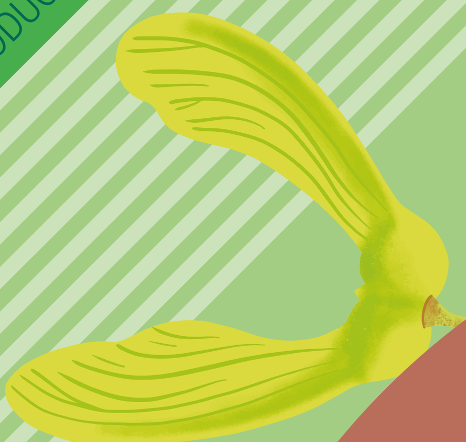
EUFORGEN

FOCUS ON FOREST GENETIC DIVERSITY

PRODUCING AND USING FOREST REPRODUCTIVE MATERIALS



THEME 3

SEED ORCHARDS

Key considerations in establishing and using clonal and seed orchards for forest reproductive materials

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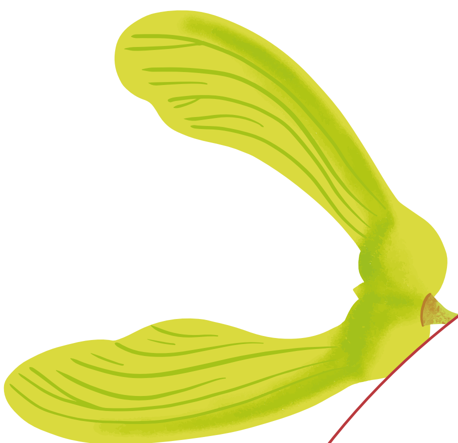

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Key considerations in establishing and using clonal and seed orchards for forest reproductive materials

The European Forest Genetic Resources Programme (EUFORGEN) is an international cooperation programme that promotes the conservation and sustainable use of forest genetic resources in Europe as an integral part of sustainable forest management. Experts from member countries come together within EUFORGEN to exchange information and experience, analyse policies and practice, and develop science-based strategies, tools and methods to improve the management of forest genetic resources. EUFORGEN is hosted by the European Forest Institute and is funded by its member countries.
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SEED ORCHARDS

Key considerations in establishng and using clonal and seed orchards for forest reproductive materials

A seed orchard is a plantation of selected clones or families that is used to produce frequent, abundant, and easily harvested crops of seed. Seed orchards should be isolated from other populations of the same or related species or managed in such a way that pollination from outside sources is avoided or minimized.

Seed orchards are ‘synthetic’ populations in which superior individuals (‘plus trees’) are planted together. The reason for establishing seed orchards is mainly to improve: a) the reproduction of phenotypically superior parents to yield well-shaped offspring that are expected to grow well; and b) the reproduction of scattered and endangered species that do not reproduce well in forest stands.

Seed orchards also play an important role in forest-tree improvement programmes, providing improved genetic material for use in breeding activities (e.g., artificial crossing and collection of material for progeny testing). Seed orchards may be composed of either vegetative copies of plus trees typically obtained by grafting (clonal seed orchards) or, less commonly, generative progenies of plus trees (seedling seed orchards).

In some European countries seed orchards are a major source of seeds for several economically important tree species.

The EUFORGEN community proposes these guidelines, based on a scientific knowledge of forest tree population genetics, for consideration by all those establishing and using clonal and seed orchards for forest reproductive materials.

01 ESTABLISHING A SEED ORCHARD

Fig. 1: A seed orchard is a managed plantation of selected clones or families, designed to produce abundant, high-quality seed while minimising external pollination.

Choice of plus trees

The choice of which plus trees to use to establish a seed orchard (whether a clonal or seedling seed orchard) depends on the tree species involved and the objective of the seed orchard. For example, seed orchards with selected, or even tested, plus trees are often established for tree species with high economic importance in forestry. In Europe, these are mainly stand-forming tree species that are usually managed in long- or medium-term rotations. Selecting plus trees that meet a number of selection criteria, such as growth performance, vitality, and disease resistance, and quality traits such as stem form, ensures production of seed of high genetic quality. Therefore, seed orchards have the potential to produce higher-quality seeds than approved seed stands.

Geographic origin

Information on suitable geographic regions of origin for materials to be combined in a seed orchard can be obtained from numerous provenance tests and field experiments. Field tests, especially older ones, have great value as they provide information on large-scale differentiation of tree species populations and provide long-term observation data on growth performance, quality traits, and disease resistance in different deployment regions or breeding zones. Knowledge on heritability of resistance to many environmental stressors is of great importance when choosing regions for plus trees selection, especially in those facing unfavourable conditions caused by climate change.

Within-orchard genetic diversity

The within-orchard genetic diversity in the seed crop should be matched to the rotation period of the tree crop. The longer the planned rotation period of the tree crop, the more diversity is needed in the seed crop to allow for adaptation to changing environments. This means that a balance must be found between improved performance of the seed orchard in terms of selection (genetic gain) and broad diversity as a prerequisite for long-term stability.

Spatial configuration of seed orchards

The spatial structure of a seed orchard affects both the ease of management and the productivity of the orchard, as well as the level of inbreeding. From a genetic point of view, arranging clones in a pattern that ensures that ramets of the same or related clones are not placed in close proximity favours outcrossing. This may increase the yield of full, viable seed and can reduce inbreeding. Note that while in some species inbreeding does not necessarily reduce seed yield, it is still detrimental to the genetic quality of seed crops.

Choice of location

Aspects to be considered in the choice of a suitable location for a seed orchard include the following.

- **Accessibility:** as seed orchards need to be maintained and managed, they should be concentrated near seed extraction plants or nursery centres.
- **Isolation:** to avoid contamination due to the exchange of pollen, seed orchards should be isolated from stands or seed orchards of the same species that are of poor quality or that

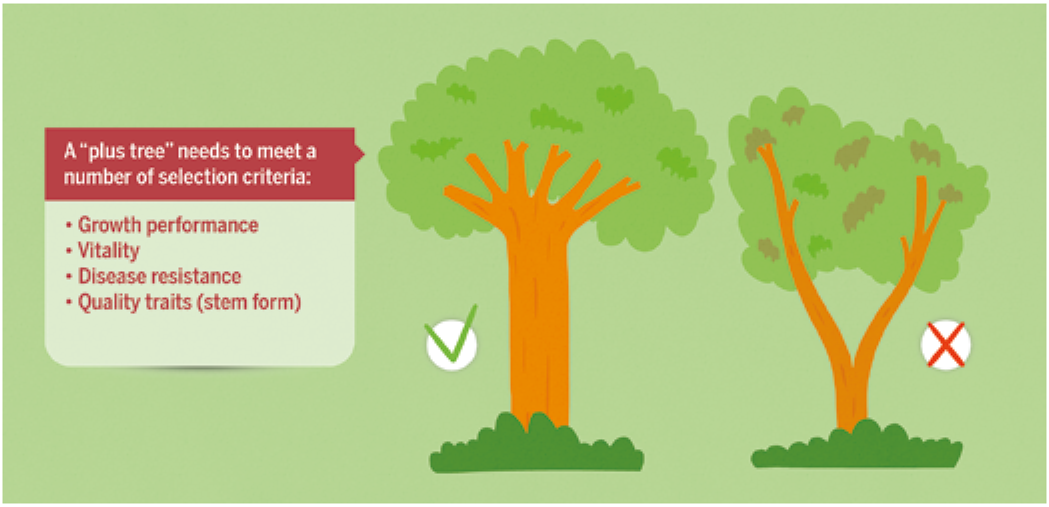

Fig. 2: Selecting plus trees based on growth, vitality, disease resistance, and stem form ensures the production of genetically high-quality seed.

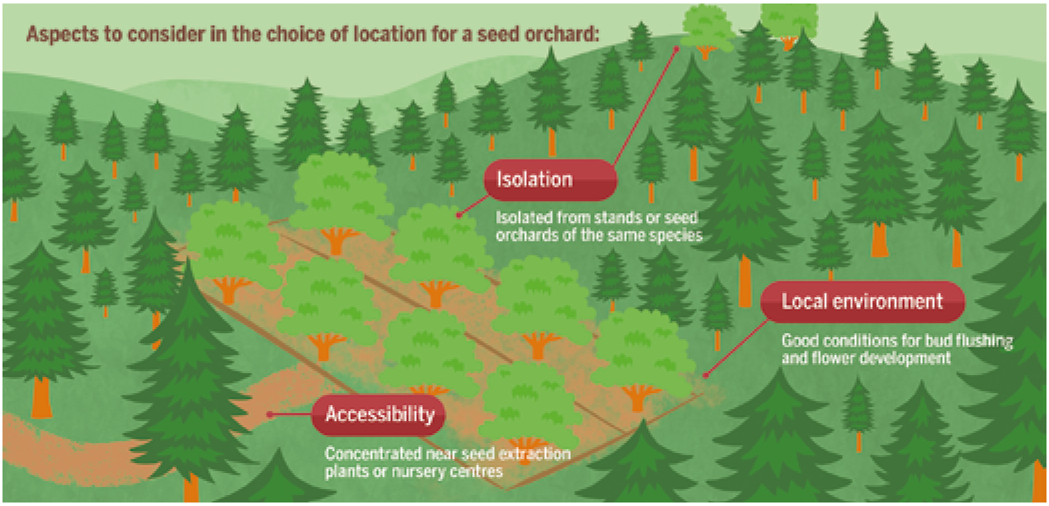

Fig. 3: Factors in selecting a seed orchard site.

do not correspond to the origin of the seed orchard clones.

- **Local environment:** seed orchards should be sited where topography and aspect produce favourable microclimates for bud flushing and flower development. Poor soils should be avoided.

Designing new seed orchards for future needs

Seed orchards should be designed to maximize genetic and economic benefits. Many tree improvement programmes are now in advanced generations of breeding, and this makes orchard design considerations more complex. Advanced-generation orchards may contain either offspring selected from a new base population (forward selections) or original first-generation selections (backward selections), or a mixture of both. The selection of plus trees and the subsequent establishment of seed orchards with selected clones is always based on phenotypes developed in the past as an interaction of genotype and environment. To meet future needs, the expected shifts of climatic parameters and added uncertainty need to be accounted for by using a broad genetic base.

Forest seed orchards can be designed in several ways. Existing seed orchards can be used by extending or adapting their recommended employment regions. Alternatively, new seed orchards can be established using materials from larger or more diverse regions of clone origin. Such new seed orchards permit sexual recombination between genotypes originally adapted to different environments. In principle, such offspring could express greater adaptability but outbreeding depression[1] is also possible. Therefore, further research on assisted migration is needed. The effect of epigenetic changes[2] should also be taken into account.

In general, breeding populations and clonal seed orchards from more-or-less natural populations and managed forests are managed separately. However, in the long term, they need to incorporate genetic resources from the species as a whole, including permanent adaptation processes as far as is possible. In view of this, sustainable breeding programmes always include measures for preservation of genetic resources.

02 GENETIC DIVERSITY IN SEED ORCHARD CROPS

The genetic diversity of seed orchards is mainly determined by the number of clones or, considering possible relatedness, the effective number of clones. In practice, clonal seed orchards in Europe often consist of between 20 and 50 clones. Current regulations in Germany require a minimum of 40 clones for main commercial tree species, while in Poland the minimum number of clones is 40 for important coniferous forest trees and 30 for other species. In Slovakia the current minimum number is 50, although 100 clones is preferred. However, if the aim of a clonal seed orchard is to ensure both genetic gain and genetic diversity the recommended census population size is 50 to 100 genotypes.

Some studies have found that the genetic diversity of seed orchards is similar to, or higher than, that of natural populations of the reference species, and genetic distances to source populations are small. Few forest practitioners and environmentalists are aware of this; most think that clonal seed orchards provide limited genetic variability in the seed produced. However, careful attention should be paid to ensure proper spatial distance between plus trees, as related clones often belong to the same half-sib family or even clone and may share recessive lethal or S-locus[3] alleles. Having too many closely related clones in a seed orchard reduces genotypic diversity and increases the proportion of 'empty seeds' (i.e., seeds without embryos or associated structures) or offspring suffering from inbreeding depression.

Seed orchards in breeding programmes

Clonal seed orchards are used in forest-tree breeding programmes, and selection intensity and population size are usually considered in the breeding strategy. Currently, a small breeding population size is favoured because of the high heritability of traits targeted by selection, efficient breeding strategy, high additive variance at the age of maturity, low annual budget, expensive testing methods, and a low value assigned to gene diversity.

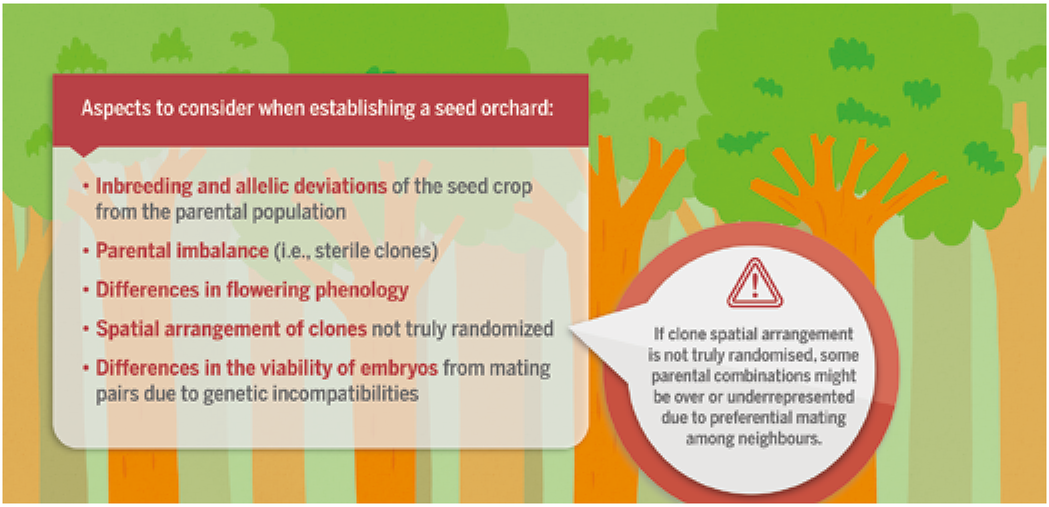

Fig. 4: Genetic and physiological factors in seed orchard design.

Genetic considerations for seed orchards

Genetic diversity in seed orchard crops depends on effective population size, which is affected by the number of clones in the seed orchard, seed orchard design, fecundity, and pollination from the outside. The way in which seed orchards are established and managed needs to ensure maximum genetic and genotypic diversity in the seed produced. The many genetic and physiological aspects that must be considered while establishing seed orchards include:

- Inbreeding and random deviations of the allelic structures of the seed crop from those of the parental population
- Parental imbalance (i.e., sterile clones)
- Differences in flowering phenology
- Spatial arrangement of clones not truly randomized
- Differences in the viability of embryos from particular mating pairs due to genetic incompatibilities.

The spatial arrangement of clones is also important: if it is not truly randomized, some parental combinations may become overrepresented - and others underrepresented - in the seed crop, due to preferential mating among neighbours.

Effective population size in seed orchards

Clonal seed orchards established from vegetative copies (ramets) of phenotypically selected or tested plus trees generally contain fewer genotypes than seed stands, while seedling seed orchards usually include a broader genetic base than clonal seed orchards because of the larger number of individuals involved in producing the seed from which they are established. However, seedling seed orchards generally provide lower genetic gain than clonal seed orchards because their pedigrees are not fully known.

The best way to estimate the genetic consequences of the processes linked to genetic variation in seed orchard crops is to assess mating patterns reflecting female and male fecundity. These in turn are related to flowering phenology and spatial design. This approach involves the estimation of various types of effective population size. The effective population size relates the state (i.e., inbreeding, co-ancestry, or genetic drift) of a real population (e.g., a seed orchard) to that of an ideal panmictic population[4]. In other words, the effective population size in a seed orchard quantifies the number of clones that have equal reproductive success, the same inbreeding or co-ancestry coefficient, or same variance of gene frequencies. This is commonly expressed in a relative manner, i.e., as a fraction of the number of clones in the actual seed orchard. As the assessment of factors such as phenology, genetic incompatibility, and male flowering is labour-intensive and costly, the easiest option to control of the genotypic diversity in seed orchard crops is to calculate the effective number of clones and the number of ramets per clone and, to ensure adaptation to environmental stresses. Note that pollination from surrounding stands of trees can increase the effective population size of the seed orchard.

Parental balance among clones

Trees may produce a large number of seeds that lack a viable embryo and/or surrounding internal structures. Such 'empty seeds' often appear similar to full, viable seeds and thus cannot be recognized during collection. As a result, the actual contribution of different maternal genotypes to a given seed lot may differ from the apparent cone or seed crop, resulting in parental imbalance.

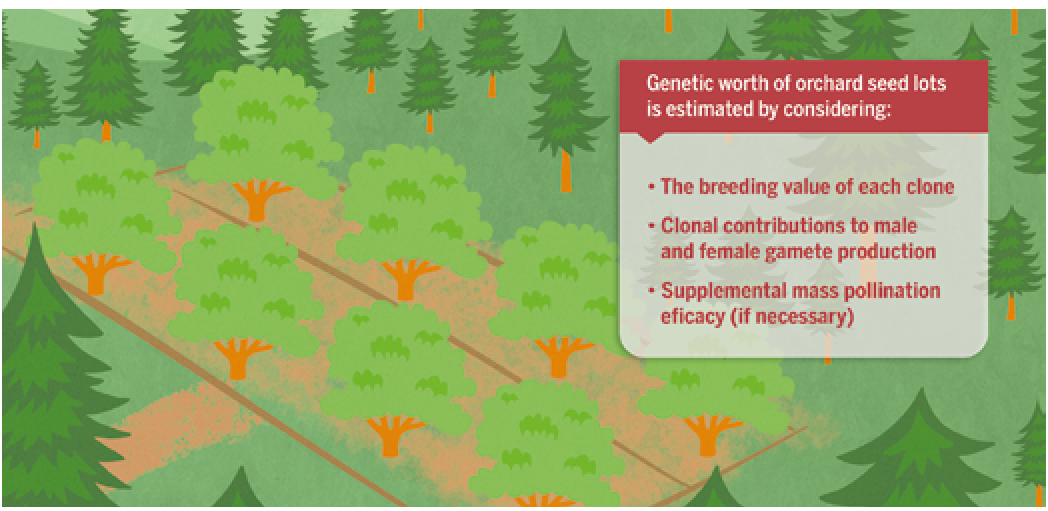

Fig. 5: Genetic worth of orchard seeds is based on clone breeding values, gamete contributions, and pollination efficacy.

Parental imbalance may also occur from the paternal side. The differential paternal mating success of individual clones (due to phenological asynchrony), variation in male fertility, and postzygotic barriers can reduce the effective population size of male parents compared with the census number of the population. To maintain parental balance among clones when establishing a seed orchard, forest managers should avoid clone relatedness, improper clonal arrangement in the seed orchard, resulting in selfing, and flowering asynchrony, etc.

Genetic worth of orchard seed lots

The genetic worth of orchard seed lots is estimated by considering the breeding value of each clone, clonal contributions to male and female gamete production, and, if necessary, supplemental mass pollination efficacy. In some orchards at risk, the calculation will also include the proportion of contaminant pollen during the period of receptivity of female flowers.

03 SEED ORCHARD MANAGEMENT TECHNIQUES

Maintaining flowering balance

Flowering abundance is partly determined by genetics, with most trees or clones flowering infrequently. However, seed orchard clones that flower prolifically do so in consecutive years. Differences in flowering and other aspects of reproductive phenology are evident in many species (e.g., phenological lags in receptivity of female flowers) and flowering phenology often affects male reproductive success. Therefore, both the selection of clones and the management practices affecting flowering abundance and phenology have a genetic bearing.

Flower stimulation

Flower stimulation techniques may be used to create artificially favourable conditions for initiation and differentiation of reproductive buds, especially with conifer species. The best results can

Fig. 6: Female flower of European black pine (Pinus nigra).

generally be obtained with a cultural treatment (e.g., nitrogen fertilization, stem girdling, root pruning, etc.) combined with hormonal treatment (gibberellin GA4/7 injection). Management measures such as pruning, fertilization, and irrigation are commonly used to enhance seed production in seed orchards. However, as they are usually applied to the whole seed orchard in a uniform way, they are unlikely to have significantly different effects on the different clones, and thus do not contribute to parental imbalance.

When establishing seed orchards to provide forest owners with forest reproductive material (FRM) of high genetic quality, it is important to ensure that the quantitative and qualitative objectives are not antagonistic. There are differing opinions on whether to use flower stimulation. On the one hand, induction treatments may favour random mating because they increase the number of flowering genotypes and thus the number of contributors to the seed lot. On the other hand, it has been reported that these treatments are particularly effective for genotypes with innate good flowering ability and thus may increase the parental imbalance of fertility and reduce random mating.

Although studies have shown that the impact of flower induction on parental contributions depends on species, years, and treatments, no antagonism has been found between quantitative and genetic objectives in any orchard. In conifers, this may be the result of two factors: first, highly flowering trees produce smaller cones with lower seed potential than lesser-flowering trees, which tends to balance parent genotype contributions; and second, the treatments that promote female flowering effectively also favour pollen production in most coniferous species. This results in more even contributions from the parent genotypes for both female and male gamete production.

Although flower stimulation may lead to a reduction in seed weight and/or germination rate, such treatments are highly recommended because of their positive impact on seed production and genetic quality, both in terms of diversity and genetic gains.

Location as induction treatment

The choice of site where a seed orchard is established can itself be considered an induction treatment. Seed orchards can be located either indoors, where environmental conditions are under strict control, or at outdoor sites that are isolated from stands of the same species to avoid pollen contamination. The deviation from panmixia is less when environmental conditions are favourable to flower initiation, pollination, and seed development. Thus, such sites should be sought when establishing new seed orchards, especially if managers do not intend to use flower stimulation treatments or if the species does not respond to standard induction techniques. Very warm sites should be avoided because of epigenetic after-effects being likely to produce maladapted FRM. Selecting phenologically compatible genotypes with a good ability to produce female flowers, pollen and sound seeds enhances genetic quality. This means the choice of genotype as a flower simulation treatment is considered.

Assisting pollination

Supplemental mass pollination is the wide application of pollen to strobili that are not isolated from wind-borne pollen to increase yield of sound seeds and realized genetic gains. Controlled pollination, carried out by qualified and experienced personnel, can be used to increase genetic gain in seed orchards and reduce pollen contamination. It is mostly used to cross genotypes with a high specific combining ability or to produce hybrid seeds. Artificial pollination can be carried out using both fresh and stored pollen.

Proper seed collection

The objective of seed collection is to maintain a basic level of gene diversity in seed orchard crops. In Europe, there are no absolute legal restrictions regarding the number of clones to be harvested or seed lot size per clone, but the whole seed crop is expected to be harvested. Several European countries do have simple regulations relating to seed collection. For example, in Slovakia and Poland, cone or seed collection in seed orchards is only allowed when more than 50% of clones flower.

Genetic diversity is assessed based on clonal contributions to male and female flowering, using the concept of effective population size (*Ne*) or state number. It corresponds to the number of unrelated and non-inbred clones in an ideal seed orchard with a panmictic rearing regime. All seed lots must exceed a pre-set minimum threshold (*Ne* = 15) due to the difficulty of evaluating the flowering percentage of the different clones and the non-synchrony of the flowering of the different clones.

High seed quality depends on the collection of seeds only upon maturity or the use of appropriate after-ripening techniques needed for some species. The level of maturity of the seed affects germinability, in particular the germination energy and the viability of the seed in storage. Immature seeds are also more susceptible pathogenic or saprophytic fungi. Furthermore, physiological maturity of seeds can influence their germinal response to different environmental conditions and affect their need for and response to dormancy-breaking treatments. However, different genotypes vary in the timing of seed maturation. Such genetic differences may be more pronounced in populations at the extremes of the species distribution range, where full maturation does not always occur.

Harvesting cones/seeds from only the most productive grafts/trees is not desirable, as they are likely to belong to a limited number of genotypes.

For more information on proper seed collection, please refer to Theme 5[i] in this series: *Seed harvesting, processing, storage, and nursery practices. How management practices can affect or influence genetic diversity of forest reproductive materials* (EUFORGEN 2023).

Clones and clonal mixtures

Vegetative propagation is a traditional method used for clonal reproduction of selected plant genotypes. Clonal propagation techniques, such as grafting, budding, cutting, and layering have been used for thousands of years in horticulture to reproduce grape or fruit plants with outstanding qualities. Plants for forestry purposes were traditionally grown from seed and use of clonal material was, until recently, common only in the case of fast-growing trees, such as poplars or willows.

Use of clonal reproduction in forestry has both advantages and disadvantages. The primary advantage is increased genetic gain based on improved utilization of additive genetic variance and more uniform products. Disadvantages include lack of genetic diversity and high ecological and economic risks. The risk level usually depends on how many clones are used, the genetic diversity among the clones, how the clones are mixed in the plantations, and landscape. Genetic variation is deliberately excluded to maximize the desirable characteristics of a particular individual or individuals. Limits on the minimum number of clones to use in plantings are set at the country level.

Specialities in vegetative propagation

According to international rules (OECD[ii], EU legislation[iii]), clonal material must be genotypically identical, homogeneous, and stable in all phases of production and use. The requirements regarding these characteristics are summarized in the distinctness, uniformity, and stability criteria published by UPOV[iv] (1981). Vegetative plant propagation is specified in detail by certification systems such as the OECD Forest Plant Scheme and EU legislation, which summarize the technical requirements for specific issues (e.g., clonal identity, homogeneity, selection and testing for production categories, etc.). For instance, clonal reproductive material shall only be marketed in the category 'Qualified' or 'Tested', which are classified by minimum requirements related to applied genetics (e.g., phenotypic selection, testing approaches, genetic evaluation, types of basic materials, etc.).

Which type of clonal FRM to choose depends on the production system. In the case of plantation forestry for producing either biomass or timber, single clones are preferable to simplify silvicultural techniques and to allow the use of cultivar-specific technologies. For restoring natural forests, such as riparian forests, the use of a clonal mixture of trees of a variety of species such as poplars and willows is preferable.

Propagation methods and techniques

The whole production chain of clonal reproductive materials is regulated by certification schemes, including rules for collection and production of vegetative plant parts. According to these, the vegetative propagules (the parts of plants such as cuttings and layers) must be harvested from registered basic materials (stool beds or stock plants) under the control of designated authorities.

The vegetatively propagated materials must be:

- Appropriately homogeneous and the plants optimally vigorous.
- Maintained to guarantee the clonal identity of all propagated plants.

Materials for clonal mixtures must be:

- Heterogenous.
- Kept separately as much as possible.
- A mix of component clones that are optimally adapted to local site conditions.

Clonal reproductive material can be produced by using cuttings, grafting, or *in vitro* methods.

Cutting

The production of cuttings is the simplest and most common way of multiplying clonal plants of fast-growing broadleaved species, such as poplars and willows. This production method has many advantages, such as cost-effective mass-production and traditional cultivation techniques with well-defined standards and simple procedures.

Grafting

Grafted material can be used for clonal multiplication of species that have no ability to reproduce auto-vegetatively. Although the production of such material

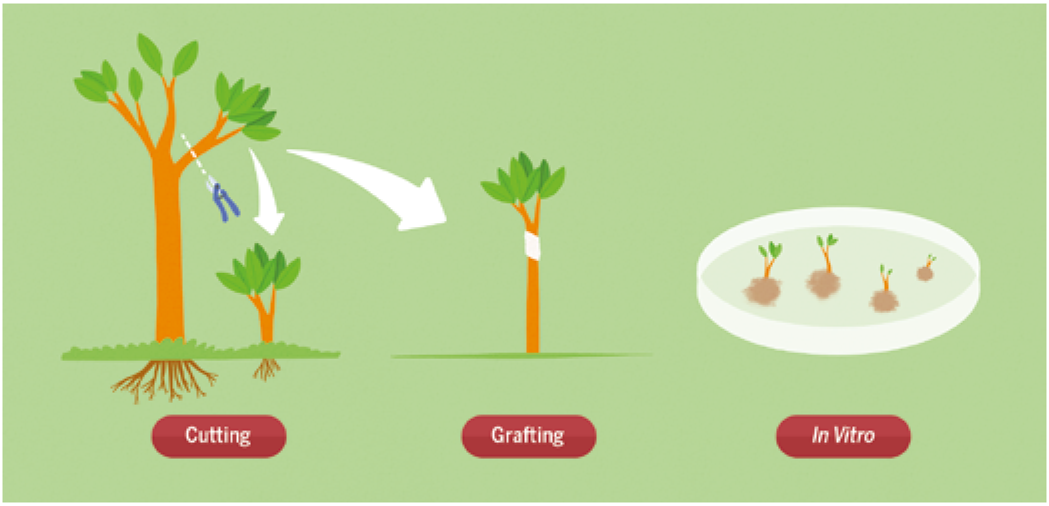

Fig. 7: Clonal reproductive material can be generated using cuttings, grafting, or in vitro techniques.

is more complex and expensive, it has the advantage of increased phenotypic variability of grafted material, due to the interactions of the scions and rootstocks. In addition, dependence upon environmental conditions can be overcome by selection or suitable rootstocks. The use of grafted plants on various forestation sites is also limited since they are often threatened by biotic stress factors or infections. Nevertheless, grafting is often the only available method for establishing field (*in vivo*) gene banks or breeding collections of selected plus trees.

In vitro

In vitro culture is used for the propagation of species (e.g. conifers) which prove difficult to multiply in other vegetative ways, or for preserving the existing gene pools of endangered tree species, and increasing their variability by thus capturing any somaclonal variability. Furthermore, the *in vitro* plants can be used for establishing basic materials to produce FRM in the next phase of the production chain. Tissue culture can also be used for producing virus-free clonal material that can be used in common vegetative propagation.

Choice of basic clonal materials

The type of basic material used to establish a seed orchard may differ depending on various aspects, such as species, purpose of use, and cost effectiveness. The most common types of basic materials used in forestry are stool beds[9], stock plants[10], and *in vitro* culture-propagated plants[11] via organogenesis[12] or somatic embryogenesis[13].

A combination of vegetative and generative reproduction systems can successfully be applied to some broadleaved tree genera (e.g., *Populus* spp. and *Salix* spp.), which makes them well adapted to colonizing specific riverside habitats. A plant's natural ability for clonal reproduction has traditionally been exploited by humans and many tree species can be propagated economically by using cuttings. This reproduction ability is also used for establishing clonal collections. However, when establishing *ex situ* clonal collections, it is important to capture a high-enough level of genetic variation to preserve the gene pool of the species' populations. Clonal collections and stool beds for genetic conservation purposes should include genotypes that have been selected without using traditional breeding selection criteria, since the selection of specific traits leads to a drastic reduction of genetic variation. As a result, the *ex situ* collections should include a large number of clones with at least a minimum of phenotypic information.

Clonal collections can also be used for breeding purposes. In this case, the collection must include clones that have been selected for phenotypic traits of economic importance, such as straight stem, fast and high growth, and resistance to frost or drought.

Pest management

Cone and seed pests pose a considerable problem to the seed production of some important tree species in European forestry. For example, infestation rates of cone insects have been reported to be as much as 95% to 100% in *Picea abies*. From a genetic point of view, the most crucial issue is if pest damage affects some genotypes more than others. Finding effective pest management practices, which are currently limited, could increase both the productivity of seed orchards and the genetic diversity of FRM. There are indications that the geographical distribution of some seed insects and the severity of the damage they cause will change due to climate change. New, alien pest species, such as the western conifer seed bug, *Leptoglossus occidentalis* Heidemann, are also expected to appear. The impact of these and other seed pests on FRM production needs to be studied further.

Fig. 8: Pest management is crucial in seed orchards to protect seed production and genetic diversity.

04 USING FRM FROM SEED ORCHARDS

Post control of clonal varieties and clones

Planting materials must be regularly compared with reference trees in post-control tests (e.g., comparative field trials) to evaluate both clonal identity and vigour of planting materials. During a long rotation (vegetative production) period, clonal genotypes are produced under strong mutagenic pressure and their genome can be significantly modified. The main reason for post-control tests on planting material lots is to confirm the homogeneity of the basic materials and their plant vigour in the place of origin.

When can we use clonal FRM?

Many countries have national regulations that determine the production and use of reproductive materials in plantation forestry. These influence whether clonal FRM can be used.

Most clonal FRM is used for plantation forestry outside the European continent. Clonal FRM is commonly used in Europe for poplars (*Populus* spp.), willows (*Salix* spp.), and eucalyptus (*Eucalyptus* spp.), and less so for other tree species, such as Norway spruce (*Picea abies*) and wild cherry (*Prunus avium*). Its use in multifunctional forestry is limited by the inherent advantages and disadvantages of clonal materials, such as high breeding value versus low genetic variation. According to a review on the theoretical benefits and risks of using clones in forestry, 530 clones provide as much 'safety' as would be experienced in infinitely large populations, and the optimum level of diversity might be around 18 clones, with a minimum of around six clones. However, both genotypic and allelic diversity in such stands is drastically reduced and this may lead to many unanticipated problems.

Genotype-by-environment interactions have a much larger impact on clones and clonal mixtures than on sexually propagated materials, and a pathogen infestation could have more serious consequences on clonal stands than in a genetically diverse stand. On the other hand, reduction in diversity is not necessarily a problem in terms of loss of adaptability of a clonal stand as a whole, provided enough natural or close-to-natural stands are preserved. In plantation forestry, the risks associated with the disadvantages of using clonal materials (e.g., limited genetic variation, high ecological or environmental risks by use) can be mitigated by appropriate management.

The use of clonal FRM should be carefully considered to mitigate the effects of climate change, and remains an option for the diversity of actions in regeneration.

In general, when using clonal FRM the objectives should be to:

- Maintain an assortment of tested clones, ensuring the optimal application of appropriate clones for certain sites.
- Restrict the use of clones that have not been tested locally or regionally.
- Limit use of non-tested clones (e.g., maximum plantation size and use for testing purposes exclusively).
- Use a diverse set of regional and local clones. It is not advised to mix clones within a stand, but in a larger area the use of a diverse set of clones can minimize ecological risks and increase landscape diversity.

How much genetic gain can we achieve?

In the Nordic countries, which have a long history of conifer breeding, timber yield of offspring from first-generation seed orchards is estimated to be about 10% higher than that from unimproved FRM. Timber yield is estimated to be up to 25% higher in the second round of Norway spruce seed orchards. For Scots pine (*Pinus sylvestris*), mean annual yields have been modelled to be 24% higher in 1,5-generation seed orchards than in unimproved stock. Offspring from seed orchards also have higher quality than unimproved stock, which is as might be expected given that quality traits are commonly more heritable than quantity traits. This genetic gain is naturally reflected in financial gain from the sale of logged offspring trees.

END NOTES

1. Outbreeding depression is the decrease in fitness caused by crossing between phylogenetically distant genetic lineages.
2. Epigenetic changes are modifications to DNA that regulate whether genes are turned on or off. These modifications are attached to DNA and do not change the sequence of DNA building blocks.
3. S-locus (self-incompatibility locus) – a locus containing few closely linked genes preventing self-fertilization in plants.
4. A "panmictic population" is a population in which mating is entirely random and any two individuals (male and female) are equally likely to mate.
5. Stool beds: plants propagated by mound layering. Stool bed layering or mound-layering is used to propagate willow, poplar, apple, and a wide variety of other woody perennial plants.
6. Stock plants: rhizomes, shoots, leaf or stem cuttings, roots, or tubers used in plant production.
7. *In vitro* culture-propagated plants the process of growing entire plants using tissue culture techniques.
8. Organogenesis: culturing explants to form organs.
9. Stomatic embryogenesis: developing plant embryos.

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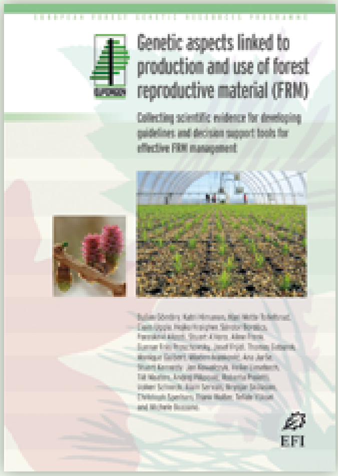
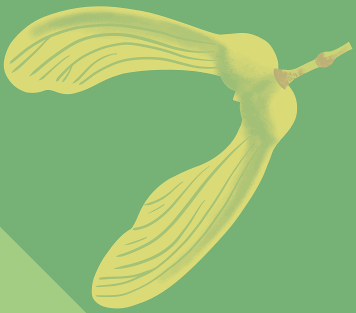
These guidelines and recommendations have been synthesized from the EUFORGEN publication:



D. Gömöry, K. Himanen, M. M.Tollefsrud, C. Uggla, H. Kraigher, S. Bordács, P. Alizoti; S. A'Hara, A. Frank, G. F. Proschowsky, J. Frýdl, T. Geburek, M. Guibert, M. Ivanković, A. Jurše, S. Kennedy, J. Kowalczyk, H. Liesebach, T. Maaten, A. Pilipović, R. Proietti, V. Schneck, A. Servais, B. Skúlason, C. Sperisen, F. Wolter, T. Yüksel and M. Bozzano. 2021. *Genetic aspects linked to production and use of forest reproductive material: Collecting scientific evidence to support the development of guidelines and decision support tools.* European Forest Genetic Resources Programme (EUFORGEN), European Forest Institute. 216 p.



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