EUROPEAN FOREST GENETIC RESOURCES PROGRAMME

EUFORGEN

Use and transfer of forest reproductive material

in Europe in the context of climate change

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Bioversity
International

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PREFACE

Forest regeneration, whether natural or artificial, is based on the utilization of forest genetic resources (i.e. genetic material of forest trees that is of actual or potential use for humans). Natural regeneration relies on genetic material that is already available on a particular site, while artificial regeneration, carried out through seeding or planting, typically involves transferring forest reproductive material (FRM) (i.e. the parts of a tree that can be used for reproduction) from other locations to the site. In Europe, much of the material used for artificial regeneration is produced and transferred within a single country. However, FRM, usually in the form of seeds or cuttings, is increasingly traded across national borders, especially within the European Union. As forest managers and owners seek to minimize the costs of establishing new forests, mistakes are made in matching the material purchased with ecological site conditions, and in ensuring high genetic and physiological quality of the material.

This phenomenon is nothing new as FRM has been traded in Europe for centuries. However, climate change is likely to increase the future demand for imported FRM as forest managers and owners try to identify tree species and provenances that will be able to grow in their land under new climatic conditions. According to the Intergovernmental Panel on Climate Change (IPCC), the global average surface temperature (combined land and ocean temperatures) has increased by nearly 1°C during the period 1901–2012[1]. The recent IPCC report concludes that it is very likely that temperature will continue to increase throughout the 21st century in different parts of the world, including Europe. In the same report, the IPCC projects that summer temperature (June-August) will increase by 3–4°C in most part of Europe by 2081–2100, and even 4–5°C in some places in the Mediterranean region. This will alter the environmental conditions to which European forest trees are adapted and may even create novel climatic conditions. As a result, some parts of the current distribution ranges of forest trees are expected to become unsuitable while new areas are likely become suitable for many species in higher latitudes or altitudes. The accelerating speed of climate change has raised serious concerns on how tree species can cope with the projected changes. Furthermore, the warming climate will probably facilitate the spread of pests and diseases, creating an additional threat to forest trees and their populations.

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[1] IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 1535 p. doi:10.1017/CBO9781107415324.

Most European countries have recommendations or guidelines for selecting species and provenances that can be used in a given site or zone. However, these recommendations are mostly based on present or past climatic conditions. They therefore provide limited advice for selecting FRM so that the next tree generations will thrive until the end of their rotation periods under rather different climatic conditions than today. More and more FRM is traded across borders but the national guidelines rarely offer help in deciding where the imported material should be used.

Solutions for these problems and challenges have been explored through European collaboration on forest genetic resources. Various European projects have tested the feasibility of harmonizing national provenance regions across the continent and have re-evaluated existing provenance trials to predict how climate change will affect forest growth and how individual species and provenances will perform under changing climatic conditions. Unfortunately, much of the new information produced by these efforts is being discussed and debated only by scientists, while forest owners, managers and policy-makers often remain unaware of the potential that the use of forest genetic resources offers for facilitating the adaptation of forests to climate change.

During the past decade, the European Forest Genetic Resources Programme (EUFORGEN) has increased its efforts to promote the conservation and sustainable use of genetic resources that can be adapted under climate change and to facilitate dialogue among scientists, forest owners, managers and policy-makers on this issue. EUFORGEN was established in 1994 to coordinate pan-European collaboration on forest genetic resources as part of the Ministerial Conferences on the Protection of Forests in Europe (now called the FOREST EUROPE process). During Phase IV (2010-2014), EUFORGEN had three objectives: (1) promote appropriate use of forest genetic resources as part of sustainable forest management under climate change; (2) develop and promote pan-European genetic conservation strategies and improve guidelines for management of genetic conservation units and protected areas; and (3) collate, maintain and disseminate reliable information on forest genetic resources in Europe.

This report presents the findings and recommendations of the EUFORGEN working group on FRM. The report presents possible approaches for the use and transfer of FRM under climate change and identifies critical factors; it does not attempt to provide field-level guidelines for using and transferring the material. The working group held two meetings, the first one hosted by Bioversity International in Maccarese, Italy, 28–30 March 2012, and the second one by the Bavarian Office for Forest Seeding and Planting (ASP) in Freising, Germany, 4–6 July 2012. The EUFORGEN Steering Committee discussed an earlier draft of this report during its 8th meeting, held in Paris, France, 27–29 November 2012. The updated draft report was then presented to a larger group of experts for further discussion at the EUFORGEN workshop on FRM that was organized in Kostryca, Poland, 1–3 October 2013. After the workshop, the working group incorporated the comments received to the revised draft report and presented it to the Steering Committee at its 9th meeting, held in Tallinn, Estonia, 3–5 December 2013, for approval. The Steering Committee endorsed the draft report, provided some additional minor comments, and requested the working group to finalize the report for publication. The working group members gratefully acknowledge inputs and comments received from all national experts who contributed to the preparation of this report.

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ACRONYMS USED IN THE TEXT

ABS	Access and Benefit Sharing
COST	European Cooperation in Science and Technology
EST	expressed sequence tag
EUFORGEN	European Forest Genetic Resources Programme
FAO	Food and Agriculture Organization of the United Nations
FGR	forest genetic resources
FRM	forest reproductive material
G×E	genotype-by-environment
GEBV	genomic estimated breeding values
GIS	geographical information system
GWAS	genome-wide association studies
INC	Intergovernmental Negotiating Committee
IPCC	Intergovernmental Panel on Climate Change
IUFRO	International Union of Forest Research Organizations
masl	metres above sea level
MAT	mutually agreed terms
MPBS	Multiple Population Breeding System
NGS	next-generation sequencing
OECD	Organisation for Economic Co-operation and Development
PIC	Prior Informed Consent
RAD	restriction-site-associated DNA [marker]
QTL	Quantitative Trait Locus
SNP	Single Nucleotide Polymorphism

EXECUTIVE SUMMARY

Forest regeneration may be natural or artificial. Both depend on forest genetic resources, but while natural regeneration relies on what is already available on a given site, artificial regeneration often makes use of the deliberate transfer from elsewhere of forest reproductive material (FRM). This material may be in the form of seeds, seedlings or cuttings.

The selection of suitable FRM has assumed a new importance both because trees are long-lived species and because rapid climate change will have an impact on the environmental conditions of the trees as they grow and mature. The long-standing importance of FRM to forestry and the cross-border trade in FRM have resulted in several European countries exercising some control over sources of FRM and their selection. Climate change is one reason why countries need to re-evaluate and modify their policy framework and guidelines on the use of FRM. An important additional practical challenge is that to an unprecedented degree forest managers must now consider the climate that a new generation of trees might experience in future, in order to select material that will thrive now, under the present climate, and also be able to withstand predicted climate. Furthermore, many forest owners think of FRM as a cost to be minimized rather than as an investment for which they should be seeking better returns.

Against this background, a working group under EUFORGEN was tasked to report on the use and transfer of FRM to respond to the challenges of climate change. The working group examined scientific research on provenance and adaptation, including several case studies of transfer, the existing regulatory framework and recent policy developments, guidelines on FRM transfer and their scientific basis, and future challenges and opportunities.

The group concluded that:

- Transfer of FRM is a valuable option to adapt forests to climate change, although there may be limits to the transfer of FRM.
- Local provenances may not always be the best source of FRM.
- Before considering changing tree species, forest managers should consider deploying other, well-tested provenances of the existing tree species. At the European level, recommendations on FRM transfer must be revised and harmonised

and at the same time, all stages of production and marketing should be more stringently controlled..

- Tree breeding also offers opportunities to assist forests and forest management to adapt to climate change.
- Improved documentation is crucial to ensuring that today's use of FRM can inform tomorrow's choices, just as past efforts have helped to guide today's recommendations.
- Basic research on adaptation of forest tree populations, along with provenance research, should continue and be strengthened, and the results disseminated in forms that forest owners and managers and policy makers can use.

Provenance, adaptation and suitability

The term "provenance" refers to the source of FRM, and material of known provenance has been a feature of forest regeneration for many decades. The working group considered historical and current uses of FRM of known provenance, including the use of provenance trials to supply additional information. Provenance trials, where material of different provenances are planted in a single place (common garden trials) or at different locations spanning a range of environmental conditions, have been instrumental in revealing genetic variation among provenances, as well as differences among provenances in the plasticity of phenotypic responses to fluctuating environmental conditions. A key conclusion is that local provenances are often outperformed by other provenances for many traits.

In long-lived species like trees, populations have been experienced natural selection, possibly over multiple generations, on a given site. However, the original population on which natural selection acted consisted only of those seedlings present at the start of selection. They may not have the genetic diversity or phenotypic plasticity to guarantee good performance under changed conditions. A different population from further away, which may have experienced selection under conditions more like those forecast for the site to be reforested, might represent a more suitable seed source. Modern molecular tools and other analytical approaches offer new scientific methods for evaluating the suitability of different provenances for different sites, in addition to underpinning a deeper understanding of adaptation. Research can also deepen understanding of the strong GxE interaction (interaction between genotype performance and environmental conditions) that operates on many forest tree species. The best provenance on one site is unlikely to be the best on a different site.

The scientific breeding of tree species, like all forms of selection, inevitably results in the loss of genetic diversity. Nevertheless, intensive tree-breeding efforts are useful in improving FRM, provided attention is given to traits that will be most important in the future under different climate regimes. Drought resistance and phenotypic stability (i.e. the ability to maintain superior productivity across a range of sites) could be useful targets for breeding, which will be helped by molecular techniques such as marker-assisted breeding, high-throughput phenotyping and others.

Law and policy

Council Directive 1999/105/EC provides the legal basis for regulating the production and marketing of FRM within the European Community, and all Member States have enacted national legislation to meet the goals of the directive. The working group examined the details of the directive and of national legislation, along with other sets of standards, and points out that none of them currently takes account of climate change. The report identifies opportunities to change some aspects of regulation, for example making use of modern genetic tools for provenance control. A fruitful avenue may be to extend control from the production and marketing of FRM to its use, possibly in the form of decision-support tools to help forest managers to choose the best source of FRM.

Going forward, the European Commission is currently reviewing the control of plant reproductive material. This review will result in a Regulation, rather than a Directive, harmonising pan-European approaches. The implications of the Nagoya Protocol for the exchange of forest genetic resources for research and development purposes remains unclear.. The Nagoya Protocol can potentially hamper research and development efforts by, for example, increasing transaction costs.

A suitably adapted policy framework could do much to improve the outlook for the transfer of FRM in response to climate change. To ensure that such policy framework can be put in place, however, additional research will be needed, along with the dissemination of research results in usable form.

INTRODUCTION

The use and transfer of forest reproductive material (FRM) (i.e. seeds, cuttings or other propagating parts of a tree) have a long history in Europe. Millennia ago, ancient Greeks and Romans cultivated chestnut (*Castanea sativa*) and stone pine (*Pinus pinea*) mainly for food production, and also traded their seeds across the Mediterranean region (Conedera *et al.,* 2004; Vendramin *et al.,* 2008). In the 18th century, seeds of several forest trees, such as Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), European larch (*Larix decidua*) and oaks (*Quercus* spp.), were widely traded and transferred for forestry purposes across European countries (Tulstrup, 1959). The field testing of tree species and their different seed sources, including several tree species introduced from North America, started more than two hundred years ago (see König, 2005, for a comprehensive review on provenance research in Europe). These early testing efforts revealed that the origin of the seed had a major influence on the success of tree planting efforts. This is considered the starting point for modern provenance research, which has increased our understanding on the effects of climate, site conditions and genetic resources on tree growth (König, 2005).

Throughout the 19th century and early 20th century, the international transfer of seeds continued in large quantities in many parts of Europe. The demand for seed was high as many countries started to regenerate artificially their overexploited forests. Despite the fact that the importance of using appropriate seed sources was demonstrated by practical experiences and the early scientific studies, many reforestation efforts seem to have paid little attention to this aspect. Historical documents indicate that the reforestation efforts were not always successful and that several countries tried to limit the use of foreign or unknown seed sources.

At the beginning of the 20th century, more systematic assessment efforts were initiated for several tree species in Europe (see König, 2005). The first international provenance trial for Scots pine was established in 1907 under the auspices of the International Union of Forest Research Organizations (IUFRO). This was followed by the establishment of a second series of IUFRO trials for Scots pine in 1938–39, and then a third series in 1982. As part of the IUFRO collaboration, an international provenance trial was also established for Norway spruce in 1938. Later on, many countries established additional provenance trials for these and several other native tree species, such as silver fir (*Abies alba*), Mediterranean firs (*Abies* spp.), European larch (*Larix decidua*), sessile oak (*Quercus petraea*) and pedunculate oak (*Q. robur*), as well as introduced tree species (e.g. grand fir (*Abies grandis*), Sitka spruce (*Picea sitchensis*) and Douglas fir (*Pseudotsuga menziesii*)). Subsequently, several European countries launched breeding programmes for many of these tree species in the 1950s and 1960s.

In the 1990s, when climate change started raising concerns, the provenance trials were re-discovered as they offer readily available empirical data for studying the impact of climate change on tree growth in field conditions (e.g. Mátyás, 1996). Although European forests are relatively well managed, climate change is considered to be an additional threat, especially for many scattered tree species and marginal populations of even common and widely occurring species. Tree populations have three options to avoid extinction under changing climate: (1) local persistence using their inherent flexibility (or "phenotypic plasticity") to a wide range of environmental conditions; (2) local persistence via reproduction and increased genetic adaptation to new conditions; and (3) survival through migration (Aitken *et al.*, 2008). The provenance trials have shown that trees exhibit different phenotypic responses to different environmental conditions (e.g. Rehfeldt, Wykoff and Ying, 2001; Rehfeldt *et al.*, 2002) and the degree of this plasticity varies among populations and species (Aitken *et al.*, 2008; Skrøppa and Kohlmann, 1997). Climate change is likely to favour genotypes with high levels of plasticity, whereas low plasticity may lead to extinction (Rehfeldt, Wykoff and Ying, 2001). However, the buffering capacity offered by phenotypic plasticity is limited (e.g. Mátyás, 2007). Furthermore, the natural migration speed of forest trees is considerably slower than the pace of climatic changes (Jump, Mátyás and Penuelas, 2009) so their migration potential is also limited.

In the past, environmental conditions largely guided the selection of FRM to be used in a given site. Now climate change makes this more difficult as forest owners and managers will also have to consider what sort of climate the new tree generation might experience during the next 50–100 years and try to select material which would not only thrive under the present climate but also withstand the predicted changes in climatic conditions. Unfortunately, many forest owners and managers do not pay enough attention to this. Furthermore, they rarely consider the selection and purchase of FRM as an investment, but rather as a cost that should be minimized.

The use and transfer of FRM in the context of climate change was one of the topics which was discussed during a FOREST EUROPE workshop organized by EUFORGEN and IUFRO in 2006 (see Koskela, Buck and Teissier du Cros, 2007). The workshop noted that the impacts of climate change on forests will vary in different parts of Europe, bringing both opportunities and threats. It stressed the fact that forest genetic resources play a key role in maintaining the resilience of forests to the threats and in taking advantages of the opportunities. Furthermore, the workshop recommended development of pan-European guidelines for the transfer of FRM on the basis of the latest scientific knowledge, to maintain the productivity of European forests and to facilitate the adaptation of forests to climate change.

Between 2005 and 2009, the EUFORGEN Forest Management Network also focused on issues and problems related to the use of FRM. Experts participating in this network conducted two surveys in 2006–2007: one on relevant policies and practices related to genetic resources and forest management, and another one on tools and mechanisms to promote the use of high-quality FRM. The surveys found that many countries promote tree planting efforts through legal and policy instruments. However, several of these countries promote largely the use of local provenances, and some countries have even banned the use of non-local provenances or introduced tree species. In addition, some countries have specific provenance requirements as part of their grant schemes supporting tree planting efforts.

The Forest Management Network noted that the production part (seed sources and seed supply) works rather well in European countries, while there are some problems with the information. Scientists and forest professionals have a wealth of information, which is not always easily accessible or available for forest owners and those who are contracted to plant seedlings. When the information is available, it is sometimes neglected by forest owners and tree planters. The Network concluded that the use part is the most critical issue, as lack of knowledge, market forces and trade mechanisms often work against the use of high-quality FRM (in terms of both genetic and physiological quality). The Network also found that, when low-quality material was used or when the material was not well adapted to site conditions, it usually took 5 to 10 years for problems (e.g. frost damage; low vigour; susceptibility to pests, diseases, wind or snow; etc.) to become visible. However, in some cases, these problems surfaced only after more than 30 years.

In 2010, the EUFORGEN Steering Committee, consisting of representatives from all member countries, decided to establish a working group to review the latest information available on the use and transfer of FRM in the context of climate change, and to make recommendations for further action at the pan-European level. More specifically, the Steering Committee requested the working group to:

1. Review existing work from EUFORGEN Networks and relevant European projects.
2. Synthesize existing (national) guidelines.
3. Select (widely used) model species.
4. Identify critical factors related to climate change and future needs associated with transfer of FRM.
5. Summarize lessons from provenances trials for seed transfer.
6. Analyse if any relevant information should be added to the *accompanying documents* as specified in the EC Directive and other relevant schemes covering the movement of FRM.
7. Compile a list of existing models and tools that can be used for future forest management planning and transfer of FRM.
8. List the issues related to the climate change context.
9. Prepare a draft report (including recommendations).

This report presents in detail the findings and recommendations of the working group.

CLIMATE CHANGE AND THE USE OF FOREST REPRODUCTIVE MATERIAL

Genetic diversity is the basis of evolution. Selection, gene flow and drift together form the engine of evolution, the processes by which genetic diversity can be modified when environmental conditions change. Without genetic diversity, adaptation to novel environmental conditions is nearly impossible. Because of climate change, local conditions will be severely modified throughout species distribution ranges by the end of the 21st century. Choosing the right FRM is a challenge for forestry when average and critical environmental conditions are changing fast.

The impact of natural processes and biological factors on genetic variation

The suitability of FRM to a particular site is judged by its ability to survive, grow and reproduce at that location. This ability derives from how particular genes and gene combinations are expressed at the location, i.e. what phenotypic traits will arise under critical biotic and ecological factors at that site and whether these traits can be modified when environmental conditions change (i.e. phenotypic plasticity). Genetic diversity is the term used to describe differences in DNA sequence between individuals (or groups of individuals) as distinct from variation caused by environmental influences. The unique genetic composition of an individual (its genotype) will determine its performance (its phenotype) at a particular site. Successful deployment of FRM can be achieved, now and in the future, by assessing genetic variation and understanding how it is structured at the individual, population and species levels.

Genetic variation can be categorized into two types: neutral and adaptive. Neutral variation results from DNA sequence differences among individuals that do not directly affect their ability to survive and reproduce. Adaptive variation results from DNA sequence differences which do affect the overall fitness of an individual and thus can be selected for or against in a given habitat. Several key evolutionary processes affect genetic variation: mutation, drift, gene flow and natural selection (Box 1).

A part of the observed heritable phenotypic variation does not result from DNA sequence changes but rather from changes in gene expression triggered by particular environmental conditions during key life stages. This

Box 1. The major processes that affect genetic diversity within and among tree populations

Mutation is a rarely occurring event that acts on the DNA to create new genetic variation within a species. It is a random event that can alter both neutral and adaptive genetic variation. Mutations at adaptive genes can either confer a selective advantage or, more frequently, disadvantage, for the individual, or have no effect at all.

Gene flow and migration Gene flow – the migration of genetic variants via natural dispersal of seed, pollen or vegetative propagules – acts to homogenize both neutral and adaptive variation between tree populations. This connectivity may increase the capacity of a given forest to respond to changing selection pressures by providing a regular input of genetic material from trees adapted to different ecological conditions. However, gene flow can also be maladaptive, particularly towards range margins or at ecologically marginal sites, because the material that arrives at a new location may come from a habitat with widely differing ecological conditions.

Natural selection is any factor that prevents or reduces reproduction of certain individuals in a population, and represents a selection pressure. Since mortality is often highest when trees are at the seedling or sapling stage, this is the point at which natural selection could have its greatest influence, at least for certain traits. Natural selection acts on phenotypic traits, thus on the adaptive variation, but it can also be indirectly observed in neutral variation if selection has caused demographic bottlenecks.

Genetic drift is the random reduction of genetic variation in a population of finite size. Genetic drift affects mostly neutral genetic diversity. It increases when population size decreases and its effects are largest in small isolated populations, typically at ecological and range margins.

potentially reversible variation is referred to as "epigenetic". Epigenetic changes are generally induced by environmental stimuli; in this way, a tree may "remember" the environment it is exposed to and transmit this information to its progeny. There is evidence for such memory effects and their epigenetic nature for phenology in conifers (Johnsen *et al.,* 2005; Skrøppa *et al.,* 2009), but such phenomena may be much more widespread and apply to other fitness-related traits as well. Both genetic and epigenetic variation influence how trees survive, grow and reproduce in a given location. The extent of this variation can be measured using common-garden trials and molecular markers. Common-garden trials, also known as transplant experiments, i.e. field tests that compare genetic material of different geographical (provenance) or genealogical (progeny) origins in a common environment, have a long history in forestry. They have been used for assessing adaptive variation and selecting material for breeding. Up until recently, molecular techniques typically provided information on neutral variation (drift and gene flow) and mating patterns in natural populations and seed orchards. Recent advances in molecular techniques are beginning to allow links to be made between adaptive traits and molecular variation, and to decipher the genetic and molecular basis of adaptation in forest trees.

Identification of critical factors for persistence under climate change

Life history traits, such as duration of juvenile and adult phases, timing and intensity of growth, onset of aging, or the temporal sequence of events and processes such as reproduction, nutrient storage, seed dispersal or some physiological or morphological characteristics (i.e. bark thickness or sprouting ability) are traits of species, populations or individuals that are shaped by the interplay of biotic and abiotic factors. They are associated with variation in fertility and survival throughout life and, thus, have evolutionary implications. Life history traits are subjected to complex trade-offs that have been shaped over long evolutionary time scales and constitute evolutionary strategies under mostly stable environments. Although a part of the circum-annual ontogenetic rhythm is internally regulated and proceeds almost regardless of external signals, climatic conditions play an essential role in the temporal regulation of growth and reproduction. Timing of biological processes in plants results from evolutionary trade-offs between conflicting needs. In the case of vegetative phenology (budburst, shoot growth cessation, frost hardening, etc.), for example, the trade-off is mainly between the length of the growing season and the risk of frost damage (Gömöry and Paule, 2011; Leinonen and Hänninen, 2002). Under rapidly changing climate conditions, these strategies and trade-offs are severely challenged (Pigliucci and Marlow, 2001; Roff, 2000).

Climate change may push species beyond their ecological niche limits and thus drive tree populations to local extinction. Alternatively, extreme weather events or shifts in annual weather pattern may disturb climatic signals received by plants and consequently disrupt adaptive strategies and trade-offs. Extinction of local populations is the ultimate consequence of these processes, and even when tree populations manage to persist (for example through processes such as phenotypic plasticity and genetic adaptation), productivity losses are a serious concern for practical forestry. Furthermore, if climate change adversely influences reproduction processes, it may also endanger the persistence of tree populations. Mitigation of, and adaptation to, climate change through a proper choice of FRM requires that there is genetic variation in resistance or tolerance to climate-associated damaging factors. Several abiotic factors and life history traits are critical for European FRM under climate change.

Among the critical abiotic factors, drought stress is generally considered to be the main problem. Most climate scenarios predict increasing temperatures and prolonged drought periods, resulting in increased continentality in much of Europe (IPCC, 2007, 2014). High temperatures in combination with water stress disturb physiological processes such as nutrient uptake or photosynthesis (Saxe *et al.*, 2001). Physiological effects of a single severe drought may last not just one growing season but can persist over several years (Jonard *et al.*, 2012). In addition to decreasing tree growth (Cailleret and Davi, 2011), reproduction may also be threatened by recurrent droughts. Summer droughts have been demonstrated to decrease seed crops and seedling recruitment in many tree species (e.g. Perez-Ramos *et al.*, 2010; Silva *et al.*, 2012). Plants react to drought stress by a variety of heritable physiological and structural mechanisms, such as changing morphology or anatomy of assimilatory organs or root systems (Ahuja *et al.*, 2010; Kozlowski and Pallardy, 2002; Newton *et al.*, 1991). Ultimately, drought stress can lead to adult tree dieback and mortality. Xerothermic conditions (when high temperatures combine with intense drought) may be accentuated in the Mediterranean, where summers are already dry and year-to-year variability of rainfall is high (Scarascia-Mugnozza *et al.*, 2000). The Mediterranean region of southern Europe is expected to lose almost one-quarter of its plant species by 2100 (EEA, 2007; Thomas *et al.*, 2004; Bakkenes, Eickhout and Alkemade, 2006).

Increased drought and xerothermic conditions throughout Europe will make wild fires a more widespread threat and selective force than it is currently. Forest trees exhibit two basic responses to endure fire: they can either recover through a fire-triggered germination of a seed-bank (e.g. low elevation Mediterranean pines like *Pinus halepensis/brutia*) or they can survive and regenerate the destroyed aboveground biomass (Mediterranean evergreen broadleaved species). Increased frequency of forest fires due to climate change can have a detrimental effect on species that do not have mechanisms to endure forest fires, such as mountain conifers like *Abies* spp., *Picea abies, Pinus nigra, Pinus sylvestris* or *Pinus leucodermis*, as they can severely reduce population sizes and consequently increase genetic drift. Even fire-adapted low-elevation Mediterranean forest trees can be at risk if the frequency of forest fires increases beyond the age of reproductive maturity.

Changed winter precipitation patterns represent another threat. Heritable features of tree architecture, such as crown shape or branching form, frequently result from evolutionary adaptation to snow pressure and occurrence of hoarfrost and ice (Geburek, Robitschek and Milasowszky, 2008). A shift of wet and heavy snow towards higher altitudes may bring excessive damage and thus important economic losses.

Elevated-temperature events during winter may induce winter desiccation in conifers, when frozen soil does not allow take up of water lost by transpiration. This has reportedly caused damage in the form of needle loss in Douglas fir (Larsen, 1981) and Norway spruce at high latitudes (Kullman, 1996). As winter temperatures are expected to increase more than summer temperatures under climate change, winter desiccation associated with xylem cavitation and needle loss may thus decrease productivity in coniferous forests.

Changed temperature patterns (mainly the timing of seasonal temperature changes) in autumn and winter may influence the frost hardening and de-hardening processes. Frost hardening is a mechanism that prevents damage to cell membranes due to ice crystal formation. Warmer autumns and winters may induce shallower levels of hardiness (Saxe *et al.*, 2001) causing frost damage in the case of sudden frost events. The phase during which maximum cold hardiness is ultimately achieved is induced by freezing temperatures (Weiser, 1970) and is associated with structural changes in cells. As growth processes require a normal physiological state of cells, the whole process is reversed in the spring. Warm minimum temperatures decrease hardiness after a few days, but low minima can slow or even reverse de-hardening, resulting in fluctuating levels of frost hardiness (Leinonen, Repo and Hänninen, 1997). However, temperature-driven ontogenetic development towards budburst is irreversible, and once budburst begins, the shoots cannot harden again in response to low temperatures (Repo, Makela and Hänninen, 1990; Leinonen, Repo and Hänninen, 1997). Changed temperature patterns due to climate warming can thus lead to lower winter hardiness and premature de-hardening, with the risk of frost damage to shoots in spring.

Formation and growth of new shoots and vegetative organs and cessation of growth are other cyclic sequences of phenomena associated with the annual cycle. In addition to photoperiod, they are partly related to temperature during a year. Shoots and vegetative buds enter a state of dormancy in the autumn. Growth cessation is triggered primarily by night length, but low minimum daily temperatures may induce earlier growth cessation (Hänninen and Tanino, 2011). However, even when only photoperiod plays a role, entering dormancy in a time when temperature still allows further growth would mean that trees do not fully exploit the growing season.

Dormancy means that cell division and growth have ceased and bud development is completed. Thereafter, buds require chill temperatures (along with night length) to become responsive to warm temperatures. Chilling requirements differ among species and genotypes within species: trees with low chilling requirements flush earlier. The process of cell growth and division resulting in budburst is induced by temperature sum accumulation. The lack of chilling caused by climate warming can cause abnormal budburst in some species (Morin *et al.*, 2009). Moreover, elevated air temperatures during dormancy induction in late summer increase depth of dormancy, meaning that more chilling is required to break the dormancy and more degree-days need to be accumulated to induce budburst (Granhus, Floistad and Sogaard, 2009). Finally, leaf unfolding patterns during bud break vary strongly depending on life history traits such as evergreen vs. deciduous and shade tolerant vs. shade intolerant (Davi *et al.*, 2011). The final effect of climate change on the course of budburst phenology is thus hard to predict (Hänninen and Tanino, 2011).

Reproduction, i.e. flower and seed production, undergoes similar cyclic development triggered by climatic signals, physiological trade-offs and possibly predator escape strategies, a phenomenon known as masting (Herrera *et al.*, 1998). Saxe *et al.* (2001) argued that trees can afford the risk of losing or damaging reproductive organs as these can be easily compensated for by a heavy seed crop during a more favourable year. This is true if such losses or damages remain a rare event. Frost events can significantly reduce seed crops, but so can unfavourable climatic conditions during seed maturation (for example high summer temperatures), which are predicted to increase under most climate change scenarios. Moreover, a changing climate can de-synchronize pollen production and female flower receptivity, leading to low effective density and poor seed quantity and quality (e.g. increased inbreeding in self-compatible species) (Alizoti, Kilimis and Gallios, 2010), particularly at range edges (Restoux *et al.*, 2008). With increasingly temporally distant suitable seed crops and proper recruitment conditions, the persistence of local populations can be endangered in the long term.

What is 'local' and is the local forest reproductive material always the best?

Environmental conditions vary between sites and therefore the degree of selection pressure also varies in different populations. This process leads to differentiation in adaptive traits of tree populations between sites. Natural selection operates to remove the least suited genotypes at a site and this is used as a basis for the "native species and local provenances should be preferred where appropriate" principle (MCPFE, 1993). In sites with a long period of occupancy (multiple generations), trees that are present currently are considered to have the most optimal genotypes after having undergone several cycles of natural selection. However, Gould (1997) argued that natural selection can only work on the material that is available. Therefore, the adult genotypes at a given site are only the best ones among those genotypes that were present at the site at the seedling stage, rather than being the best possible option for that site. In addition, it is difficult to define the exact size of a local population in forest trees (such as for those trees that exchange genes during reproduction), particularly when there are no strong environmental gradients and in species where pollen is dispersed over long distances. Topography, population density, flowering intensity and phenology and life history traits all influence the size of the local population. In wind pollinated European ash species, for example, adaptation operates at very broad scales of up to several hundreds of kilometres, whereas geographical distances influence differentiation more strongly in the insect pollinated *Fraxinus ornus* (FRAXIGEN, 2005).

The genetic diversity of a given FRM is the product of the original genetic material that colonized the site on which natural selection, drift and gene flow have acted. The relative influence of evolutionary and demographic factors can be investigated using a combination of molecular markers and provenance trials to provide information on the geographical scale of local adaptation. This information is crucial for selecting and using FRM in different sites and habitats.

The challenges of using the right forest reproductive material under climate change

The current pattern of genetic variation in forest trees and their adaptation to climatic conditions has occurred over evolutionary time scales lasting from thousands to millions of years. The rate of adaptive responses to environmental changes at population level depends on several factors, such as the level of genetic variation among inter-breeding individuals, the size of the population, the heritability of fitness-related traits, gene flow between populations, and the intensity, direction and duration of the selection pressure. Many forest tree species are known, or believed, to have high genetic variation in important adaptive traits (Petit and Hampe, 2006). They also have high fecundity, which creates a large gene pool for natural selection to work on. However, the unprecedented pace of anthropogenic climate change (Loarie *et al.,* 2009), coupled with the comparatively long generation time of many forest trees, means that there may be insufficient time for natural selection to give rise to populations adapted to new climatic environments (Jump *et al.,* 2006). Only when a tree population is initially large, environmental changes are not too severe and evolutionary potential is high, can it effectively survive by genetic adaptation (Gomulkiewicz and Holt, 1995).

Concerns that there is insufficient time left to ensure that adaptation occurs before tree populations face extinction have provided the impetus for intervention in the form of assisted migration (Aubin *et al.,* 2011; Hoegh-Guldberg *et al.,* 2008), i.e. in the context of this report, man-made transfer of FRM to a non-autochthonous place. The rationale behind assisted migration is that the predicted future habitat at the location to where the material is translocated matches the current habitat of stands from whence the material is taken. However, current and future habitat similarity is judged based on climate, which is far from enough for defining a suitable habitat. Also, the translocated FRM being significantly different from the local material, complex genetic interactions between the autochthonous and translocated FRM will occur, with uncertain results in terms of adaptation. The impact of this introduced diversity will depend upon the scale of planting, relative to that of the local population, and the degree of genetic difference between the populations.

Genetic adaptation will depend on the amount of genetic variation present in natural populations, as it is unlikely that new variation will be created via new mutations. Heritability measures the part of the variability of a phenotypic trait that is heritable in a population. The higher the heritability of a trait is, the more efficient selection is for a new, more adapted, phenotype is. Heritability of cold hardiness or flushing date is low to moderate (Bower and Aitken, 2006; Rweyongeza, Yeh and Dhir, 2010). Phenological traits frequently exhibit clinal variation along longitudinal, latitudinal or altitudinal gradients, as demonstrated by common-garden experiments with different provenances (Dæhlen, Johnsen and Kohmann, 1995; von Wuehlisch, Krusche and Muhs, 1995). This gives good prospects for FRM recommendations related to phenology. However, the responses to increasing temperature in the timing of various processes associated with the annual cycle have been demonstrated to differ among species, i.e. the same change in temperature may accelerate a bud-burst in one group of species, but delay it in another (Hänninen and Tanino, 2011). The question is whether such differences in reaction also exist among genotypes or provenances within a species. Research has not sufficiently addressed this issue. Moreover, a part of the heritable variation is epigenetic. In conifers, day length and temperature during zygotic embryogenesis and seed maturation (associated with both latitudinal and altitudinal differences) affect spring flushing, autumn growth cessation, height growth and frost hardiness (Johnsen *et al.*, 2005; Skrøppa, 1994). Ultimately, such epigenetic memory leads to rapid changes in phenological behaviour of the offspring of transplanted provenances after one generation (Skrøppa *et al.*, 2009). At present, no reliable mechanistic models of phenological processes are available as there is much uncertainty about the background physiological processes and external factors triggering them. The existing models accurately simulate past long-term phenology records, even if different models are based on substantially different assumptions (Saxe *et al.*, 2001). It remains questionable, however, whether any reliable predictions can be made about phenological behaviour of transferred material under climate change.

Several options are offered by FRM for mitigating climate change and adapting forests to climate change. However, there is no general consensus on the best way to use FRM, either for favouring local adaptation or for assisted migrations. Options on how to use FRM will depend on the objectives of management (production, protection, amenities), on the evolutionary past of the forest (whether it is genetically diverse or not), on its position in the distribution range of the species (rear edge, core, or leading edge) and within the ecological niche of species (marginal or central). Research, particularly provenance research and molecular genetics and ecology, will be foremost in helping design proper strategies, and legal requirements and regulations for implementing them.

LEGAL AND POLICY FRAMEWORKS

Council Directive 1999/105/EC

The legal framework in the European Union for the production and marketing of forest reproductive material (FRM) within the Union is based on Council Directive 1999/105/EC[1] which applies to all EU Member States. EU Directives lay down certain end results that must be achieved in every Member State. National authorities then have to revise their national laws to meet these goals, but are free to decide how to do this. The requirements of Directive 1999/105/EC are organized in relation to four different categories of FRM ('source-identified', 'selected', 'qualified' and 'tested').

The Directive sets up rules for the approval of basic material (determined by each member state) for the production and marketing of FRM. It also prescribes a registration, labelling and control system to allow the identification of FRM from the collection phase to the delivery to the end user.

The objectives of this Directive are to:

- ensure free movement of FRM within the EU;
- protect against the introduction and spread of organisms harmful to plants in the EU;
- provide high quality and genetically suited FRM for the various site conditions; and
- conserve forest biodiversity, including genetic diversity.

The scope of the Directive is limited to 47 species and artificial hybrids important for forestry purposes (listed in Annex 1 of the Directive). The Directive provides a common set of minimum requirements, but allows the EU Member States to impose additional and more stringent requirements for the approval of basic material and production of FRM in their own territory, using their national legislation. The exception is marketing – no other restrictions are

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[1] Available at http://ec.europa.eu/food/plant/propagation/forestry/forestry_leg_en.htm

acceptable other than those provided in the Directive. This provides special flexibility for Members States to regulate the production and marketing of FRM of the category 'source-identified' concerning the approval of basic material and the marketing to the end-user. The Directive does not include requirements concerning the end use of FRM, but Member States are free to determine requirements for this in their national legislation.

OECD forest seed and plant scheme

The Council Directive on marketing of FRM is harmonized with the OECD Scheme for the Certification of Forest Reproductive Material Moving in International Trade[2]. This voluntary scheme is open to all Members of the OECD as well as to any Member of the United Nations. There are four categories of reproductive material under the scheme ('source-identified', 'selected', 'qualified' and 'tested').

According to the decision of the European Union, forest seed and planting stock of all four categories produced in six non-EU countries under the OECD scheme and officially certified by the national authorities shall be considered equivalent to seed and planting stock complying with Council Directive 1999/105/EC.

National law on forest reproductive material – similarities and differences

Council Directive 1999/105/EC has been implemented into national law by all 28 Member States. Supplementary third states, such as Serbia, have adopted similar rules. Turkey has also adopted the text of the Directive and applies it strictly. All definitions concerning the type of material and categories were introduced without changes into national laws and regulations and are fully accepted by national authorities, forest owners and producers of FRM. The term 'production' is adopted in a uniform way when seed processing and handling is considered. The multiplication of parts of plants or *in vitro* propagation is considered as production of FRM only in some countries.

In all Member States, regions of provenance (also called seed zones) are delineated, based on a number of criteria, including ecological units or vegetation zones, phenotypic or genetic similarities, or a combination. The number and size of regions of provenance vary greatly between countries due to different approaches used for delineation, the complexity of site conditions, the composition of forest ecosystems in a country, and the economic importance of the species. Aspects related to climate change are not yet taken into consideration.

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[2] Available at www.oecd.org/fr/tad/code/46092739.pdf

Generally, the national legislations follow the requirements for approval of seed stands from the Directive. In nearly all Member States, an official inspection service checks the basic material before approval. In states with federal structures, such as Germany, Italy and Spain, this is done not at the national but at the regional level. Review of the approved basic material is recommended at between 10 years (most countries) and 15 years (e.g. Italy). In some national laws (e.g. Germany), no revision period is indicated, but revision is being done continuously. Italy applies special legislation concerning forest tree clones due to the economic value of poplar clones in the country.

Generally, an FRM supplier needs an official licence for trading material for forestry purposes. In many countries a register of suppliers is maintained. The licensing and registration is done by official bodies, but professional and ability tests are not always requested.

The master certificate is issued in all countries by a public authority, generally the local forest service or the local office of the national body. Seed testing is also done by authorized laboratories under public authority.

The official control is done with different intensities across countries. It includes field inspections with different temporal regularity and control of books and accompanying papers (master certificate and delivery papers). To facilitate the control for cross-border transfer, a Commission recommendation was adopted in February 2012 on guidelines for the presentation of information for the identification of lots of FRM and the information to be provided on the suppliers label or document. This document contains harmonized identification codes for different requirements, as listed in Article 13 of Council Directive 1999/105/EC, and serves as numerical translations of the text in the supplier’s documents or labels[3].

In many countries there are restrictions related to marketing of FRM, based on the protection of valuable local genetic resources. The restriction to marketing of FRM is based on results of ecological and genetic tests for certain species. In the case of ‘source identified’ it is based on quality criteria for approval of basic material of this category, which in these countries is subject to ‘more stringent requirements’ regarding criteria for approval, or restriction of this category for certain species as a whole.

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[3] Available at http://ec.europa.eu/food/plant/propagation/forestry/forestry_leg_en.htm

Table 1. Additional regulations, schemes and recommendations made by countries on forest reproductive material (FRM) (details are based on replies of member states to a questionnaire of the Working Group)

Detailed specification	Countries
1. Legal framework	
1.1 Controls or limitations regarding the production & commercialization of FRM (basic material, collection, breeding, controls	
Limitations concerning list of species	BE, FR, SI, IE
Additional list of species	HU, ES
Limitations for category source identified	BE, FR, DE, HU, LU, SI, CZ, IE, RS, IT,SK
Ministerial authorization for import of non-EU material	BG, FR; PL, HR, RS, SI (after professional opinion by SFI)
Voluntary certification scheme including reference samples	BG, FR, DE, UK, SI, NL (for additional non-directive species)
Re-inspection of seed stands	HU, PL
1.2 Requirements for maintaining minimal genetic diversity	
Number of individuals to collect from seed stands, varying by species and category	BE, CY, BG, HR, DK, DE, GR, IT, LU, NO, RO, SI, SK, UK, CZ, PL
Number of clones in seed orchards	HR, EE, FI, FR, DE, HU, NO, SK, SE, SI, CZ, PL, IT, SI
Minimum area to collect from	DE, GR, HU, LT, SI, UK, CZ, PL, IT (for selected species)
Distance between trees to collect from	BG, IT, PL, CZ, SI
Age of seed stands; number of mature trees to collect from	DE, HU, CZ, PL, SK
Designation of trees to collect from	BE, SI
Minimum number of genetically different trees	NL
Special rules for source identification	UK, NL (specifically for autochthonous seed sources), IT (collection and use within the same region of provenance), SI (additional criteria for approval)
1.3 National or regional regulations for the use of FRM in the forest	
Rules, specific exceptions, limitations, administrative authorization for transfer of FRM into and between eco-geographical regions or regions of provenance	BG, CY, HR, EE, FR, LT, NO, SK, SI, SE, UK, RS, PL
Species adapted to site conditions	BE, BG, FI, FR, GR, LT, SI
Species restrictions in protected areas (Natura2000, National parks, etc.)	BE, HU, SK, IE, HR, CZ, ES
Provenances adapted to site conditions for important species	BE, EE, FI, FR, GR, LT, NO, SI
Limitations on exotic species	BE, BG, CY, EE, FI, GR, HU, NO, PL, SK, SE, SI, ES (national legislation with list of invasive exotic species)
Use of local FRM required	GR, CZ (only in genetic conservation units), SI (recommended, but with a ranking of appropriateness)
Limitation on clonal FRM	SE, SI
1.4 National or regional regulations regarding subsidies linked to FRM	
Forest subsidies funding only if recommended FRM used	CY, FR, DE, GR, IT, PL, SK, SI, ES, UK, IE, CZ, RS
Forest regeneration funding linked to special conditions and/or use rules of FRM, like natural hazards, use of local FRM, adaptation to site conditions	FI, LT, LU, SI, RS, ES
Funding for production of FRM	SI, FI, RS
Funding for promotion of hardwoods	SE, IE, RS, ES
Funding according to positive list of FRM	DK, ES
2. Guidelines and recommendations	
2.1 Transfer of species or provenances (documents, web, etc.)	BG, FI, FR, HU, LT, SK, SI, ES, SE, UK, CZ, IT, NO
2.2 Use of species by ecological regions (documents, web, etc.)	BE, BG, DK, FR, HU, LT, LU, RO, SK, SI, ES, SE, UK, CZ, IT
2.3 Use of provenances by ecological regions (docs., web, etc.)	BE, BG, DK, FR, DE, HU, LT, NO, ES, SE, UK, IE, CZ, IT, SI
2.4 Other guidelines and recommendations	
Number of trees to be collected	FR, NO, DE, ES, SI
Production of FRM: diversity, no. of trees, no. of ramets per clone	ES, FI, DE, SI
Diversity recommendations for state forests	PL
Use of FRM for close to nature forestry	DK
Quality requirements for marketing of FRM	ES

RECENT DEVELOPMENTS IN POLICY AND LEGAL FRAMEWORKS

New traceability and certification systems for forest reproductive material by means of genetic markers

For official controls, proper documentation through master certificates and delivery papers is an important element. The often long-distance transport during production, from seed harvest to planting, facilitates mislabelling or erroneous declaration of the origin of FRM. Therefore, methods to specifically test the origin of FRM, irrespective of at which step the samples are taken (harvesting sites, seed lots, or reproductive material grown in nurseries), are clearly needed. DNA markers open up possibilities for control techniques that are yet more precise and more efficient. Such systems are used to verify the origin of FRM, to check the number of trees from which the seed was collected, to identify tree species, hybrids or clones, and to check the parent-offspring relationships. Control tools based on genetic tests are generally not foreseen in the legislation, but they can be implemented under private law.

In Germany, two almost identical certification systems are currently in place, i.e. the Certification Scheme for Tracing the Origin of Forest Reproductive Material in Southern Germany (ZüF; http://www.zuef.de/) and the FfV Certification, supported by ISOGEN and the Association of Forest Seeds (ISOGEN; http://www.isogen.de/) (Konnert and Hussendörfer, 2002; Konnert and Behm, 2006; Konnert and Hosius, 2008). Both systems aim to verify and trace the origin of FRM from harvesting and seed processing to the raising of seedlings in nurseries. They are essentially based on reference samples and on the comparison of their genetic composition using a species-specific array of different molecular markers. The reference samples are collected at different stages of FRM production (harvest, cleaning of seed and/or mixing of the seed lots, and plant delivery) and they are centrally stored. To increase the efficiency and to reduce costs, only a randomly selected subset of samples is selected and analysed. The molecular marker allele frequencies are used to assess the genetic similarity or dissimilarity of the reference samples. Both systems are open for producers of FRM in all European countries.

In Austria and Slovenia, reference samples are taken from every tree harvested for seed and stored for prospective controls. In Slovenia, the regulation on confirmations and master certificates for FRM and its modifications (UL RS 11/2003, 19/2004, 55/2012) demands that the responsible person of the producer collects a sample of living tissue (e.g. a living branch, three wood cores including living cambium, cones, conelets, beechnuts, etc.) from each tree used for seed production, delivers it to the authorized professional field officer, who then sends all material together with a copy of the confirmation document to the Slovenian Forestry Institute (SFI). Once the material is received, DNA is extracted and stored at -85°C until processing.

A new approach based on DNA fingerprinting can efficiently verify the origin of seed sources without the above-mentioned use of multiple reference samples (Degen, Holtken and Rogge, 2010). The authors used only a sample of adult trees within oak seed stands and the control was directly made for each suspicious plant or a group of suspicious plants by the use of multi-locus genotype assignment. However, this new method is not yet in general practice.

The Nagoya Protocol on Access and Benefit-Sharing

In October 2010, the 10th Conference of Parties to the Convention on Biological Diversity (CBD) adopted an international agreement called the Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization (Access and Benefit Sharing – ABS). The aim of the protocol is – in very simple terms – to facilitate access to genetic resources and to ensure the fair distribution of benefits arising from their use by establishing a clear and transparent legally binding framework. The “utilization of genetic resources” is defined in the Nagoya Protocol as “to conduct research and development on the genetic and/or biochemical composition of genetic resources, including through the application of biotechnology” (CBD, 2011). Therefore, the protocol does not apply to the use of genetic resources for production purposes, such as obtaining seeds for growing and planting seedlings as part of normal forestry operations. The Nagoya Protocol requires that users, including scientists, companies and individuals utilizing genetic resources, and traditional knowledge associated with these resources, from other countries for research and development purposes, have to obtain in advance:

- Permission from the country of origin of the genetic resource and a written endorsement, termed “prior informed consent” (PIC).
- After obtaining the PIC, the user of the genetic resource has to negotiate conjointly on a bilateral level with the country of origin the terms and conditions of the exchange (including a set of benefits on “mutually agreed terms” – MAT).

The protocol is intended to increase legal certainty and transparency for the exchange of genetic resources and related information. Rights and obligations deriving from any existing international agreement shall not be affected by the implementation of the protocol. In October 2012, the European Commission presented a proposal for an EU ABS Regulation to implement the elements on compliance of the Nagoya Protocol for the European Union. Subsequently, the European Parliament and the Council adopted Regulation ((EU) No 511/2014) on ABS on 16 April 2014. It entered into force on 9 June 2014 and applies from the date the Nagoya Protocol itself entered into force (12 October 2014).

There is a consensus that the exchange of forest genetic resource (FGR) for research and development needs to be facilitated and intensified under climate change. However, at the moment it is not entirely clear how the implementation of the Nagoya Protocol and the EU regulation ((EU) No 511/2014) will affect the exchange of forest genetic resources for research and development, including between EU member states in order to maintain the free circulation of FRM on the EU internal market. Unfortunately, it is expected to increase transaction costs and create administrative hurdles before countries have managed to establish fully functional and transparent national ABS regulatory systems (e.g. Koskela *et al.*, 2014).

CURRENT GUIDELINES AND RECOMMENDATIONS RELATED TO FOREST REPRODUCTIVE MATERIAL

Recommendations adopted by FOREST EUROPE

The FOREST EUROPE process (formerly the Ministerial Conference on the Protection of Forests in Europe – MCPFE) has adopted several resolutions on forest genetic resources, including FRM.

Strasbourg Resolution S2 (1990) set up principles for the conservation of forest genetic resources in Europe and the cooperation between the countries in this field. It requested the establishment of a functional but voluntary instrument of international cooperation to promote and coordinate: (1) *in situ* and *ex situ* methods to conserve the genetic diversity of European forests; (2) exchanges of reproductive materials; and (3) monitoring of progress in these fields. Subsequently, EUFORGEN was established in 1994. Resolution S2 also recognized that the use of genetically-improved materials is of great importance for afforestation and restocking, in particular where this is for the purpose of the production of timber. Furthermore, Resolution S2 requested that countries keep records, at least for public forests, of the exact identity of the reproduction materials used for planting and regeneration.

According to **Helsinki Resolution H1** (1993), native species and local provenances should be preferred where appropriate. The use of species, provenances, varieties or ecotypes outside their natural range should be discouraged where their introduction would endanger important or valuable indigenous ecosystems, flora and fauna. Introduced species may be used when their potential negative impacts have been assessed and evaluated over sufficient time, and where they provide more benefits than do indigenous species in terms of wood production and other functions. Whenever introduced species are used to replace local ecosystems, sufficient action should be taken at the same time to conserve native flora and fauna.

Helsinki Resolution H2 states that the conservation of genetic resources of forest taxa should be recognized by countries as an essential element of sustainable forest management. Furthermore, **Helsinki Resolution H4** encouraged studies on genetic variability of regionally important tree species in response to climate change and increased concentration of carbon dioxide, and on the degree and rate of evolutionary processes and adaptation.

The **General Declaration of the Lisbon Conference** (1998) preferred the use of native species and local provenances for reforestation and afforestation. Annex 1 of **Lisbon Resolution L2** introduced a quantitative indicator on changes in the proportions of stands managed for the conservation and utilization of forest genetic resources (gene reserve forests, seed collection stands, etc.). According to the management guideline of Annex 2 of Lisbon Resolution L2, adequate genetic, species and structural diversity should be encouraged and/or maintained to enhance stability, vitality and resistance capacity of the forests to adverse environmental factors and to strengthen natural regulation mechanisms. Furthermore, it stated that management plans should take account of endangered or protected genetic *in situ* resources, and that only those introduced species, provenances or varieties should be used whose impacts on the ecosystem and on the genetic integrity of native species and local provenances have been evaluated to avoid or minimize negative impacts.

The **Vienna General Declaration** (2003) recalls the importance of the maintenance, conservation, restoration and enhancement of biological diversity of forests, including their genetic resources, both in Europe and on a global scale. According to **Vienna Resolution V4**, countries should promote the conservation of forest genetic resources as an integral part of sustainable forest management and continue the pan-European collaboration in this area. Furthermore, it again urged countries to promote natural regeneration, and regeneration with native tree species and provenances.

In 2008, the **Warsaw General Declaration** recalled the maintenance, conservation, restoration and enhancement of the biological diversity of forests, including their genetic resources through sustainable forest management.

In 2011, the **FOREST EUROPE** process decided to launch negotiations for a Legally Binding Agreement on Forests in Europe. An Intergovernmental Negotiating Committee (INC) for this agreement started its work in 2012 with the aim to conclude the negotiations by 2013. The draft negotiated text, as it stands after the resumed fourth negotiating session (Geneva, Switzerland, 7–8 November 2013), does not include any direct reference to the use of FRM or the conservation of forest genetic resources. However, they are indirectly covered by the provisions of the draft agreement. One of the objectives of the draft agreement, for example, is to "to maintain, protect, restore and enhance forests, their health, productivity, biodiversity, vitality and resilience to threats and natural hazards, and their capacity to adapt to climate change as well as their role in combating desertification". In October 2015, an extraordinary Ministerial Conference will discuss those issues that could not be agreed by the INC.

Regional activities – the *Silva Mediterranea* example

Silva Mediterranea, which became an FAO statutory body in 1948, is an international forum dedicated to Mediterranean forests. It incorporates countries from three continents (Europe, northern Africa and Near East) that not only have very different legislation and environmental, social and historical backgrounds, but also different organizational structures and needs. *Silva Mediterranea* uses the OECD scheme as its main reference for FRM certification, but some of the general criteria and guidelines are supported and/or influenced by European Directive 1999/105/CE, especially in the Northern Mediterranean region. The FRM work of *Silva Mediterranea* focuses on the creation of common criteria in order to facilitate international trade. For example, Topak (1997) carried out an inventory of the basic material present in 17 *Silva Mediterranea* countries according to the OECD scheme. *Silva Mediterranea*, and especially its Working Group on “Forest Genetic Resources in the Mediterranean Region”, promotes the use of existing knowledge and expertise through dissemination and training to match local needs.

Silva Mediterranea established provenance trials in collaboration with IUFRO in the 1970s. These trials were located in nine Mediterranean countries and included the Mediterranean pines, firs, cedars and cypress as well cork oak (Besacier et al., 2011). The provenance trials have been inventoried recently for the establishment of a new database (Pichot, 2007; http://w3.avignon.inra.fr/ForSilvaMed/), developed by INRA-Avignon and Silva Mediterranea partners. This work was partly carried out in the framework of the TREEBREEDEX project (www.treebreedex.eu).

According to its work plan, the FGR Working Group of Silva Mediterranea will promote the development and training of a new generation of researchers able to communicate and develop scientific and technical capacities to adapt FGR and forests to climate change (Ducci, 2009; http://www.fao.org/forestry/19318-0ebc0835b0ffd94872e2249feaf1c10d6.pdf). For this purpose, the Working Group prepared recently a European Cooperation in Science and Technology (COST) Action titled “Strengthening conservation: a key issue for adaptation of marginal/peripheral populations of forest tree to climate change in Europe” (MaP/FGR). This project was launched in November 2012 and it involves several European countries in addition to the Silva Mediterranea partners, as well as international institutions, such as Bioversity International, FAO, EFIMED and IUFRO. The project also aims at promoting the appropriate use of FRM in the context of climate change.

National provenance recommendations and support tools

As explained above, Council Directive 1999/105 only sets a framework to be subsequently addressed by the national legislation of the EU Member States. Most national laws regulate only production and commercialization, but do not regulate the use of FRM. In order to secure the correct use of FRM, some Member States have included in their national laws recommendations to forest owners on the use of FRM. In other Member States, forest administrations make recommendations for the use of provenances in different regions. They mostly rely on the concept of provenance regions, which are areas within which reproductive material can be transferred with little risk of being poorly adapted to their new location. They are generally based on the results from provenance trials and the long-term experiences of practical forestry. In general, climatic parameters are not given any preferential consideration.

Provenance recommendations often have the role of a decision support, and forest owners are not obliged to follow them. However, they can be binding in some countries under subsidiary schemes. Financial support for those recommendations is crucial for successful implementation. European countries have reached different levels of implementation of these recommendations. In many European countries, the provenance recommendations are given for either all or only a sub-set of species in the national lists.

The form of publication of the recommendations is also different from country to country. They range from paper documentation to internet-based interactive decision tools linking the planting site in an ecological zone with recommended FRM available in a nursery. Most recommendation systems are a combination of documents and maps available on the internet.

In Germany, for example, the forest administrations of the federal states provide forest owners with recommendations for the use of provenances in different regions. They differ in the presentation form between the states, but follow a common consensus: the local provenance is preferentially recommended (e.g. for Bavaria see: http://www.stmelf.bayern.de/wald/asp/014927/index.php).

In France, recommendations for the use of French FRM are published under http://agriculture.gouv.fr/conseils-dutilisation-des-provenances-et-variet-es-forestieres. A revision of the French recommendations is currently ongoing in the context of climate change. The seed tree company Vilmorin also gives recommendations for the utilization of seed from Douglas fir seed orchards, based on site characteristics, budburst, growth performance (wood production) and genetic variability (see www.vilmorin-tree-seeds.com).

In Italy, several modes are used to provide guidelines and recommendations. These include formal guidelines, technical papers issued based on the results of research programmes (http://www.ricercaforestale.it/), and networks of regional forest services and research institutions coordinating relevant activities.

In Slovenia, the Forest Act requires that site-adapted FRM has to be used in any reforestation or afforestation with planting and sowing. Accordingly, the use of FRM in the same or in different provenance regions and elevation zones has recommendations defined by categories, from most appropriate, very appropriate, appropriate, less appropriate, appropriate only in exceptional circumstances. The recommendations are part of the regulation on delineation of provenance regions and its modification (Ur.l. RS 72/2003, 58/2012). Additionally, the Slovenian Forestry Institute published (in Slovenian) the EUFORGEN Technical guidelines for conservation and use of forest genetic resources with Slovenian recommendations for the use of FRM.

In the United Kingdom, the Forestry Commission publishes Information Notes, which provide recommendations for provenance selection for UK conditions. The first choice of provenance should be a "selected" seed stand, preferably growing in the same region of provenance as the planting site. As an alternative, material from selected stands in northwestern Europe (Netherlands, northwest France, northern Germany and Belgium) is indicated. Seed stock from central and eastern continental Europe should not be planted, as it is poorly adapted to the UK in terms of growth rate, survival, phenology and resistance to foliar diseases. In some respects, the climatic dimension is taken into account by the statement that northward movement of genetic material (by hundreds of kilometres) may result in a gain in vigour compared with local-source provenances, whereas any southward movement is considered ill advised.

In Ireland, the Forest Service (Regulatory Authority) provides recommendations for provenance choice based on results from an extensive series of provenance trials. Seed collected from registered seed stands in Ireland should be used when possible. A comprehensive table of acceptable seed origins is provided in the guidelines, and for European species it is required that the first choice is registered Irish material. If this is unavailable, then registered British (English or Welsh), French (north of Paris), Belgian, Dutch, Danish or German (north of Frankfurt) reproductive material from selected seed stands should be used.

In Spain, the Ministry of Agriculture, Food and Environment, in collaboration with the Spanish Forest Research Centre (INIA-CIFOR), has published the regions of provenances and recommendations for the use of FRM for those tree species that are covered by the legislation at the national level. There are also recommendations at the regional level, such as those in Castilla y Leon, and private forest owners should follow them if they want to receive grants from the public administration.

Some recommendation systems are interactive decision tools, internet-based, linking plant sites in ecological zones with recommended FRM available in nurseries. In Austria, an online platform (www.herkunftsberatung.at) was created by the Research and Training Centre for Forests, Natural Hazards and Landscape (BFW) in collaboration with the forest administration to support forest owners in provenance selection. This online service is based on the national register of approved seed sources, results of provenance trials in Austria and annually declared seed collections.

In Denmark, the Danish Nature Agency of the Ministry of Environment, in cooperation with the University of Copenhagen, provides species and provenance recommendations through a web-based tool that guides and helps users to select appropriate material suitable for the planting purpose and locality (www.plantevalg.dk). The system has two components: a database where information about species and seed sources is available, and a recommendation function through which guidelines for selection of species and seed sources for different planting purposes are made available. The guidance process has three levels: the first level is a species recommendation (including planting purpose), the second level consists of the recommendations for provenances and selected material (seed producing), and the third level is information on where to buy the plant material (i.e. availability of seed sources in different nurseries). The system is a web-based geographical interface, where users can locate their forest within 13 ecological zones. The selection criteria are transparent and well documented. Information on possible subsidies is included. The system also allows the user to provide comments in order to improve the system.

Norway has an internet-based recommendation system, which is hosted by the Norwegian Forest Seed Centre (www.skogfroverket.no). Customers can choose their planting location and elevation and will get suggestions for suitable seed lots, with differentiation between optimal and usable (according to the internal Norwegian transfer rules). After choosing a certain seed lot, the customer will also get information about which nursery is producing plants from that lot at that time. The suggestions for seed lots from stands are made according to current legislation, and no climate change effects are considered. Recommendations for deployment zones for improved orchard material are made with a certain regard for possible climatic changes. As the prediction of future site conditions in Norway is very difficult because of the mountainous landscape with steep elevation changes within small distances, tree breeding and the connected trials are considered a very important tool to explore and use the "genetic abilities" of the species in an adaptation process to future climate.

Sweden has a similar recommendation system, which is hosted by Skogforsk (http://www.skogforsk.se/sv/KunskapDirekt/Alla-Verktyg/Plantval/). Suggestions for suitable seed lots are made with respect to future climate scenarios.

Scientific and practical considerations on the choice of provenances under climate change

The success of tree planting efforts depends fundamentally on the use of appropriate FRM that is able to survive and thrive at the planting site. The decisions taken today on selecting suitable material for forest regeneration must be made in the light of the climate projections for the next 30–200 years, when the trees planted now will be mature, even if this leads to stands that are adapted sub-optimally to the current and future conditions. The use of appropriate FRM and the ability to verify the origin of FRM is therefore of vital importance for our efforts to prepare for and manage the effects of climate change on European forests.

Genetic diversity provides the raw material for adaptation and it therefore has an important role in maintaining resilience of forest ecosystems in the face of threats associated with climate change. A high level of genetic diversity in a population increases the probability that a proportion of the genotypes survive into the future by increasing the adaptability of that population. Therefore, it is imperative that FRM with high levels of genetic diversity should be chosen to maintain genetic adaptability at a particular site. This is particularly true at the rear edge of geographical distributions, where local conditions might already be ecologically extreme and where climate change effects are expected to be high. Conversely, FRM from these marginal populations can demonstrate local adaptation to xeric conditions and be a valuable source of FRM for reforestation under climate change (St. Clair and Howe, 2007; Mátyás, 1994; Robson *et al.,* 2011).

There are different approaches to preserve or increase genetic diversity and to prepare forests for the future. One option could be to adopt a so called "portfolio" approach and plant a mix of provenances alongside the current population, using climate change predictions to guide the choice of provenances for the future (e.g. Hubert and Cottrell, 2007). A second, higher-risk, approach would be to introduce FRM from a single provenance from a location with a climate similar to that predicted for the site. The assumption is that the translocated provenance would contain genes more suitable for survival in the future climate. A third option is to rely on natural regeneration and harness the high genetic variability and phenotypic plasticity occurring in most forest tree species, and use forest management to create conditions where selection can occur on naturally regenerated seedlings – the stage at which tree species experience the most severe selection pressures.

Alternative approaches for seed zone delineation and seed transfer recommendations under climate change

Traditionally, the approach to seed transfer regulation on both legislative and voluntary levels has been a geographical one, based on seed zones or regions of provenances, which should contain populations with identical or similar adaptive features. This was criticized by Mátyás (2007), for example, who argued in favour of using climatic criteria rather than geographical origin as a basis for seed transfer. Moreover, seed zones were often delineated based on environmental (mainly climatic) homogeneity rather than genetic variation patterns or homogeneity of adaptive responses demonstrated by field trials. Therefore, new approaches to the delineation of seed zones or regulation of seed transfer have appeared in recent years.

In Canada, the first seed collection zones were delineated in 1940 on Vancouver Island. In 1962, Haddock proposed seven seed collection zones for the entire British Columbia. This concept was later refined in the early 1970s, when 67 zones for seed collection were delineated in all provinces (Ying and Yanchuk, 2006). The basis for the delineation was a preliminary approximation of ecological classification of forest lands. A new revision, done in the early 1980s, also took into account results of provenance trial results from 24 seed zones. Simultaneously, for the first time, the "floating principle" of seed transfer was introduced (Rehfeldt, 1983). It means that seed transfer limits are no more given by the fixed seed zone boundaries but rather they are defined along adaptive clines along geographical distances. In practice, this means that seedlings may be planted outside the seed zones in which the seed was collected, so long as the transfer is within the adaptive limits of the seed source based on a statistical model (e.g. Wu and Ying, 2004). The model defines the degree and direction of local optimality along longitude and elevation. Beside this scientific approach, the operational version of seed transfer guidelines in British Columbia incorporates knowledge and experiences of local foresters to cover specific situations across large forested landscapes that cannot be predicted by models.

The introduction of the climatic (ecological) distance concept (Mátyás, 1994, 1996) opened the possibility of applying climatic variables instead of geographical ones for transfer guidelines. With the improvement of statistical models and software able to convert physical to climate distance, Hutchinson (2004) and Wang *et al.* (2006) included climate variables in seed transfer rules. On the basis of this, the seed transfer rules in British Columbia were re-examined and slightly changed in light of climate change (British Columbia Ministry of Forests, Lands and Natural Resource Operations, various dates). Now it is allowed to move most species in most areas 100 to 200 m upwards in elevation.

In the Pacific Northwest (Oregon and Washington States), seed zones were first established in the late 1960s, especially following requests from the expanding tree improvement programmes for Douglas fir. A seed zone was defined by a certain geographical area within which seed can be collected and replanted, with the expectation that the resulting stands will be adapted to the conditions of the area. First seed zones were based on differences in climate and vegetation and they were subdivided by elevation (150 m or 500 ft) (Johnson *et al.,* 2004). These zones were slightly revised in 1973 (Tree Seed Zone Map, 1973). Based on new results on adaptive traits from common-garden studies and provenance trials, the tree seed zones were reviewed, extended and made species-specific (Randall, 1996; Randall and Berrang, 2002). The new recommendations for seed movement in this region are mainly based on genecological research using common-garden experiments (Johnson *et al.,* 2004; St. Clair and Howe, 2007; St. Clair, Mandel and Vance-Borland, 2005). In nursery studies, dozens of adaptive traits and environmental parameters were measured. To simplify the analysis of the complex data sets, these traits were combined into a few principle components that summarize most of the variation. St. Clair, Mandel and Vance-Borland (2005) showed that two composite variables explain much of the variation among individual traits and among locations.

The first principle component, highly related to minimum temperatures in winter months and dates of last spring and first autumn frost, showed an east-west cline associated with elevation and temperatures. Low temperatures appear to have resulted in natural selection for traits of earlier bud-set, presumably to avoid autumn frost, and faster emergence presumably to promote seedling establishment as soon as conditions are favourable in the spring.

The second principle component was correlated with precipitation and maximum temperatures in the summer months, and shows a north-south cline. According to the authors, selection for earlier budburst could be a mechanism to ensure sufficient early growth before summer drought becomes a limiting factor. The risk of maladaptation was defined as the proportion of non-overlap between the normal distributions of the current population and the population in the future (predicted based on climate scenarios) for the first composite variable. Based on this kind of studies, researchers can develop seed movement guidelines in the context of climate change. The results of the above-mentioned study suggest, for example, that Douglas fir populations should be moved 450–1130 m higher in elevation and 200–540 km northward to match climates expected by the end of the 21st century. Ukrainetz, O'Neill and Jaquish (2011) used this approach to develop both seed zones and guidelines for "floating-principle" (focal-point) transfer for *Picea glauca* and *P. engelmannii* in British Columbia. They concluded that the focal-point approach offers larger areas to which FRM can be transferred at a given risk level of maladaptation.

In Austria, the outcomes of extensive provenance experiments with Norway spruce established by K. Holzer were used to develop transfer guidelines for the Alpine region (Kapeller *et al.*, 2012). The authors used a population-response approach based on an annual heat-moisture index, where the response functions were calculated both for individual populations and clusters of populations based on the present provenance regions, altitudinal belts and climatic data. This approach allowed identification of best-performing population groups under current climate as well as under climate projection to 2080. Interestingly, populations showing the best productivity indices originate from regions phylogenetically distinct from the core distribution area of Norway spruce, suggesting that population history might explain part of the variation in climate response among populations. The authors suggested that populations from currently warm and drought-prone areas seem to be well adapted to the respective climate conditions, and may be appropriate candidates for extended utilization in the future.

Enhancing the genetic potential of tree population to adapt to climate change is also an option that needs to be considered. Savolainen *et al.* (2004) quantified genetic variation of growth and hardiness traits within Scots pine populations in Finland. They found relatively high heritabilities of phenological traits and a strong genetic differentiation between northern and southern populations (Q_{ST} = 0.86). The authors used a simulation approach to test whether Scots pine in northern Finland can change to the new predicted optimum through migration and local selection during the next 100 years, assuming that the new phenotypic optimum can be deduced based on the current match of temperature sums and phenotypic means. The simulation showed that the adaptive response to climate change will lag behind the moving optimum. Although no particular recommendations for human-mediated provenance transfer are given, the authors suggest that artificial regeneration with suitable seed sources can increase the proportion of adapted genotypes.

SCIENTIFIC BASIS FOR FOREST REPRODUCTIVE MATERIAL TRANSFER GUIDELINES

Methodological aspects of forest reproductive material transfer based on provenance research

The molecular basis of adaptation has been the subject of intensive studies during the last decade, using methods of both forward and reverse genomics. However, adaptive molecular markers are generally still under construction and have not been used for large-scale mapping of genetic variation to an extent comparable with neutral markers. Therefore, common-garden experiments, and especially provenance trials, remain the main source of information about adaptive processes and their outcomes in forest trees.

The main aim of the provenance research is the identification of flourishing and sufficiently adapted tree populations that can be used as seed sources for reforestation (König, 2005). Nevertheless, provenance trials also have other objectives, some of them purely scientific, namely the identification of the character (ecotypic or clinal) and main geographical trends of variation of phenotypic traits.

The existing spatial frameworks for the recommendations on FRM transfer (regions of provenance, seed zones and breeding zones) are generally based on climatic or biogeographical zoning rather than outcomes of provenance trials. The idea underlying this approach is that local adaptation is the most important ecological force shaping genetic variation, and that climate and photoperiod (i.e. factors associated with the geographical location) are the main drivers of natural selection. There is, however, no unanimity about the reasonable size or number of such zones among countries. Neither there is a consensus about the principles and methodologies on which they should be based. Sometimes empirical data provide no support for the existing zones (Isik, Keskin and McKeand, 2000).

Empirical information about the behaviour of the transferred FRM in terms of yield, growth, survival and tree quality has been used for a long time in decisions about appropriate material for reforestation. They were based mainly on practical experience (e.g. import of Slavonian oak to central Europe) or anecdotal information from provenance trials about the best-performing provenances. The term ‘provenance’ is used here in a very narrow sense, denoting a local population or a very small region (such as Polish spruce provenances Istebna or Rycerka). However, a strong genotype-by-environment (G×E) interaction is typical for forest trees, meaning that the 'best' provenances need not necessarily be the best everywhere.

In modern provenance experiments, numerous provenances have been repeatedly planted on a series of trial plots under a wide range of environments. Such experimental set-ups allow testing of the reactions of provenances to transfer: on the one hand, determining the environment where a particular provenance performs best; on the other hand, choosing the optimum provenance for a particular site. To derive climate-related responses of tree populations from broadly designed provenance trials, two primary approaches have been developed: general transfer functions, and population response functions (Aitken *et al.*, 2008; Rehfeldt *et al.*, 1999). They can be used as an alternative basis for provenance recommendation (Ukrainetz, O'Neill and Jaquish, 2011) and may provide support for the delineation of provenance regions.

General transfer functions relate fitness-related traits of the planted trees to geographical or climatic distances between provenances and common-garden locations (i.e. the difference of geographical or climatic variables between the site of origin and the site of plantation (cf. Mátyás, 1994; Rehfeldt *et al.*, 1999). The response of a population to transfer is expected to vary along the ecological-distance gradient in a non-linear manner. The maximum of the response function determines the rate of transfer at which the performance of a population is the best. Various types of unimodal response functions have thus been used to model this relationship (Gaussian, Weibull, beta, 2nd order polynomial). Typically, data from different test sites, even from different experiments, are pooled together to develop a general transfer function, assuming that the shape and peak locations of transfer curves do not vary significantly among environments (Rehfeldt *et al.*, 1999).

Population response functions describe the norm of reaction of an individual population to a range of test site environments. Methodology is very similar to general transfer functions, but the provenances are not considered jointly. Naturally, this approach requires that a provenance is repeatedly planted over a representative number of trial plots covering a sufficiently broad range of climates. Optimal transfer rates of populations may differ from each other, but they frequently exhibit geographical continuity, and sometimes range-wide trends. They can be thus used for the delineation of adaptively homogeneous areas, where populations exhibit similar reactions to climatic conditions.

The choice of proper climatic proxies is the crucial issue in any approach based on a mathematical modelling of tree-climate relationship. The reactions of tree populations on transfer need not follow geographical gradients (longitude or latitude), and crude climate indicators, such as mean annual temperatures or vegetation-season precipitations, do not necessarily describe properly those aspects of climate that are actual drivers of adaptation. Various types of climatic indices have frequently been used for this purpose (cf. Mátyás and Yeatman 1992; Rehfeldt *et al.,* 1999, 2002). The problem with these indices is their applicability in practice. No forester would probably be willing to calculate, say, degree-days (>5°C)-to-annual precipitation ratio (Rehfeldt *et al.,* 2002) of the reforestation site and all potential FRM sources to decide which FRM source is the proper one. However, such indices can be used in geographical information system (GIS)-based automated decision-support systems incorporating geographical distributions of climatic variables.

Alternatively, transfer rules have been generated by other statistical and geostatistical approaches. Beaulieu, Perron and Bousquet (2004) and Campbell (1986) proposed relative risk assessment, based on the extent of mis-match between the normal curves of the genotypic distributions of the local and the transferred provenances at a plantation site. Hamann *et al.* (2000) predicted the performance of seed sources at unknown locations with ordinary kriging based on provenance data from tests sites, and generated seed-transfer guidelines by principal component analysis of predicted reaction norms. Hamann, Gylander and Chen (2011) applied multivariate regression trees to partition genetic variation, using a set of environmental or geographical predictor variables as partitioning criteria in a series of dichotomous splits of the genetic dataset, again based on provenance trial data. St. Clair, Mandel and Vance-Borland (2005) identified relationships between traits and environmental variables at source locations by canonical correlation analysis. Regression equations were then used to map genetic variation as a function of the environment, using GIS tools.

Inferences about natural populations from provenance trials are associated with several caveats. One applies to the nature of what we call "provenance" and representativeness of provenance samples for the maternal population. Seeds for establishing trials, especially when extensive international experiments are organized, may in some cases be drawn from commercial seed lots. In that case, they might represent a mixture of only a few open-pollinated families, sometimes collected from a single stand, and typically represent the seed crop of a single year. Even when a seed crop is harvested from many mother trees, it may not properly represent the genetic structure of the whole mother stand. In a year of a poor crop, only some of the trees participate in fertilization. Moreover, genetic structures were shown to differ significantly also between crops of mast years (Konnert and Behm, 2000).

Another problem is associated with the manner in which experiments are established. Typically, seedlings are grown under optimal nursery conditions, and then planted in the field. Opportunities for natural selection at juvenile stages are largely circumvented by nursery practices. Early mortality is modified by wide spacing, control of the competing vegetation, and protection against large herbivores, rodents and pests.

Older provenance trials usually did not include ecologically marginal sites and do not cover the whole breadth of a species' distribution (Aitken *et al.*, 2008). With increasing age, mortality cannot be assessed because a part of trees need to be removed by thinning, and the number of standing trees may fall below the limit of representativeness. Most studies are based on measurements at juvenile age. For instance, a thorough study of climate responses of Norway spruce in Austria based on an extensive experiment (389 provenances on 29 sites) was published by Kapeller *et al.* (2012); however, height at 15 years was used here as a surrogate of growth vigour. It remains questionable as to what extent inferences based on such measurements can be extrapolated to adult age, which is more relevant from a practical point of view, unless juvenile-mature correlations for the traits of interest were found to be strong in previous experiments. Finally, the idea that provenance experiments may guide assisted migration as a measure for the mitigation of climate change (Mátyás, 1996) relies on space-for-time substitution. We do not have enough knowledge about the validity of this approach in this particular case. Even taking into account all these limitations, provenance experiments provide a huge resource for evolutionary ecology and climate change studies, and represent the most reliable basis for practical recommendations.

Case studies and transfer recommendations in selected species

The following case studies are intended to illustrate the principles explained in the previous sub-section, with examples of those tree species for which enough knowledge has been gathered by previous genetic studies and provenance experiments at the range-wide, or at least regional, level. Consequently, the choice is biased towards widespread, commercially important species, because the research in the past primarily focused on this group of species. Although the selection of species is partly unbalanced from the point of view of life-history traits, it is at least balanced with respect to distribution: boreal (Scots pine), temperate (European beech, silver fir) as well as Mediterranean species (Greek fir, Bornmüller's fir, Nordman fir, Aleppo pine, Calabrian pine) are represented. Douglas fir was also included as an example of an introduced tree species that is widely used in European forestry.

Scots pine (*Pinus sylvestris*)

Scots pine is a pioneer species that spontaneously regenerates after major natural or human disturbances, if weed competition and grazing pressure are low. The species grows mainly on poorer, sandy soils, rocky outcrops and peat. The species is wind-pollinated and has both male and female flowers on the same tree. Flowering is regular; female flowering starts at the age of 20–30 years. Abundant male flowering appears some years later. Mast years are relatively frequent but at the boreal forest limit seed maturation is impeded by the short growing season; mast years may occur as seldom as once or twice in 100 years (Mátyás, Ackzell and Samuel, 2004). The high migration potential of both pollen and seed results in effective gene flow within the contiguous range, causing a distinct, clinal pattern of variation within the species, at least for adaptive traits. This is typically the case with growth and phenology characters, which are determined primarily by temperature. The selection of Scots pine as one of the model species for case studies was motivated by the importance of Scots pine as a valuable commercial forest tree species in large parts of its native distribution, which covers the whole Euro-Siberian range, making Scots pine one of the most widely distributed tree species on earth.

Towards the end of the 19th and the beginning of the 20th century, seed of forest trees was transferred across Europe without any regulation. Substantial amounts of Scots pine seed and cones were imported into Germany from Belgium, France, Austria, Hungary and Russia (Lüdeman, 1961). In Sweden and Livonia (present-day northern Latvia and southern Estonia), poor results were experienced with seed from central Europe, particularly seed from 'Pfälzer' pine from southwest Germany, which since then has a bad reputation (Langlet, 1938; Kurm, Meikar and Tamm, 2003). This experience underlined the importance of the origin of the reforestation material. For Scots pine, many provenance tests have been established (Giertych, 1991). The results show a significant differentiation in growth among populations with respect to the long-distance transfer of FRM. In general, transfer of northern populations from 57–67°N southwards results in reduced height growth and stem volume (Giertych, 1979; Oleksyn and Giertych, 1984). At the same time, populations originating from the central part of the species' range in Europe grow as well or better than local provenances at northern latitudes. This indicates that the Central European populations of Scots pine have a greater growth potential than the northern European populations. Statistical modelling approaches have revealed that climate change may lead to short-term plastic responses in contemporary populations of Scots pine, including large losses in growth and productivity in the central and southern parts of eastern Europe, modest losses in growth and productivity along the southern periphery of the species' distribution in Asia, and gains in productivity in the northern and eastern part of the distribution range (Rehfeldt *et al.,* 2002). Results indicate that provenance experiments can be efficiently used to predict growth response reactions of FRM transferred to new environmental conditions.

European beech (*Fagus sylvatica*)

European beech is an example of widespread broadleaved species with more or less continuous distribution in the centre of the range, although small and isolated populations occur at outer or inner range margins. As a wind-pollinated species, it is expected to be predominantly outcrossing and to exhibit high levels of gene flow, which has partly been confirmed by genetic studies (Merzeau *et al.,* 1994). In spite of this, within-stand spatial genetic structures indicate strong isolation-by-distance patterns (Chybicki *et al.,* 2009). The glacial history and Holocene migration of beech differ from most European widespread tree species. Although there were several glacial refugia in southern Europe, many refugial populations have not expanded, or have colonized only restricted areas, because the spread was blocked by lowlands with big rivers. The major part of the present-day range of beech (except Italy and southern Balkans) was colonized from a single source, located in Slovenia and Istria (Magri *et al.,* 2006). This explains the relatively low differentiation for neutral nuclear loci generally observed in European beech. The initial gene pools of beech subjected to natural selection were relatively homogeneous, except a gradual decline of allelic richness towards the range margins caused by recurrent founder effects during the Holocene migration (Comps *et al.,* 2001), which was only partially compensated for by gene flow. Therefore, clinal patterns for several phenotypic traits (especially phenology and cold resistance) observed in common-garden experiments are unlikely to result from isolation by distance and can be attributed to adaptation.

In the early 1990s, a large-scale international beech provenance experiment was established, containing 202 seed sources planted in two series of plantations (field trials), comprising 23 and 24 plantations, respectively. These trials are located in 21 European countries. The Apennine and Balkan peninsulas are strongly under-represented in the collection of the tested material in this experiment.

During 2006–2010, an integrated evaluation of the beech provenance experiment was accomplished within a COST action. In general, trial sites proved to have the most important effect on survival and growth (the respective variance components ranged from 30% to 70% of the total variance). The effect of seed source origin was considerably smaller, amounting to only 0% to 7%. At the same time, a significant provenance × trial-site interaction was observed for most growth traits, with variance component of 4% to 21% (Alía *et al.*, 2011). When averaged over the sites, no clear geographical trend in the performance of individual provenances was identified for survival, and only a weak correlation with latitude and climate parameters of the site of origin was observed for height growth. There was also no clear spatial pattern of the stability of the provenances (Finlay-Wilkinson joint regression model). Concerning height growth, it seems that there are populations that perform well over a broad range of environments.

In spite of significant G×E interactions, which obscure overall spatial trends in growth and survival, responses of provenance to transfer show quite clear geographical patterns. Gömöry (2010) analysed provenance-level response functions. He found clear geographical patterns for almost all combinations of response and the underlying climatic and geographical variables. In general, correlations between optimum transfer rates and the underlying variables were strong and significantly negative, whereas optimum environments were nearly the same for all provenances. This indicates that the extent of local adaptation is rather limited, probably due to big phenotypic plasticity of beech.

Mátyás *et al.* (2011) found that the growth performance of beech populations at the xeric limit of the distribution generally deteriorates with transfer into more continental climate (as quantified by the Ellenberg index). At the provenance level, there is marked differentiation. Maritime provenances show improving performance with warming and drier conditions, while continental populations display the opposite. The results propose a relationship between the climate of origin and the character of response to changing climate.

Spring and autumn vegetative phenology are generally considered important fitness-related traits. A comprehensive evaluation of leaf flushing done by Robson *et al.* (2011) confirmed that heat accumulation during the winter and spring (degree-hours >5°C) is the most important determinant of the timing of budburst, but photoperiod, chilling period and summer drought may play a role as well. The total span of average flushing times of provenances was 11 to 12 days almost independently of planting site. Irrespective of altitude, there is a general trend for provenances from the southeast of Europe in the Mediterranean and warm-continental regions to flush early in comparison with late-flushing provenances from the north and west of Europe, where Oceanic influences on the climate are strong.

Gömöry and Paule (2011) showed that late-frost damage is almost entirely determined by the budburst date. Strong correlations between height/diameter growth and length of vegetation season indicate that the timing of leaf flushing and shedding results from an evolutionary trade-off between effective use of the vegetation for photosynthesis and the avoidance of frost damage. If late frosts become frequent under climate change, transfer of reproductive material from the West to the East may become a viable mitigation option. Robson *et al.* (2011) suggested considering provenances from the southwest of Europe for future use under climate change, as they are adapted to Mediterranean environments and yet flush relatively late, and thus may be candidates to withstand climate change without being susceptible to late frost. However, these provenances are typically less productive.

Silver fir (*Abies alba*)

Silver fir is an example of a conifer species that has suffered serious range reductions over the last centuries, mainly through human influence (silvicultural preferences for monocultures of Norway spruce). Its natural range extends from 52°N (northern Germany) to 38°N (southern Italy) and from 22°E (eastern Romania) to 03°W (western Pyrenees) (Cremer, 2009). Its distribution is characterized by a central core in central and eastern Europe, and a fragmented marginal range with isolated populations. Silver fir is a monoecious and wind-pollinated conifer species and its seed are dispersed mainly through wind.

In the mixed mountain forests of central Europe, silver fir exhibits a specific role as a stabilizing element due to its deep seated root system and its ability to regenerate and survive long periods under shade (Cremer, 2009; Schütt, 1994). In the climate change context, silver fir is promoted by management plans in many parts of its natural distribution range as it is seen as a low risk alternative to the more vulnerable Norway spruce (*Picea abies*) (Brosinger, 2011).

From numerous genetic studies, it is known that as a result of migration history after the last ice age, human influence on forest ecosystems and natural selection processes, silver fir shows a high level of genetic differentiation at both a macro- and a micro-geographical scale (Konnert and Bergmann, 1995; Konnert, 1993; Vendramin *et al.*, 1999; Liepelt *et al.*, 2008). High genetic variation was found in Calabria (Bergmann, Gregorius and Larsen, 1990; Vicario *et al*., 1995; Camerano *et al.*, 2012), whereas populations at the northern edge of the natural distribution in northern Bavaria, Thuringia and Saxonia show very low genetic diversity (Konnert, 1993; Llamas, 1994). In this area, silver fir generally is of bad quality and shows decline symptoms. Seed harvests in these stands have, without exception, a high proportion of empty seeds, indicating genetic depression.

The large genetic differences are illustrated also by a variation in adaptive traits (Sagnard, Barberot and Fady, 2002) and growth behaviour in provenance trials (e.g. Wolf, 1994; Commarmot, 1995; Ruetz, Franke and Stimm, 1998; Ruetz, 2002). Even provenances originating from the same micro-geographical region (e.g. Calabria) differ significantly in height growth and budburst date (Hansen and Larsen, 2004).

The first provenance trial for silver fir was installed in 1905 by Engler in Switzerland (see Pavari, 1951). In 1924, Italy and France started an international trial with 20 provenances from the Pyrenees, the Alps and the Apennines (Pavari, 1951). Results showed a higher survival rate and resistance to drought effects in southern provenances (especially from Calabria) and a lower resistance to more continental climate conditions, compared with provenances from the Alpine region. The stronger "oceanic" disposition of the Calabrian provenance Serra S. Bruno was also confirmed by a two-site test carried out in Denmark (Hansen and Larsen, 2004) on 13 provenances from southern Italy (Calabria), central Italy, Germany (Black Forest), Romania (Carpathians) and Denmark. Height after 15 years, budburst and mortality varied significantly among provenances. In particular, in the field trial that was well protected against late frost in the spring and early frost in the fall by a shelter wood of larch, a high variance in height growth was observed.

Between 1986 and 1989, a silver fir provenance trial was established in southern Germany (Ruetz, Franke and Stimm, 1998). A total of 21 provenances covering the entire natural distribution range were planted in seven sites. After 20 years, provenances from the Carpathians in Romania and Slovakia showed the best growth and the lowest mortality. Among the central European provenances, those from the Vosges Mountains in France and from southwest Germany (Black Forest), performed particularly well. Below-average growth was detected in provenances from western France, Italy, Macedonia and populations from the northern border of the natural distribution range in northeast Bavaria. Populations from Calabria and Serbia had high mortalities (Ruetz, 2002). Based on results from genetic inventories and provenance trials, silver fir from the Carpathian region, especially from Slovakia and Romania, is recommended for planting to improve the situation of silver fir in southeast Germany. A prior condition is that material with provable identity is available (verification of the origin by means of genetic methods is possible, and done at random). This recommendation is based on practical reasons and it does not include any considerations of climate change.

Mediterranean firs

Eleven fir species, gathered under the term Mediterranean firs, occur in the Mediterranean Region. They grow at higher elevations, between 800 m and 2800 m, depending on the latitude, from the Pyrenees, to the Alps, the Apennines, Sicily and the Balkans (*Abies alba* Mill., *Abies nebrodensis* (Lojac.) Mattei, *Abies borisii-regis* Mattf., *Abies cephalonica* Loud.), to the Turkish Pontus and Near East (*Abies bornmuelleriana* Mattf., *Abies cilicica* (Ant. et Kotschy) Carr., *Abies equi-trojani* Aschers. et Sint.) Mattf.), and to the Caucasus range (*Abies nordmanniana* (Stev.) Spach.). The western group of species extends to the Iberian peninsula (*Abies pinsapo* Boiss) and to the Atlas mountains in Northern Africa (*Abies marocana* Trabut., *Abies numidica* Carr.). These species are able to produce hybrid species in introgression areas, such as *A. borisii-regis* (Panetsos, 1990) or geographical variants, e.g. between *Abies bornmuelleriana* and *A. equi-trojani* (Ata, 1990). Similar to *Abies alba,* the genetic differentiation of Mediterranean firs generally exhibits a geographical pattern in both neutral markers and phenotypic traits (Fady and Conkle, 1993; Parducci *et al.,* 2001; Ducci *et al.,* 2004).

The distribution range of some Mediterranean firs is very fragmented and often reduced to single, scattered and isolated populations, which are characterized by a very small effective size. *Abies nebrodensis*, *A. pinsapo* and *A. numidica* are the most endangered species with regard to climate change, with an expected upward shift of altitudinal zones.

In the 1970s, several international trials with Mediterranean firs were set-up within the IUFRO network. One of the first tests was established with the participation of France, Italy and Greece, containing provenances of *Abies bornmuelleriana*, *A. equi-trojani*, *A. nordmanniana* and *A. alba*. At the same time, FAO *Silva Mediterranea* expanded the trial with provenances of *Abies cephalonica*, which varied considerably in survival and growth.

In Italy and Greece (Panetsos, 1990; Ducci *et al.*, 2011), *A. cephalonica* populations from Mainalon (Veti and

Kapo), Parnassos (Koro and Mevr) and Cephalonia Island (Ceph) performed best, although the last-named was sensitive to late spring frost. In southern France, the Greek provenances Mainalon and Parnon yielded the best results and were therefore recommended for reforestation (Fady, 1993). Furthermore, *A. cilicica* has an interesting potential within the same bioclimatic range as *A. cephalonica*. Even though *A. bornmuelleriana* and *A. equi-trojani* are of interest for southern France, their cultivation should be restricted to acidic, high elevation and high rainfall sites.

Among the firs of the Pontus region, *A. bornmuelleriana* proved to have great vigour even in relatively arid environments. *A. bornmuelleriana* provenances from Kangal and Arag and the *A. equi-trojani* provenance Kazdag showed good performances for both height and diameter growth rates, whereas provenances of *A. nordmanniana* presented the worst results. Due to the popularity of *A. nordmanniana* and *A. cephalonica* as Christmas trees, reproductive material of these species is spread throughout Europe.

Mediterranean pines of the *halepensis* group (*Pinus halepensis* and *Pinus brutia*)

Pinus halepensis and *P. brutia* are among the 11 species of pines growing in the Mediterranean bioclimatic region. They are pioneer, prominent, low-elevation conifers with extensive distribution across the Mediterranean basin. The ability of both species to grow in the adverse climatic conditions of the Mediterranean region, combined with their fast growth on favourable sites, make them very important multipurpose species for forestry, while their ability to endure forest fires through specific mechanisms, render them irreplaceable for the special and sometimes delicate Mediterranean ecosystems (Aravanopoulos *et al.*, 2004; Alizoti, Bailian & Panetsos, 2004; Chambel, *et al.*, 2013).

Provenance testing was launched in the early 1970s in most of the Mediterranean countries, following international initiatives coordinated by FAO and IUFRO that resulted in the collection of seed from 50 provenances (33 of *P. halepensis* and 17 of *P. brutia*) and the establishment of numerous provenance trials of the two species across the whole Mediterranean basin. Later on, other international collaborative initiatives exploited the already existing network and established also new trials for the two species (FAO *Silva Mediterranea*, IUFRO and EU projects). *P. halepensis* provenance trials have been established in Greece, Italy, France, Spain, Israel, Morocco and Tunisia, while *P. brutia* trials are mainly located in Turkey, Greece, France and Italy. The purpose of the provenance trials is not only the evaluation of survival and growth of the two species, but also their adaptive potential across different and sometimes limiting environmental conditions (Chambel *et al.*, 2013).

Results of the above established networks of trials indicate the existence of high plasticity for growth traits and significant G×E (genotype by environment) interaction across sites. The relative ranking of provenances tends to remain rather stable, indicating that the G×E interaction is rather quantitative and not qualitative (Chambel *et al.*, 2013). G×E interaction for traits like stem form and frost resistance was lower than that for growth traits, both at a species and at a provenance level. Results also indicate the existence of ample adaptive genetic diversity for both species, with *P. halepensis* provenances being in general more water-stress tolerant, while *P. brutia* provenances being less susceptible to frost damage (Calamassi, Falusi and Tocci, 1980; Falusi, Calamassi and Tocci, 1983; Calamassi, Falusi and Tocci, 1984; Grunwald and Schiller, 1988; Atzmon, Moshe and Schiller, 2004; Voltas *et al.*, 2008). *P. brutia* has also been proven to be more resistant to the insect *Pissodes notatus* (Ducci and Guidi, 1998). *Pinus halepensis* exhibits a well-established north-east – south-west cline for adaptive traits, with the north-eastern provenances showing higher early growth rates and better stem forms than the southern Iberian and North African provenances (Chambel *et al.*, 2013). Similar geographical trends for early reproductive allocation have also been reported by Climent *et al.* (2008), indicating that the eastern and northern populations are less precocious for cone bearing than southern Iberian and North African provenances. Differences for growth and adaptive traits have been also revealed for *P. brutia* populations growing at different altitudinal gradients (Kaya and Isik, 1997; Pichot and Vauthier, 2007). Eco-physiological studies carried out on *P. halepensis* provenances in harsh, near-desert, environmental conditions, showed the existence of significant inter- and intra-provenance variation and indicated that populations exhibiting higher heterozygosity, higher drought resistance and water-use efficiency survived and performed better (Schiller and Atzmon, 2009; Klein *et al.*, 2013). Regarding neutral genetic diversity, high levels of differentiation has been recorded among populations, but rather low within populations, with a tendency to increase from west to east. It has been suggested that the above-mentioned genetic patterns may have emerged due to a combination of factors, such as the Pleistocene climate, the species' migration strategies, and impact of wild fires (Fady, Semerci and Vendramin, 2003; Fady, 2012). Climate change is expected to result in temperature increase and more pronounced and frequent droughts in the Mediterranean basin. In northern Mediterranean regions, though, increase of growth or expansion of the distribution in the face of climate change has been postulated for *P. halepensis* (Rathgeber *et al.,* 2000; Thuiller, 2003). At the edge of the distributions of both species a notable growth decline has been recorded via dendrochronological methods, i.e. for *P. halepensis* in the very dry coastal areas of south-eastern Spain (De Luis *et al.*, 2007) and for *P. brutia* in some of the Aegean Sea Greek Islands (Körner, Sarris and Christodoulakis, 2005; Sarris, Christodoulakis and Koerner, 2007). Frost damage can be another risk that primarily *P. halepensis* might encounter in mountainous or continental areas due to climate change, given the lack of hardiness of the species to cold temperatures and the expected abrupt temperature changes due to global warming (Fernández *et al.*, 2003; Climent *et al.*, 2009).

Transfer of *P. brutia* FRM from Turkey is currently approved in several countries, i.e. Italy, France and Spain. Specifically in Italy, the material imported is the one that exhibited the best survival and performance in the FAO/*Silva Mediterranea* field trials. *P. halepensis* FRM is produced across the Mediterranean countries by genetic material sampled from national provenance regions and seed stands. Use of introduced and maladapted *P. halepensis* reproductive material (i.e. Algerian and Italian provenances) for afforestation purposes in south France resulted in high mortality due to frost damage and cold winter temperatures (Tabeaud and Simon, 1993; Bedel, 1986).

Given all the above, it is recommended that *P. halepensis* FRM produced from national provenances should be used, based on the results obtained from the networks of the existing experimental trials. Genetic material proved to be tolerant to extreme, near-desert, conditions could be considered for planting in sites with potentially high temperature and drought indices. Transfer and use of *P. brutia* FRM should be based on the species requirements and adaptation limits, as well as on results obtained from the field trials.

Douglas fir (*Pseudotsuga menziesii*)

Douglas fir has one of the widest natural ranges of any tree species and the largest south-to-north distribution of any commercially used conifer in North America, extending from 19°N in Mexico to 55°N in western Canada. Within this large geographical area with strongly contrasting climatic conditions, Douglas fir occupies many habitats. Populations are generally regarded as being closely adapted to different environments. Two types or varieties are recognized: the typical coast or green variety (var. *menziesii* or *viridis*) extends from Vancouver Island and the coastal mountains of British Columbia along the Pacific slope into California, and has a nearly continuous distribution from sea level to an elevation of around 1800 m. On the eastern slope of the Cascades and in the Rocky Mountains from northern British

Columbia into the southwestern United States of America and Mexico, botanists recognize the *glauca* variety, known also as "interior" or "blue" Douglas fir. This variety differs from *menziesii* in foliage colour, cone form, growth rate and environmental requirements. It has a patchier distribution, especially in the south and a wider elevation range, of 500 to 3500 m. This variety mingles with the coastal variety in southern British Columbia and northeastern Washington (Hermann, 1985).

Douglas fir (*Pseudotsuga menziesii*) has been grown in Europe for over 120 years and it is one of the most important introduced species in many European countries. Beside site conditions and silvicultural treatment, the provenance is crucial for a successful introduction of this non-native species. Until the late 1960s, in the majority of import cases, nothing was known about the introduced provenances. In the mid-1960s, seed zones for Douglas fir were established for the Pacific Northwest. At the same time (1967–1968), an IUFRO provenance trial was started with provenances from Oregon and Washington State in the United States of America and from British Columbia in Canada. More than 120 provenances were planted in more than 100 field tests in 33 countries all around the world, but mainly in Europe. This is one of the largest international provenance trials installed for forest trees. Parts of the numerous trials still exist (Kleinschmit and Bastien, 1992). In 1990, researchers from INRA-Orleans presented range-wide results based on data collected from 108 trials and from 20 institutions in 15 countries (Breidenstein, Bastien and Roman-Amat, 1990). The results of this study demonstrate a better adaptation and growth of coastal provenances (var. *menziesii*) on nearly all European sites. In central Europe, the best performing provenances originated from Washington State (below 600 masl), whereas provenances from northern Oregon grew fast only on sites with a mild climate. In general, mortality was low to moderate on nearly all sites (15–30%). Higher mortality was observed on provenances from British Columbia, whereas the Washington State provenances showed the lowest mortality. In nearly all tests, provenances of the *glauca* variety (interior Douglas fir) exhibited excellent survival in the first years (Kleinschmit *et al.*, 1974, 1991) but poor growth performance in later stages.

In the Mediterranean region, and especially in Italy, several tens of thousands hectares of planted Douglas fir are growing in mountain ranges with very good performances and good technical characteristics. In this area, more than 120 provenances from British Columbia to California, New Mexico and the interior were compared with provenances introduced earlier to Italy. The results indicate that for Italy, the most appropriate provenances are from the Coastal Range in Oregon and in California (higher elevations). All those provenances showed in general a low G×E interaction, very good performance, high survival rate, low percentage of forked trees, good stem form and low number of branches. Also some Italian landraces ranked among the best, particularly the Calabrian provenance Mercurella and the northern Tuscany seed stand Acquerino (Ducci *et al.*, 2003). In Spain, the best materials came from north Oregon and south Washington from latitudes north of 45°N (Zas *et al.,* 2003).

As a conclusion of these tests, recommendations for selecting provenances for different planting sites throughout Europe are given. In central and eastern Europe, the choice of Douglas fir reproductive material is restricted to the middle-elevation zone of the Cascade range in northern Washington State, as provenances from high latitude and elevation have slow growing rates. Only at sites with a harsh climate, Douglas fir provenances from high elevations could be interesting. In southern and Mediterranean Europe, provenances from low elevations in northern Oregon and southern Washington State seem to be of high interest.

The IUFRO provenance collection stimulated numerous other seed collections for Douglas fir in the 1970s. For example, to refine provenance recommendations in southern Germany (Bavaria) more than twenty supplementary field tests were installed between 1971 and 1976. These include provenances from which promising results are expected, including an altitudinal sampling up to 1000 masl in some areas (Ruetz, 1987). As a result of these trials, new guidelines for Douglas fir seed import and use were developed based on seed zones and elevation (Ruetz, 1987). These guidelines also became part of the provenance recommendations in Bavaria. For regions without summer drought, provenances from the west slope of the Cascades in Washington from low and middle elevations are recommended. For the mildest regions of Bavaria and on dry sites, provenances from north Oregon and from the east slope of the Olympic Peninsula in Washington State are preferred. Provenances from the Washington coast ranges have generally performed well and have had little spring frost damage. Thus they are recommended especially for sites susceptible to late spring frosts.

CHALLENGES AND OPPORTUNITIES

Potential of tree breeding to meet conservation needs and climate change challenges

Tree breeding activities differ in their intensity, focus and impact on forestry among different regions of Europe. Intensive breeding programmes have generally focused on a few forest tree species. Typically, breeding is organized as a recurrent cycle of selection, testing and production. Intensive breeding may lead to the loss of diversity, but it also provides the opportunity to increase diversity substantially by a proper management of the genetic resources used.

Breeding is one tool with which to face climate change. The control of the genetic factor through tree improvement is expected to produce trees that are better adapted to certain environmental conditions. As the combined effect of increasing temperatures and decreasing precipitation, i.e. drought stress, is considered the major problem associated with climate change, planting of drought-resistant trees may represent a mitigation option. Drought tolerance is a trait with moderate heritability (Cumbie *et al.,* 2011; Newton *et al.,* 1991) so there is potential for genetic improvement. Several current breeding programmes include drought tolerance (Butcher, 2007; Dalla-Salda *et al.,* 2009), resistance to pests and pathogens (whose incidence is expected to increase under climate change), vegetative and flowering phenology or physiological characters as target traits. Recent development in forest tree genomics, especially progressing discovery of biologically relevant SNPs by means of association genetics may considerably accelerate progress in this respect (Hamanishi and Campbell, 2011; Neale and Kremer, 2011). Research is being conducted to identify candidate genes related to traits that will respond to climate change (budburst, bud set, winter hardiness, drought resistance and water-use efficiency). However, the achievements obtained so far are not yet at the stage of introducing these genes (by crossing or other means) into commercial varieties.

Phenotypic plasticity, the ability of a genotype to produce different phenotypes under different environments, may be considered a trait of its own, which is heritable and may thus be subject to selection. Phenotypic plasticity is favoured by evolution in spatially and temporally heterogeneous environments. Phenotypic change may vary not only in the amount and pattern, but also in the speed of expression, reversibility, and ability to occur at different developmental stages (Schlichting and Smith, 2002). Both spatial and temporal heterogeneity apply to forest trees, which form large populations covering typically plenty of climatically and edaphically differentiated microsites. As long-living organisms, trees are also exposed to environmental changes, even during their lifespan. The term has been widely applied in forest genetics literature, not always according to the original definition, which was the environmentally sensitive production of *alternative* phenotypes. The interpretation of the term was increasingly becoming liberal and tree breeders often used the term for expressing the breadth of site condition variation, successfully coped with by the population or genotype. It is therefore advisable to use instead the term **phenotypic stability** to express the ability to maintain fitness (growth superiority) across a wide range of sites, often surpassing locally adapted populations. Phenotypic stability is expressed by reaction norms or transfer functions calculated from comparative tests, such as provenance trials. The trait is genetically determined and becomes increasingly important in climatically changing environments. Breeding programmes should prioritize the selection and improvement of this trait.

Definitions for the stability of phenotypic expression are nearly as numerous as their applications. In general, measures of phenotypic stability attempt to quantify a genotype’s tendency to exhibit constant phenotypic expression in different environments (Lynch and Walsh, 1998). In forestry, the patterns by which different FRMs (e.g. seed lots from selected seed stands, seeds from tested families in seed orchards or clones) respond to environmental conditions are primary determinants of the FRM’s desirability in different environmental conditions. Stability of FRM performance across a broad range of environmental conditions is usually essential from breeders’ points of view. Removing unstable families is an alternative to reduce the impact of G×E interaction in breeding populations (Mata, Voltas and Zas, 2012). Many authors have suggested considering the genotypic stability across sites as a screening trait in selection processes (Johnson, 1998). Selection based on stability parameters is also a safeguard decision regarding the current global change scenarios. Selection for specific adaptation at present may lead more easily to easing future adaptation concerns in the deployed material (Ledig and Kitzmiller, 1992). Removing the most interactive families indeed reduced G×E interaction, but achieving near-complete stability in the breeding population would require roguing up to 70% of the initial material. This would imply a too large reduction in genetic variability, which is, by far, not the best decision from a sustainability point of view. Applying a low intensity selection for stability, that is, removing around one-third of the most interactive families should be the option of choice as it may substantially reduce interaction effects while probably keeping a sufficient genetic pool for future activities in the breeding programme.

Selection is inevitably associated with the loss of genetic variation. Low-frequency genes, which may prove beneficial under future environments, may be lost in each breeding cycle through both selection and genetic drift associated with the small size of breeding populations (Godt *et al.,* 2001). In many countries and for many tree species, improved material represents substantial part of reforestation. This is the case for clonally propagated species such as poplars and willows, with a few clones cultivated on huge areas, but also commercially important conifers (Scots pine and European larch), where most seed stock is produced in seed orchards. The available options for raising diversity within the reproductive material produced by seed orchards are supplemental mass pollination or supplementing seed lots harvested in seed orchards with seeds deriving from other origins or other seed orchards.

There are at least two aspects of breeding that must be emphasized in connection with climate change. First, more attention needs to be paid to the choice of target environments for the improved material. This requires proper progeny testing, where field tests are established not only on optimum sites but also in climatically marginal environments. Alternatively, field trials may be replaced by indoor or nursery tests with manipulated temperature and watering regimes, whenever appropriate. Development of rapid and inexpensive early-testing procedures for drought tolerance is also desirable in order to accelerate deployment of clones, families and provenances appropriate for future climates (Dvorak, 2012). The second aspect is preserving sufficient genetic diversity within the improved material. Lindgren, Gea and Jefferson (1996) developed the concept of status number as a kind of effective population size to monitor the loss of genetic diversity in seed orchards or clonal mixtures. Gene markers can also be used to monitor the potential loss of genes. Nevertheless, the risk of gene loss is unavoidable, especially in advanced-generation breeding, although it can be diminished by appropriate breeding design. Therefore, there is a need for breeding approaches that combine the achieving of breeding targets with gene conservation measures.

One of the major challenges for tree breeding is that the high priority breeding goals set today may be of limited importance when it is time to harvest the expected gains, especially given the uncertainty of environmental conditions, which may change dramatically over a rotation time and are beyond any human control. Consequently, a successful breeding programme should be designed to match the future changes in breeding objectives and environmental change. The Multiple Population Breeding System (MPBS) developed by G. Namkoong can fulfil such requirements, as the breeding population is subdivided into smaller sub-populations of equal size that are preferentially planted over a broad span of site conditions, while the target trait might be different for the different sub-populations. The MPBS is hierarchically structured and emphasizes inter-populational diversity within an array of populations both in the traits targeted for improvement as well as for environmental adaptabilities. In this way multiple adaptive peaks can be simultaneously revealed, as within each sub-population separate trait combinations and site adaptabilities can be selected for applying recurrent selection (Namkoong 1984; Eriksson, Namkoong and Roberts, 1993), while the system can be modified to produce interpopulation hybrids. Conservation goals can also be met through the MPBS as broad sampling to establish multiple populations, and continuous development of inter-populational variation can ensure the existence of ample diversity to meet changing environmental challenges. The main advantage of the MPBS is that it combines the capture of the total existing genetic variation with a satisfactory variation within each sub-populations, and it allows the sub-populations to adapt to the prevailing environmental conditions, besides the fact that the disruptive selection and thus the speed of evolution might be higher in a sub-population than in an extensive population of thousands of trees.

According to Eriksson, Ekberg and Clapham (2006), the MBPS has been adopted in Sweden for silver birch, lodgepole pine, Norway spruce and Scots pine breeding programmes, and different sub-populations of these species have been distributed across different sites and environmental conditions. The MPBS strategy has also been adopted in many other breeding programmes across the globe.

The nucleus breeding system is another example of a long-term breeding system that has the aim of gene conservation and long-term genetic gain. This system splits the breeding population into sub-populations of unequal size. The smaller nucleus contains fewer trees, while the larger part includes a significantly greater number of trees. The most intensive breeding efforts occur within the small nucleus, while the conservation and long-term gain are secured in the larger sub-population. Transfer of genetic material from the larger population to the nucleus can minimize inbreeding within the nucleus despite the loss of genetic gain.

Marker-assisted breeding and genomics approaches

During the past 20 years, great progress has been made in assessing neutral DNA variation in tree species using a range of molecular techniques that have been developed over that period. Isozymes, RFLPs, RAPDs, AFLPs, microsatellites and, more recently, non-coding SNP markers, have all proved extremely valuable in establishing the demographic patterns of neutral genetic variation. From the FRM viewpoint, this neutral variation does not provide any information on phenotypic or adaptive variation, which is crucial when considering the transfer of material in the context of climate change. The next major technological advance is likely to be harnessing the recent development of affordable, rapid and informative diagnostic techniques to evaluate large numbers of adaptive genes and genetic variation at both the individual and population levels. Understanding the adaptive genetic potential of forest tree populations is fundamentally and critically important for evaluating their vulnerability to climate change and suitability for transfer.

A genomics approach aims to account for the way in which the total gene complex of an individual contributes to its phenotype. Genomics encompasses a range of approaches that aim to integrate traditional genetic disciplines with the emerging cutting edge technologies in molecular biology, DNA analysis and bio-informatics, which are all evolving at an astonishing rate. Current genomic approaches include transcriptomics – sequencing the expressed genes in an organism or specific tissue type and producing expressed sequence tag (EST) libraries, which reduces the genome complexity and hence sequencing effort; proteomics and metabolomics – analysing the proteins and primary and secondary metabolite profiles; and genetic mapping aimed at understanding of genetic architecture. Genetic maps are extremely useful as loci controlling quantitatively inherited traits (QTL) have been already identified in many forest trees for a variety of growth, wood quality, and other economic and adaptive traits. However, such traits are generally controlled by small contributions from a large number of genes and there is currently a move away from the QTL method towards the whole genome scanning approach.

The various genomic approaches create synergies to provide valuable information regarding tree genome organization and function. These approaches are only possible because of the progress that has been made in DNA sequencing technologies. Next-generation sequencing (NGS) technologies can produce thousands or millions of sequences at once and generate gigabytes of data in a matter of days at a much reduced cost.

Rigault *et al.* (2011) used the power of NGS to confirm and enhance the *Picea glauca* gene catalogue by providing a deeper coverage for rare transcripts, by extending many incomplete clusters and by augmenting the overall transcriptome coverage. With this availability of sequence information at thousands of putatively important genes or regulatory regions, the characterization of adaptive genetic diversity and the association with phenotypic trait variation is becoming more accessible. The progress that has been made with sequencing technologies is particularly important for studying the large and highly repetitive genomes of conifer species. This has involved applying both the sequencing of lower complexity targets, i.e. transcriptome ESTs or restriction-site-associated DNA markers (RADs), and the whole-genome sequencing approach.

One of the ultimate practical objectives for tree genomics is to gain the ability to identify genes under selection due to geo-climatic factors, determine their allelic diversity, and then apply that knowledge in management decisions related to the use and transfer of genetic resources.

The discipline of landscape genomics has recently emerged, combining population genetics and landscape ecology to study patterns of demographic and adaptive genetic variation across heterogeneous landscapes. Since forest tree species often have broad contiguous populations, yet which demonstrate local adaptation, they are excellent models for empirical study in landscape genomics.

A study that is underway at the University of California in the United States of America aims to generate complete polymorphic transcriptome information from eight conifer species across California, select genes showing adaptive variation, and then design dense (20 000 SNPs) Illumina Infinium genotyping chips to genotype 2000 trees from each of the eight species (16 000 trees in total). The scale of this project could not have been foreseen even 5 years ago.

A commercial whole-genome sequencing service has been launched recently, with a two-week turnaround for US$ 9 500. Third-generation sequencing technologies utilizing a nano-scale sensor to electronically read the sequence of a single DNA molecule may make the cost of human whole genome sequencing fall to below US$ 1 000. Progress of this sort would enable tree geneticists to embrace the concept of genome-wide association studies (GWAS), involving scanning large sample sizes with hundreds of thousands of SNP markers located throughout the genome with a subsequent comparison of the frequencies of either single SNP alleles, genotypes, or multi-marker haplotypes, between phenotypically different cohorts. This analysis identifies loci with statistically significant differences in allele or genotype frequencies between phenotypes, pointing to their role in the trait. In contrast to candidate gene studies, which select genes for studies based on known or suspected mechanisms, GWAS permits a comprehensive scan of the genome in an unbiased fashion, and thus has the potential to identify novel factors.

Genomic selection (Nakaya and Isobe, 2011) is a form of marker-assisted selection (MAS) that selects favourable individuals based on genomic estimated breeding values (GEBVs). GEBVs are also used in animal breeding, but have not been a popular index in plant breeding. They are defined as "the sum of the estimate of genetic deviation and the weighted sum of estimates of a breed's effects" which are predicted using phenotypic data from family pedigrees. GEBV has become a feasible approach with the recent advances in high-throughput genotyping platforms.

What once cost millions of dollars and took years to achieve may soon cost less than many standard diagnostic tests today. Whilst such technologies may take a while to filter down to tree geneticists, it is clear that there will be a paradigm shift in the amount of sequence information generated. From the FRM perspective, the challenge will be to understand and exploit this huge amount of information in a meaningful way.

Molecular markers for genetic characterization of forest reproductive material

Most forest tree species exhibit high levels of genetic diversity that can be characterized using molecular markers and used for identifying the origin of reproductive material raised in nurseries prior to, or after planting, should a need for confirmation arise. The majority of current molecular markers are selectively neutral (neutral variation results from differences between genotypes that do not affect their ability to survive and reproduce) and they do not reflect the distribution of adaptive variation, which will be considered later. However, neutral markers can provide information on the level of genetic diversity, colonization routes and lineages, in addition to helping to confirm the origin of FRM or to ensure that the trail of material from nursery to forest is genuine.

The level of genetic diversity can be easily measured, typically with highly variable microsatellites or SNP markers. A simple example of this is the use of molecular markers to assess the genetic health of planting stock, i.e. whether it is showing signs of inbreeding. In southern Germany, the genetic diversity of all Douglas fir and silver fir stands are assessed using a suite of isozyme and microsatellite markers. If the stand shows lower levels of variation in comparison with other stands, it will be rejected as a seed source. Molecular markers are also used to determine the level of purity of oak and larch. As a further example, the inherent variability between individual trees can be harnessed with molecular markers to enable individual clone identification (e.g. cherry, apple and pear) and also for the identification of hybrids (e.g. poplars (*P. nigra* × *P. deltoides*) and larch (*L. kaempferi* × *L. decidua*)).

The choice of the most appropriate molecular method to trace the origin of FRM largely depends on the species and the current information on the spatial distribution patterns of its genetic diversity. For example, there is highly detailed information on the phylogeographical variation patterns of chloroplast DNA haplotypes in European oaks (Petit *et al.*, 2002) which makes chloroplast DNA markers an excellent tool to track the origin of oak. The utility of uni-parentally inherited variation is due to more restricted seed dispersal. In many European tree species, the highest levels of marker diversity have been found in central Europe, which could be due to ancient refugia or an admixture of genetically differentiated lineages (Petit *et al.*, 2003).

In the future, the identification of adaptive DNA markers could be of great benefit for choosing suitable FRM material that will be best suited to a particular climate scenario. There is currently a great deal of ongoing work in the field of adaptive variation. Research efforts are currently focusing on studying variation in candidate genes related to traits that will be important in response to climate change, such as budburst (Derory *et al.*, 2009), bud set (Frewen *et al.*, 2000) and water stress (Perdiguero *et al.*, 2011). For the time being, these approaches are limited to the search for candidate genes and the exploration of their diversity in extant populations (Gonzalez-Martinez *et al.*, 2006). Although genomics approaches enable the assessment of genetic differentiation simultaneously in a large number of loci, the influence of polymorphisms on adaptive variation cannot be evaluated without good quality phenotypic data and extensive breeding programmes. Current evidence from genomics studies points to a complex multi-gene inheritance of adaptive traits.

There is a clear underlying message that the gathering of basic genetic information on tree species at all levels (individual trees, stands and countries) should be done with the knowledge that the greater the amount of information that is available, the greater the opportunity to use DNA markers accurately for the identification of origin of FRM, and to understand the current genetic health of tree species. It must be remembered that trees do not follow political boundaries and therefore the use of common marker sets with common standards between countries should be encouraged.

Advances in phenotyping and phenomics

Traditionally, the set of traits assessed in field experiments with forest trees was limited to survival rate, growth, phenology, frost resistance and tree-architectural traits. Although these are the traits of primary interest for a practical forester, their potential is limited for understanding adaptation processes and explaining response patterns to environmental changes over time (e.g. climate change) and space (FRM transfer).

Due to their size and longevity, forest trees are not suitable objects for scoring phenotypic traits in as a complex way as is possible with other organisms. In biology, the term 'phenomics' as an analogy to genomics was recently coined for acquisition of high-dimensional phenotypic data on an organism-wide scale (Houle, Govindaraju and Omholt, 2010). Phenomics is an emerging trans-discipline dedicated to the systematic study of phenotypes using new methods for high-throughput scoring, and focuses on linking genetic variation assessed in genomic and gene-expression studies to phenotypic variation. It has become a recognized component of biological, medical and agricultural sciences.

All recent research projects focusing on tree genetics and breeding lay emphasis on high-throughput phenotyping. Long before the era of genomics, efficient techniques for assessing tree phenotypes were needed as key components of conventional breeding approaches (Neale and Kremer, 2011). The ability of rapid and cost-effective scoring of phenotypic traits on large numbers of trees is crucial, not only for practical breeding but also for revealing the genetic background of complex phenotypic traits. This also applies to conventionally assessed traits. Recent development of new measuring devices and computer-aided field-data collection systems, such as FieldMap, has allowed reliable and rapid assessment of growth traits, even in older trials.

Nevertheless, deeper understanding of the genetic basis of adaptation processes and predicting responses of tree populations to environmental change requires broadening the spectrum of traits assessed in all types of indoor and outdoor experiments, including common-gardens, and finding high-throughput scoring procedures for these traits. These would include those traits listed below.

- **Physiological traits.** Recently, methodologies for monitoring a large number of parameters characterizing plant carbon and water turnover have developed considerably (Kramer *et al.,* 2004; Rosenqvist and van Kooten, 2003; Seibt *et al.,* 2008) and similar improvements are also expected in monitoring nutrient uptake, frost resistance, drought tolerance, etc. At the same time, increased availability of high-resolution digital cameras and image-processing software allow documenting the growth process and reactions to time-dependent stress factors, using measurements in the full range of technically available wavelengths from infrared to X-ray imaging, or other imaging methods, such as magnetic resonance imaging (MRI) or terahertz scanning (Eberius and Lima-Guerra, 2009).

- **Wood properties.** Development of microscopy techniques associated with computer-aided image analysis has allowed identification of numerous structural and ultrastructural wood traits (Fahlén and Salmén, 2005; Xu *et al.,* 2006). New techniques have also appeared for the analysis of wood chemistry (Selig *et al.,* 2011; Zhou, Taylor and Polle, 2011). Although wood properties seem to be mainly of commercial importance, they affect tree stability, water balance and other ecologically relevant traits.
- **Pest and pathogen resistance.** Rapid development of remote sensing and image analysis allows increasing the efficiency of large-scale estimates of pest and pathogen damage in outdoor trials (King, 2000).
- **Proteome and metabolome.** Improved methods of analytical organic chemistry allow identification of numerous proteins and secondary metabolites mediating the response of a genotype to a particular environment (Ossipov *et al.,* 2008; Warren, Aranda and Cano, 2012).

Facilities allowing manipulation of the environment, such as phytotrons and climatic boxes, are available in many laboratories throughout Europe. Recent international projects, such as NovelTree or Trees4Future, have undertaken inventories of such facilities and devices suitable for high-throughput phenotyping, and allowed cross-linking and international cooperation in their utilization.

RECOMMENDATIONS

FRM transfer is a valuable option for adapting forests to climate change

Forest tree populations have (genetically) adapted over a long period (and are still adapting) to their respective habitats and, as a result of this adaptation, formed so-called provenances. Climate change is expected to alter forest habitat conditions in Europe at such a pace that the natural processes (selection, gene flow, migration) that drive evolution and adaptation will not act fast enough. Therefore, human intervention in the form of FRM transfer (assisted migration) is a valuable option to adapt forests to climate change, especially in those areas that are most severely threatened by climate change.

Local is not always best

Autochthonous local tree populations originate from complex selection processes acting on a restricted regional gene pool. For various biotic and abiotic reasons, local populations do not always demonstrate optimum fitness (for important forestry traits) compared with other FRM in common-garden experiments. In addition, in Europe, locally found populations often originate from historical FRM transfer but for which passport data are lost. Local FRM will not always be the answer to climate change challenges. As local environmental conditions change, forest managers should extend their options to both local and non-local FRM.

Use provenances instead of species in assisted migration schemes

Science has repeatedly shown that adaptive genetic diversity within forest tree species is often very large and yet it seems that, under the pressure of climate change, forest management would rather change species than provenances when designing reforestation efforts. Therefore, there is an urgent need to disseminate information and knowledge on the adaptive potential that is readily available from different FRM within tree species.

Transfer of FRM also has its limits

With increasing temperature and periods of drought there is an increasing demand from forestry for provenances from warmer southern regions. As long as extreme events such as late frosts occur, these provenances can be recommended only in exceptional cases, and the transfer of the material used has to be well documented. Short-rather than long-distance transfers will often be more ecologically relevant and should be preferred. The conservation of local genetic resources should be taken into account when assisted migration is being considered. Forest managers should protect particularly threatened FRM (mostly peripheral populations from rear edges of geographical distributions) that could be of use in other, more suitable, locations.

Revision of transfer recommendations is necessary at the pan-European level

Provenance regions or seed zones represent the spatial framework for FRM transfer recommendations in Europe. Their number and size vary greatly among countries because different approaches are used for their delineation. FRM is increasingly traded across borders but the national recommendations rarely offer help in deciding where the imported material should be used. Transfer recommendations should have a pan-European perspective and should also include climate change considerations.

More stringent control of FRM is needed at all production and marketing stages

The legal frameworks for FRM production and marketing are well defined at EU and OECD levels. However, major differences still persist at national level for controlling the origin of FRM throughout the production chain. Harmonized control mechanisms and close cooperation between control agencies in different EU Member States and collaborating countries are necessary. Recent technological breakthroughs, particularly in molecular biology, make it possible for control agencies to easily and cost-effectively monitor and trace FRM, and to disseminate information to the end-users.

The need for FRM documentation increases under climate change

The best adapted FRM of today may not prove the best adapted FRM of tomorrow under climate change. By keeping track of successes and failures in management decisions, forest managers will be able to adjust their strategies. Data on FRM – geographical origin, harvesting conditions, genetic diversity and production methods – are likely to be key information sources for plantation efforts, so that forest managers should be particularly keen to ask for and to keep a record.

Tree breeding offers opportunities for forestry under climate change

Breeding programmes have typically focused on improving yield, wood quality, and resistance to pests and diseases. Resistance or tolerance to drought or increased water stress periods are becoming a priority for new generations of breeding programmes, and so does keeping large breeding populations. Such FRM can be tailored to managers’ needs, from very specific to large portfolio uses.

It is crucial to continue provenance research under climate change

Provenance experiments provide a wealth of resources for evolutionary ecology and climate change studies, and they are the most reliable basis for formulating practical recommendations for FRM. Existing networks of provenance experiments need to be upgraded to include under-represented (e.g. peripheral) populations and sites, and need to be regularly monitored and measured. Pan-European efforts for collating, archiving and analysing data at species-range level should be continued and intensified, so that results can be transferred into practical recommendations for forest managers.

Knowledge gaps should be filled on the adaptation of forest trees

Understanding the adaptive genetic potential of forest tree populations and their response to environmental changes in time and space is fundamentally and critically important for assessing how FRM might be used in the face of climate change. In particular, the molecular basis of adaptation and the relationship between genetic variation in a large set of genes and phenotypes in environmental gradients still represent knowledge gaps. International cooperation must be intensified in this context, including collaborative utilization of shared research facilities.

Dissemination of information on the value of FRM to forest owners, managers and policy-makers needs to be improved

The scientific community has extensive knowledge and information on the potential that the use of FRM offers for facilitating the adaptation of forests to climate change. Education and training for increasing awareness of stakeholders, such as forest owners, forest and forest habitat managers, and policy-makers, needs to be continued and intensified. Ways to increase capacity building for using science-based knowledge and to foster an efficient and mutually rewarding science–management–policy dialogue, must be fully explored, more than ever before.

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ANNEX 1

List of European projects relevant for the use and transfer of forest reproductive material

Project	**Framework**	**Leader**	**Short description**
LINKTREE	BiodiverSa (2009–2012)	INIA Spain	LINKTREE uses a combination of high throughput sequencing and/or genotyping of ecologically relevant genes and quantitative genetics experiments to evaluate levels of standing genetic variation and signatures of selection in natural forests. (www.igv.fi.cnr.it/linktree)
Trees4future	FP7 - structures 2011–2014	INRA France	Trees4Future is an Integrative European Research Infrastructure project that aims to integrate, develop and improve major forest genetics and forestry research infrastructures. (www.trees4future.eu)
EUFORINNO	FP7–Regpot	SFI Slovenia	EUFORINNO addresses the strategy of SFI to become a reference centre for Central and South-Eastern Europe in the European Forest Research and Innovation Area (EuFoRIA). Between the key areas of cooperation is also the control of FRM and the establishing of a forest gene bank.
Map/FGR	COST Action (2012–2015)	CREA SEL Italy	Strengthening the adaptation of forest genetic resources (FGR) to climate change in marginal and/or peripheral populations of forest trees in Europe through appropriate conservation and management strategies
NOVELTREE	FP7 (2008–2012)	INRA France	NOVELTREE will provide an improved understanding of the biology of forest tree species and enable significant genetic improvement in the composition and characteristics of forest products in order to satisfy the needs (e.g. quality, quantity, sustainability, vulnerability) of consumers and of the forest-based sector. (www.noveltree.eu)
FORGER	FP7–KBBE 2011–2015	ALTERRA Netherlands	The FORGER project will make available sound and integrated information on genetic resources to forest managers and policy makers by improving inventories on forest genetic resources in Europe, developing a common protocol to measure and monitor genetic diversity, analysing historic and current use and exchange of forest genetic resources over Europe, and analysing how forest genetic resources are affected by climate change and forest management practices. (www.fp7-forger.eu)
TREEBREEDEX	FP6–Infrastructures 2006-2010	INRA France	The aim of the TREEBREEDEX project was to develop a European platform for research and technical collaboration on tree breeding. (http://treebreedex.eu)
Evaluation of Beech Genetic Resources for Sustainable Forestry	COST Action E52 2006–2010	vTI Germany	This COST Action had 22 countries participating. Its main objective was to evaluate jointly, for the first time, 60 international beech provenance trials located in 19 European countries, a total of 200 provenances in all.
EVOLTREE	EU FP6 Network of Excellence 2006–2010 and ongoing as EFI programme	INRA France	Evoltree associates four major disciplines – genomics, genetics, ecology and evolution – for understanding, monitoring and predicting genetic diversity, ecosystem structures, dynamics and processes in European forests.

EUFORGEN