and private seed orchards (see www.plantevalg.dk).

The State improvement programme was developed in close cooperation with researchers at the Arboretum Hørsholm and Forest and Landscape Denmark (now the Institute for Geology and Natural Resource Management, University of Copenhagen) as well as private forest owners and the State forest.

In 2005, the majority of breeding activities relating to conifers were stopped, due to political priorities and economic restrictions, and only low intensity breeding of broadleaved forest trees continued. At that time, the already established progeny trials and clonal material were preserved as well as possible. However, over time many of the progeny trials and clone archives have deteriorated. Therefore, present forest tree "breeding" in Denmark is largely a poor legacy of past breeding activities, from which one can only expect sparse improvements by 2050. "Breeding" will presumably be limited to occasional establishment of new and replacement of old orchards. Ambitious political goals for a substantial reduction in Danish fossil fuel consumption and replacing fossil fuel by biomass (Energistyrelsen 2010, European Commission 2007) have, to date, not led to any renewal of breeding activities in Denmark.

Hansen et al. (2013) and Hansen (2011) have documented a series of easy "tree-improvement activities" based on the preserved improved material. There is, for instance, a potential gain of 30–50% in volume production for Sitka spruce by using elite material from tested clones, either from the establishment of seed orchards, and/or vegetative bulk propagation of seed from top-crosses based on hedge-cutting-systems (Hansen, unpublished data or op cit.).

Furthermore, Graudal et al. (2013) analysed the impact on potential biomass and timber production as well as carbon storage from a set of forest management scenarios. Based on these model calculations, tree breeding in combination with extended use of nurse trees could improve production substantially, even from the perspective of 2050. It has been estimated that full-scale implementation of nurse trees and breeding would increase harvestable biomass by 19% in 2050 compared to current yields (Graudal op. cit. table 3.3). In addition, it was estimated that intensive breeding and full scale implementation of the use of improved material would increase the total production in Danish forest by 3% in year 2050.

Comments on the data in table 1

Plant utilisation

The most recent information about plant utilisation in Danish forestry was published by Jensen et al. (2001). The Danish State forest used a total of 4.4 million plants, from 1985 to 1998, excluding the *Abies* species, Noble fir and Nordmann fir, which are only used for greenery and bough production (Jensen et al. 2001).

Recent statistics from the Danish Nature Agency (Naturstyrelsen, unpublished) for the period 2000 to 2013 indicate a remarkable reduction to 1.5 million plants per year in the State forest. The State forest constitutes around 112,000 ha and the total forested area in Denmark is around 615,000 ha (Nord-Larsen et al. 2014). This means, that, on average, for the years 2000 to 2013, the annual use by the State forest was estimated to be 2.3 million plants, and the total countrywide consumption 12.6 million plants. A strategic change in silviculture in State owned forests towards natural regeneration can partly explain the drop in plant use (Skov og Naturstyrelsen 2002). No statistics are presented for use in private forests, but presumably it has been less influenced by the change in public forest silviculture, so the countrywide estimate of 12.6 million plants per year is conservative.

Another attempt to estimate the plant demand was based on the yearly cultivation area (Jensen et al. 2001) indicating a slightly higher use, but still of the same magnitude.

An annual average increase in the Danish forest area resulting from reforestation of farmland, amounting to approximately 1900 ha (Graudal et al. 2013), alone would consume around 4–8 million plants (based on 2000 to 4000 plants/ha). Still, the plant consumption in 2050 is presumed to be of the same magnitude as today.

Yield

The reference level for unimproved material can be based on data from the Danish National Forest Inventory (NFI). One disadvantage with such data is the influence on mean yield caused by current demography of the forests, present age class distribution, differences in site fertilities etc. (Nord-Larsen 2015, unpublished data). The mean yield is also affected by the genetic origin of the material such as provenances and genetically improved material (only conifers). The actual production level of the Danish forest according to NFI is presented in table 4.

Production estimates may also be obtained from experimental data, but extending those results to nationwide average growth may introduce large errors and a substantial set of assumptions. Direct yield comparisons of tree species are difficult even on experimental lots at the same site due to different rotation times, especially for the broadleaves. However, such data is available from a Danish nationwide series of field trials comparing Norway spruce, Sitka spruce, grand fir, Douglas fir, Japanese larch, Scots pine, oak and beech at 13 locations (Nord-Larsen, unpublished 2015). These trials were established in 1965 and the most recent analyses refer to assessments from spring 2013, i.e. after 48 years of field testing. This is a time span approaching the rotation age for conifers, but only half that of broadleaves. The timber producing conifers in Denmark are exotic tree species and defining an unimproved level is very difficult.

Table 4. Mean yield data based on results from the Danish NFI. Volume refers to stem volume for conifers and to total volume, i.e. including stem and branches for broadleaved species. The total dry matter (DM) biomass production including branches for all species, was estimated from biomass equations. Norway spruce: Skovsgaard et al. 2011. Sitka spruce, grand fir, Douglas fir and larch: Nord-Larsen & Nielsen 2014. Beech: Skovsgaard & Nord-Larsen 2012. For oak and pine, a two-step procedure was used, estimating total aboveground volume production multiplied by density (oak 570 and pine 480 kg dry matter/m^3).

Tree species		Yield, Volume m^3 ha^{-1} $year^{-1}$	Yield, DM ton ha^{-1} $year^{-1}$
Norway spruce	*Picea abies*	18.2	6.9
Sitka spruce	*Picea sitchensis*	15.1	5.6
Grand fir	*Abies grandis*	14.3	4.4
Douglas fir	*Pseudotsuga menziesii*	12.5	5.1
Larch	*Larix spp.*	9.4	4.0
Scots pine	*Pinus sylvestris*	7.8	3.2
Oak	*Quercus robur/petraea*	5.9	3.3
Beech	*Fagus sylvatica*	13.3	7.5

Provenance trials comparing seed sources from a wide range of the natural distribution area could, in principle, be used for defining a reference level as the mean of the imported provenances, which works for Sitka spruce and grand fir.

However, Norway spruce has a more than 200 year history in Denmark and the North American conifers have been grown for about 150 years, and have, to a certain extent, been domesticated. Thus, seed material from naturally adapted Danish stands has been used along with continued imports from the original source of provenances. The tree species trial was established in 1965 and the seed sources used reflect what was used in Danish forestry at the time.

The production reference levels given in table 1 are commented upon in Appendix 2 by comparing the results from the experimental lots established in 1965 and the NFI data.

Genetic gain

The state improvement programme for forest trees is closed today. Some activities, such as establishment of new seed orchards, are still carried out by HedeDanmark and a few other private companies, but based on results from former breeding activities. Therefore, the increase in predicted gains for forest production in 2050 will be small in relation to the present situation. However the rather few, although newly established, orchards will presumably be extensively used in future plantations due to their higher genetic gain.

Average gain estimates for each species based on the present status of these 'upcoming' orchards refers mostly to Seed Orchard letters (Naturstyrelsen 2014b) and to unpublished data from the Department of Geosciences and Natural Resource Management at the University of Copenhagen (Jon Kehlet Hansen, pers. comm.).
The state tree improvement programme (Anon. 2000) aimed to supply 75% of improved material from orchards and improved seed stands, but demand changed over time due to an increase in reliance on natural regeneration in State forests. Thus, for the genetically improved species Norway spruce, Sitka spruce and hybrid larch, the potential supply is presumably closer to 100%.

Detailed information on the genetic gain estimates for each species are given in Appendix 2.

NORWAY

Comments on the data in table 1

Plant utilisation and reference yields

The present number of plants sold for commercial use has been estimated from data provided by the Norwegian Forest Seed Center and this data has then been extrapolated to 2050, based on political aims.

The Norwegian regions in Table 1 are based on counties being grouped as follows:

North: Nordland, Troms and Finnmark.

Central: Southern and northern Trøndelag.

West: Rogaland, Hordaland, Sogn and Fjordane, Møre and Romsdal.

South: Vest-Agder, Aust-Agder, Telemark, Buskerud, Oppland, Vestfold, Akershus, Oslo, Hedmark and Østfold.

Reference yields for Scots pine and Norway spruce are based on the mean site index provided by the National Forest Inventory (NFI) for the period 2009-2013 (A. Granhus, NFI, pers. comm. 2014) and are most probably an underestimate of the production potential at present.
Reference yields for Sitka spruce are based on rough means from data given in Øyen (2005) and Øyen (pers. comm.).

There is very little published yield information for Lutz spruce but 20–30% lower production compared to the figures given for Sitka spruce is expected.

Figures reported for future planting of Sitka and Lutz spruce are very uncertain and are very much dependent on legislation pertaining to introduced species. The potential area for planting could be 5 to 10 times that presented in table 1, if allowed by legislation.

Genetic gain

Norwegian seed orchards for Scots pine and Sitka spruce are established from phenotypic selections and a genetic gain of 10% is expected.

The corresponding gain for Norway spruce is estimated by comparisons of seed orchard and stand seed lots from a total of around 30 progeny trials. The figures should be considered to be realised "seed orchard gain" rather than solely genetic gain and will include the effects of inbreeding, pollen contamination and seed production in a warmer climate. The latter is most important for Central and North Norway and higher altitudes in southern Norway as the seed orchards are located further south or in a warmer climate. Epigenetic effects caused by higher temperatures during embryogenesis and seed maturation have been very well documented (e.g. Johnsen et al. 2005, Johnsen et al. 2009). Delayed growth cessation seems to be positive in terms of height growth as long as the plants are sufficiently frost hardy in the autumn (Skrøppa et al. 2005, 2006, 2007). The difference in height growth between seed orchards and regular local stands of Norway spruce can be as high as 20–25% after 12 years growth in the field (Skrøppa et al. 2007). There are examples of differences of 30–40% in volume production after 30 years in single tree plot trials (Steffenrem unpublished data).

Genetic gains for Norway spruce in 2050 are estimated from genetic parameters observed in the Norwegian breeding populations, assuming a "realised seed orchard gain" as mentioned above and that the plans for the new breeding strategy are followed (Edvardsen et al. 2010).

Genetic gains for Sitka and Lutz spruce have been estimated under the assumptions that the seed orchards for Sitka spruce will still be based on phenotypic selection from stands, while a second generation seed orchard, based on selections made in progeny trials, will be made for Lutz spruce.

ECONOMIC GAIN

GENERAL

Calculating economic gains resulting from breeding is of great importance in order to determine whether investments in tree breeding can be justified. Estimated genetic gains will affect forest management and long-term plans for wood supplies. Planting genetically improved trees will increase growth, reduce damage and produce wood of higher quality. The cost of producing seed orchard seed is low, making the use of seed orchard seed profitable. Increased survival can reduce the number of seedlings planted and thereby the cost of cultivation, and at the same time increase the yield and shorten the rotation time. The possibility of producing mature trees for harvest in a shorter time would deliver the most radical change for forestry, since the rotation time is reduced and the annual area for harvest increases. All these factors connected to the use of genetically improved seed will result in an increased bare land value.

STAND LEVEL

Using gain in economic terms instead of gain in yield is, perhaps, a more interesting way to estimate the progress in genetic improvement. However, there are few results published from Nordic trials where a relevant economic evaluation of genetic gain has been performed at stand level. One example though, is a study by Ahtikoski et al. (2012), which is based on realised gain trials of Scots pine in Finland. The results from assessments at age 15–25 years, indicated a 15% higher gain in stem volume for first-generation seed orchard material compared to unimproved stand seed lots. Ahtikoski et al. (2012 and 2013) evaluated the economic effect of this genetic gain at stand level. The financial benefit was examined by using improved seedlings, taking the private forest owner's perspective (Ahtikoski et al. 2012). The results, which were based on comparisons of bare land values, showed that using improved seed material of Scots pine was financially viable in most parts of Finland at a discount rate of 3%. The absolute increase in bare land value was higher in southern than in central and northern Finland (Ahtikoski et al. 2013) regardless of interest rate (3% or 4%) or genetic gain (3% or 15%). Their findings showed that the change in bare land value was dependent on climatic conditions and the increase in bare land value was smaller in the north, mainly due to poorer growth potential. In addition, growth and yield studies, based on simulations with the MOTTI stand simulator, showed a substantial reduction of the optimal rotation age by using genetically improved material. For instance, the rotation period of 72 years for unimproved material (no genetic gain) was reduced to 57 years when using improved material with a 15% genetic gain, at sites with a temperature sum of 1350 day degrees. For 1100 day degrees, the corresponding reduction in rotation time was from 96 to 71 years.

Based on Nordic progeny trials, the genetic gain in tree height is in general approximately 10%, corresponding to a 10–15% gain in volume (e.g. Rosvall et al. 2001, Andersson et al. 2007, Jansson 2007, Ahtikoski et al. 2012, Kvaalen et al. 2008). With the assumptions that improved materials increase site index by 10% and using an interest rate of 2.5%, Kvaalen (2010) estimated economic harvest age and net present value (NPV) for site indices of G11–G23 (defined as H40, i.e. height at 40 years total age). Optimal economic harvest age was reduced by 5–10 years and the NPV increased by 30–400% depending on site index and timber price. The relative increase was highest for the lowest site indices when timber prices were low. In terms of absolute values, the difference was the opposite – the highest gain for high site indices when prices were high. The analysis showed that not only volume and harvest age influenced NPV, but the costs of harvest operations were also affected by a reduction due to bigger trees. Hence, the "moderate genetic gain" of 10% had much stronger implications in terms of NPV due to the additional effects of several factors.

An economic evaluation of European beech provenance trials aged around 65 years showed differences in predicted bare land values of 26% between the poorest and the best provenance at a 2% rate of interest (Hansen et al. 2003).

PHOTO: THOMAS ADOLFSÉN/SKOGENBILD

There was a 13% difference between the best provenance and the average of the provenances. Only the three best provenances were associated with positive bare land values at an interest rate of 4%. The bare land value estimates were based on a scenario in which seedlings were planted. In a situation where the forest owner can use natural regeneration at low cost, which is normal for beech establishment, it will not be profitable to replace the poorest provenance by planting the best provenance even with an interest rate as low as 2% (Hansen et al. 2003).

A tool for calculating profitability for different genetically improved material is available on the Swedish website "Kunskap Direkt" (www.kunskapdirekt.se). Figure 4 illustrates how a 12% genetic gain affects the economy in a Norway spruce stand with a site index of H100=28m. The interest rate used in the calculations is 2%. The improved stand increases the annual volume growth from 7.0 to 7.8 $m^3\ ha^{-1}$ and reduces the optimal rotation period by 6 years. Bare land value increases by 34% and it is more profitable to shorten the rotation time compared to a later harvest with higher stand volumes.

NATIONAL LEVEL

Rosvall (2011) estimated the economic gain of using genetically improved seedlings on a Swedish national level to amount to 1.7 billion SEK per year. This should be compared to the value of 12.3 billion SEK for the entire harvested volume in 2006. NPV of the harvests during the next 100 years is predicted to increase by 26 billion SEK due to genetic improvement at a 2% interest rate, or by 8 billion SEK at a 4% interest rate.

Ahtikoski (2000) analysed the profitability of Scots pine and silver birch breeding in Finland with emphasis on the next generation seed orchards. The profitability was calculated for state orchard seed producers and private forest owners, where NPV was used as the investment criterion. The NPVs were positive for Scots pine at a 6% discount rate for a genetic gain in growth of 12%. For silver birch NPV was positive at a 4% discount rate for genetic gains of 20% in southern and 14% in central Finland. Ahtikoski (2000) also compared direct sowing of seed orchard seed and local stand seed. The results for a private forest owner indicated that direct sowing of seed orchard seed was a profitable alternative compared to sowing stand seed even at an 8% discount rate. The overall result suggested that subsidising tree breeding in Finland is justified from society's point of view.

A Finnish cost–benefit analysis comparing direct sowing using material from seed orchards and from natural stands, was presented by Ahtikoski & Pulkkinen (2003). The emphasis of the study was on a socio-economic analysis focusing on the welfare impact of tree breeding from the public's point of view. Seedlings from seed orchards had 11% better survival than seedlings from local stand seed. The net cost of orchard seed was less than that of stand seed for a 7% yield improvement at a discount rate of 3%.

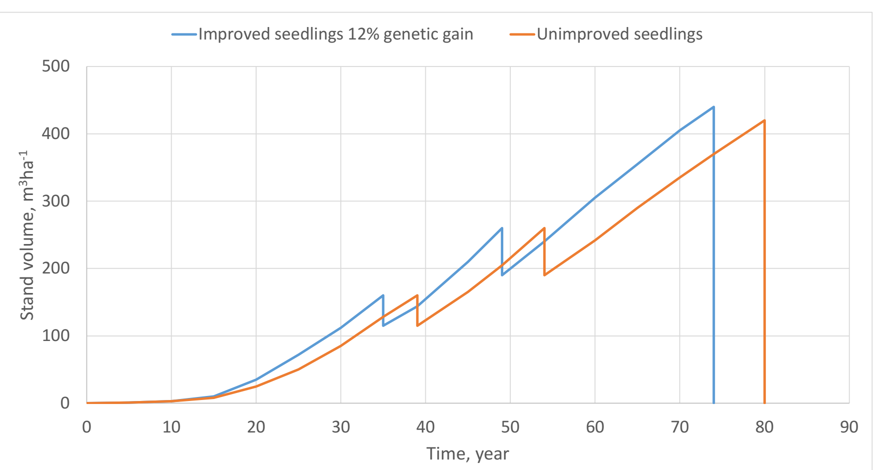

Figure 4. Example of results from the website tool in "Kunskap Direkt" where total stumpage volume in a stand with unimproved material (red curve) is compared with a stand including genetically improved material with a 12% gain (blue curve). The x-axis refers to "time, years" and the y-axis to stand volume ($m^3\ ha^{-1}$).

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PHOTO: THOMAS ADOLFSÉN/SKOGENBILD

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APPENDIX 1

DETAILED INFORMATION FOR TABLE 1 – SWEDEN

The reference level for yield

The annual mean yield (MAI) based on ordinary growth data from the Swedish National Forest Inventory (SNFI) would under-estimate the true reference yield level since these data are a random sample from the Swedish forests and include more or less heterogeneous data. The yield potential for spruce and pine was instead etsimated by using the site index (H100 and T100), which based on site properties (Hägglund & Lundmark 1977), was recorded in the field for each SNFI plot. The site index for **spruce** was used for plots where the basal area of Norway spruce was at least 65% and the site index for **pine** was used for plots with a basal area for pine of at least 65%. The site index from NFI years 2008–2012 was then transformed to yield in m^3 ha^{-1} $year^{-1}$ using regression functions (Hägglund & Lundmark 1981a, 1981b). Finally, area weighted yield means were estimated for spruce and pine respectively in each region, as presented in Table 1. The site functions by Hägglund & Lundmark (1981a, 1981b) were based on older NFI data (before 1980), i.e. the impact from improved material was very low. This means that the results for pine and spruce given in Table 1 represent a regional estimate of the growth in well managed stands on suitable sites for non-improved pine and spruce.

For **Sitka spruce** and **Douglas fir**, new results based on Swedish permanent yield plots were used (Ekö et al. 2015). For Sitka spruce, growth was in average 16 % higher than for Norway spruce which most probably belonged to the category “Transferred provenances”. Thus, here we added 8% to the 16%, i.e. a ratio of 1.25 was used as a reference to the unimproved MAI of Norway spruce. The growth for Douglas fir varied a lot between sites, probably due to establishment problems. The three most successful sites had after a mean rotation time of 90 years a MAI of 15 m^3 ha^{-1}, which roughly is on the same level as the Danish MAI estimations (Appendix 2).

For **grand fir** the same MAI was used as in Denmark (Appendix 2). This is in agreement with a study by Hausswolff-Juhlin (2010) in southern Sweden, where MAI varied from 19–28 m^3 ha^{-1}.

Siberian larch was estimated to have around 20% higher yield than Scots pine according to Martinsson (1995).

Previous studies of **hybrid larch** in Sweden Ekö (2008) have shown a slightly better growth but a rotation time half as long compared with spruce. However, new results (Ekö et al. 2015) indicate a 30 % higher MAI for hybrid larch. Here a reference MAI of 12 m^3 ha^{-1} was used.

Growth of unimproved material of **lodgepole pine** in Swedish forests has been estimated to be 30–40% superior to that of unimproved Scots pine regardless of site fertility, and its wood density is around 3% less than for Scots pine (Elfving & Norgren 1993, Elfving et al. 2001, Persson 2008). The reference yield for lodgepole pine was set to 35% higher than for Scots pine.

Since downy birch is very seldom planted, we here assumed that birch only refers to **silver birch**. The Finnish growth estimates (Hagqvist & Hahl 1998) were used for north and central Sweden and for southern Sweden the yield from a review by Rytter (2004) was used. The same review was used for estimates of the reference yield for **alder** in southern Sweden.

For **Poplars**, which here include hybrid aspen as well as other poplar species, 16 m^3 ha^{-1} $year^{-1}$ was used as a reference. This was based on estimates by Elfving (1986) for different hybrid aspen families planted on fertile sites in the very southern part of Sweden . For north Sweden, the reference was estimated to be 12 m^3 ha^{-1} $year^{-1}$ (Elfving 1986).

Oak and **beech** were assumed to be planted on fertile sites, where for oak a site index (H100) of 26 m in south and 24 m in central Sweden was used as a reference and for beech 28 m was used, corresponding to 5.2, 4.6 and 6.3 m^3 ha^{-1} $year^{-1}$ respectively (Carbonnier, 1971, 1975).

Genetic gain

Genetic gains in table 1 were estimated in the following way: For **Scots pine** and **Norway spruce**, genetic gain was based on results from a large number of analyses of genetic field trials by Rosvall et al. (2001). The seed orchard gains refer to realised gain after reduction for pollen contamination and was weighted by the seed production in actual (year 2010) and future (year 2050) seed orchards respectively (Almquist et al. 2010).

Estimates for **Sitka spruce**, **Douglas fir** and **grand fir** were based on Danish experiences (Appendix 2) since most of the plant material used in Sweden originates from Danish seed orchards.

There is one **Siberian larch** seed orchard in Sweden which was recently reactivated, thus seed production is very low. Most plant material used originates, therefore, from Finnish seed orchards including selected plus-trees, for which genetic gain was assumed to be 10%. It was estimated that in 2050 genetic gain will be roughly 20%.

Estimations of genetic gain of hybrid larch are difficult to carry out due to lack of relevant trials. A lot of the **hybrid larch** seedlings used in southern Sweden originate from the Danish seed orchards, as well as from the Swedish seed orchard in Maglehem. The genetic gain for Danish larch was estimated to 60% (Table 1), but was for Sweden reduced to 30 %, since the estimates of MAI for "unimproved" material were mainly based on material from the Maglehem seed orchard.

The existing five active seed orchards of **lodgepole pine** have an estimated genetic gain of 10% and in 2050 the gain will be around 25% (Rosvall et al. 2001).

Genetic gain for **silver birch** in central Sweden was set to the same level as in Finland (Hagquist & Hahl 1998), since the reference level is similar and almost all birch plants in this region originate from Finnish seed orchards. In the south, the estimates follow Rosvall et al. (2001).

The yield for the selected **hybrid aspen** clones on fertile sites in southern Sweden is 20–25 m^3 ha^{-1} $year^{-1}$ and slightly higher for other **poplars** (Stener, 2010). This results in a genetic gain today of around 45% in relation to the "artificial unimproved" reference level. For 2050 the gain was roughly estimated to be 35–70% depending on region.

The number of plants originating from seed orchards of **beech** and **oak** is and will be quite limited since beech nut/acorn production is usually limited. Thus, the seed crop has to be supplemented from selected seed stands unless vegetative propagation becomes an option in the future. Genetic gain is estimated to be 10% and may, due to extensive activities, increase to 15% in 2050.

APPENDIX 2

DETAILED INFORMATION FOR TABLE 1 - DENMARK

The reference line for yield

Norway spruce: In the nationwide field trial series from 1965 (F-1965), the mean annual increment (MAI) of 18 m^3 ha^{-1} $year^{-1}$ (range 8 to 24) across the test sites was of the same magnitude as for the NFI data (Table 4). The provenance used in F-1965 was F300, Rye Nørskov, which in a provenance study was very close to the average of 128 tested Danish provenances for height growth (Madsen 1989).

Sitka spruce: The MAI of 23 m^3 ha^{-1} $year^{-1}$ (range 17 to 28) across the test sites in F-1965 was substantially higher than the NFI data (Table 4). Danish domestic sources were rapidly noted as being superior to imports from the same provenance area (Nielsen 1994). Gains in volume production in the region of 30–70% under harsher conditions have been recorded and in younger trials (age 10) a gain in height of 20% was achieved. The provenance used in F-1965, F235c Frijsenborg, was 33% above the MAI average of the imports, so the reference level was set to 23/1.30=17 m^3 ha^{-1} $year^{-1}$.

Grand fir: The MAI of 24 m^3 ha^{-1} $year^{-1}$ (range 10 to 33) across the test sites in F-1965 was, like Sitka spruce, substantially higher than the NFI data (Table 4). At several sites the increment is still increasing and grand fir has, with age, improved its rank compared to the other species, i.e. production may, at this stage, be underestimated. Yield of the best Danish sources was estimated to be around 10–15% higher than the average of the imported seed sources (Hansen and Nielsen in prep.) The provenance used in F-1965 was a direct import from Vancouver Island, Comox, Canada but seemed to be among the better ones (Hansen, J.K. unpublished 2015). Thus, a baseline was estimated to 24/1.15= 21 m^3 ha^{-1} $year^{-1}$ for unimproved and unselected material.

Douglas fir: The MAI of 17 m^3 ha^{-1} $year^{-1}$ (range 11 to 22) across the test sites in F-1965 was higher than the NFI data (Table 4). The Douglas fir provenance used was F53a Wedellsborg. There are no other test results for this provenance, but anyway it was used to represent the baseline. Danish versus selected imported sources have been tested, and it seems that the best materials of both groups have similar growth potential (Larsen et al. 1997b, Larsen & Kromann 1983)

Larch: The MAI of 13 m^3 ha^{-1} $year^{-1}$ (range 9 to 18) for Japanese larch in F-1965 was again higher than the NFI data (Table 4). The estimates for Japanese larch were used as the baseline.

Scots pine: Data for pine were only available for one site in F-1965, with a MAI of 7 m^3 ha^{-1} $year^{-1}$, which was of the same magnitude as the NFI data (Table 4).

Poplars: Hybrid aspen, formerly used on a small scale in Danish forestry, has a MAI around 16 m^3 ha^{-1} $year^{-1}$ for site class 1 (Jakobsen 1976); this was used as the reference level.

Oak: The MAI in F-1965 was around 6 m^3 ha^{-1} $year^{-1}$ (range 4 to 11) and of the same magnitude as the NFI data (Table 4). The provenance used was Dutch Zevenaar and, according to Larsen et al. (1997a), it is comparable to the average of the Danish provenances of *Quercus robur* and therefore was used directly as the baseline.

Beech: The MAI of 10 m^3 ha^{-1} $year^{-1}$ (range 4 to 17) in F-1965 was less than the NFI data (Table 4), but some test sites included experienced quite harsh conditions. The provenance F128a Lundsgaard that was used has been widely planted in Denmark, but tests have shown that it is among the poorest sources (Hansen & Kromann 2005). However, the differences between sources were fairly small, and provenance F128a Lundsgaard was just 2% below average.

Genetic gain

Norway spruce: Breeding activities have been focused on improving vitality and density rather than volume production due to dieback damage, referred to as "red spruce", in the late 1980s. The existing orchards are expected to provide 100% of the required seed supply, and gain for volume is estimated to be 8%.

Sitka spruce: The trees in the seed orchards owned by the state were mainly improved for stem quality and not yield, so for these no gain in production is expected relative to provenance material. The privately owned seed orchards HedeDanmark FP625 and C.E. Flensborg have an estimated gain in volume compared to F235c standard provenances of 25% over a rotation period (HedeDanmark 2014). Close to 100% seed supply is expected from seed orchard material in the future and the average gain from a mix of orchards is estimated to be 40% both today and in 2050.

Grand fir: The best provenances produce about 25% better than the average for imported material and the best Danish sources around 15% better with respect to volume. A newly established orchard will, in the mid 2020s produce seed with an estimated gain in volume growth compared to the best Danish sources of 11%, but compared to average of provenances more than 30% (Hansen, J.K. unpublished 2015).

Douglas fir: Genetic gain for volume production today is estimated to be 8% and will be 10% in 2050 (Hansen et al. 2005, 2013) and seed orchards should supply approximately 25% of the seed demand.

Hybrid larch: Roulund (2007) evaluated nine seed orchards: six hybrid orchards were compared with three Japanese larch orchards. Superiority in volume production varying from 40% to 100% was found. Presumably the best orchards will gain the largest market share but still an average of 60% is used as average gain. Hybrids are already extensively used. Statistics on Danish seed harvests during 2008–2013 (Naturerhverv 2014a) show that 93% of the seed available originates from hybrid larch. A set of fairly new seed orchards is now established with presumably the same magnitude of gain, and thereby securing close to 100% seed orchard supply with hybrid seeds.

Scots pine: No breeding has been carried out. Most pine seed orchards have been used for gene (provenance) conservation and easy seed harvesting (Anon. 2000). The estimated number of plants used, based on the data from the Nature Agency, is probably to some extent an overestimate.

Poplars: The most commonly used poplar in Denmark has, for the past 20 years, been OP42. The MAI for this clone was 26 m^3 ha^{-1} $year^{-1}$ at age 13 in a trial including 36 clones (Nielsen et al 2014). Sampling on sites throughout Denmark indicates that OP42 produces from 9 to 40 m^3 ha^{-1} $year^{-1}$ (3 to 14 tons DM, ha^{-1}, $year^{-1}$) and 25 m^3 ha^{-1} $year^{-1}$ seems to be a realistic average (Anders Tærø Nielsen, pers. comm.), i.e. around a 55% gain in relation to the reference line. New trials have been established (Palle Madsen, pers. comm.), but results are not yet available. A conservative estimate of future genetic gain is a slight increase.

Oak: Today all seed material originates from approved stands. There is a total of 200 ha of *Quercus petraea* and 500 ha of *Q. robur* (Bruno Bilde Jørgensen, pers. comm.). Based on a number of approved stands (Naturerhverv 2014b) some seed orchards have been established (Hansen et al. 2012) with approximate gains of 6% after the second thinning at age 25. The State owned orchards are expected to cover 50% of consumption (Anon. 2000), and private orchards may add another 10%. The best Dutch provenances deliver about +10% in growth compared to average Danish material, and this is comparable to the best Danish material, i.e. F148 Tåstrup skov and its offspring (Larsen et al. 1997a). For *Q. petrea* a substantial amount is imported from Norway, but hardly any *Q. robur* is imported.

Beech: No breeding or selection has been carried out for commercial purposes, it is mainly naturally regenerated. Seed supply will be based on approved stands and provenance imports. The best Danish material, at age 37, had 6% higher production than the average (Hansen and Kromann 2005). The best imported provenance, Sihlwald from Switzerland, might add 3% genetic gain in volume production compared to normal Danish stands, but the major advantage is improved stem form (Jon Kehlet Hansen, pers. comm.). Around 50% of the future seed material can probably be sourced from Danish seed stands of Sihlwald origin.

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