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Trees Sustaining People and the
Environment

Innovative practices in the sustainable management of fast-growing trees

Lessons learned from poplars and willows and other experiences with fast-growing trees around the world



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experiences with fast-growing trees around the world**

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3.3 Genetics and conservation of fast-growing trees: adaptation, drift, selection, biotechnology, genetic pollution and habitat shrinkage

Isacco Beritognolo,¹ Mirko Liesebach,² Laura Rosso,³ Volker Schneck,⁴ Fulvio Ducci,⁵ Lorenzo Vietto³ and Maurizio Sabatti⁶

¹ National Research Council (CNR), Institute of Research on Terrestrial Ecosystems, Porano, Terni, Italy

² Thünen Institute of Forest Genetics, Grosshansdorf, Germany

³ Council for Agricultural Research and Economics (CREA), Research Centre for Forestry and Wood, Casale Monferrato, Alessandria, Italy

⁴ Thünen Institute of Forest Genetics, Waldsiedersdorf, Germany

⁵ Council for Agricultural Research and Economics (CREA), Research Centre for Forestry and Wood, Arezzo, Italy

⁶ University of Tuscia, Department for Innovation in Biological, Agrifood and Forest Systems (DIBAF), Viterbo, Italy

Summary

The fast-growing trees (FGTs) used worldwide are the result of breeding and selection activities organized around base genetic resources of several tree species and hybrids. *In situ* characterization of FGTs has revealed high genetic variability of natural populations, while *ex situ* field trials have shed light on their gene ecology. Static and dynamic conservation strategies contribute to maintaining the integrity of genetic resources and sustaining the genetic improvement of FGTs. Recurrent intra- and interspecific breeding over generations have greatly improved the growth and yield of FGT plantations. Selection and deployment of superior forest reproductive material (FRM) will be accelerated by new high-throughput tools, including genomics, phenomics and modelling. International regulations apply to the production and trade of FRM, but more countries should participate, and barriers to trade and use of FRM need to be addressed.

Keywords: Breeding; dynamic gene conservation; reproductive material; genetic diversity; genetic improvement; static gene conservation

Introduction

In recent years, interest in FGTs to produce wood and biomass as renewable raw materials has risen greatly. Joint efforts by industry, stakeholders and scientists are required to achieve more sustainable production systems and reduce anthropogenic pressure on forest ecosystems. The sustainable management and economic exploitation of FGTs require in-depth knowledge of genetic resources in terms of their geographic distribution and their genetic, phenotypic and ecological diversity. Genetic resources refer to the heritable diversity and genetic material maintained within and among plant species that are of environmental, scientific, economic or societal value. The genetic resources of a given species include selected germplasm, natural wild populations and interfertile species of wild relatives. The exploration and characterization of genetic resources provide the knowledge base for their conservation and management. Information acquired on genetic and phenotypic diversity is essential for selection and breeding to improve FGT reproductive material and ensure adaptation to future climate scenarios. New technologies are empowering the basic research and breeding of FGTs, particularly in some model species, and are opening new horizons to improve the whole FGT value chain.

Characterization of fast-growing tree genetic resources

The diversity of genetic resources is fundamental for breeding, cultivation and adaptation to a changing environment (Jactel *et al.*, 2017). Unlike crops, most FGTs belong to poorly domesticated forest species, and a wide genetic diversity is present in their natural populations (Neale and Kremer, 2011). The biological and ecological features of forest trees, such as their mating system, life history and gene flow, maintain a relatively high genetic diversity, despite the impact of climate change and anthropogenic disturbances (Savolainen and Pyhäjärvi, 2007). Breeding and propagation practices can affect the diversity and adaptation of genetic resources. Vegetative propagation is an efficient method for several purposes, but the genetically homogeneous plantations of FGTs increase vulnerability to abiotic and biotic stressors. Moreover, seed dispersal and pollination from plantations may affect the genetic diversity of surrounding natural forests (Ingvarsson and Dahlberg, 2019). This risk is relevant where cultivated exotic species can cross with local wild plants, as in the case of interspecific poplar (*Populus* L.) hybrids grown near natural stands (Vanden Broeck *et al.*, 2021). Some globally spread FGT species may also become invasive alien species and alter the diversity and structure of forest ecosystems (da Silva, Bouillet and de Paula, 2016). The characterization of genetic resources requires two levels of investigation, *in situ* and *ex situ*.

In situ studies explore existing variations of plant populations in their ecological habitats. Natural stands adapted to specific sites represent precious genetic resources for plantations in similar environments. Basic characterization of natural genetic resources addresses the genetic diversity and structure of natural populations by analysing DNA variation. In the last decade, rapid progress has been made in the field of genomics, which analyses entire genomes using high-throughput technologies, such as next-generation sequencing (NGS) technology. Genomics tools are available for a few species with long research track records, such as poplars, eucalypts (*Eucalyptus* L'Hér) and pines (*Pinus* L.) (Street, 2019).

Ex situ studies investigate the genetic basis and plasticity of phenotypic traits, the “genotype × environment interaction” and the association between genetic variants and traits (Li *et al.*, 2017). Common garden field trials are the most common experimental design in *ex situ* studies and are fundamental steps in the scientific analysis, domestication and breeding of trees (Sáenz-Romero *et al.*, 2019). Multisite trials are essential for evaluating adaptation to different environments (Chakraborty *et al.*, 2019). Some basic information on genetic resources of the main FGT species among hardwoods and softwoods is presented in this section.

Poplars have long played a role in human society as multipurpose trees for wood and specialty products (Pannucci *et al.*, 2021). The *Populus* genus includes 32 fast-growing species, classified in six sections, encompassing a wide natural range throughout the northern hemisphere. The current status of domestication and conservation of poplar genetic resources has been reviewed by Stanton, Serapiglia and Smart (2014). Initial *in situ* studies focused on phenology in wild populations of *Populus trichocarpa* Hook. and *P. deltoides* Moen. from different latitudes of North America and showed the importance of bud set phenology for breeding and selection (Pauley and Perry, 1954). Common garden experiments were then established at several locations to study the quantitative genetics of adaptive traits in *P. deltoides* and *P. trichocarpa* (Farmer, 1996). DNA markers have enabled the genetic characterization of poplar germplasm and the identification of commercial genotypes (Fossati *et al.*, 2005).

Moreover, *P. nigra* L. is a keystone species of European riparian ecosystems (Figure 2) and is a good example of how genetic resources are characterized by field and laboratory analyses. Genetic studies on *P. nigra* populations in Europe have shown high genetic diversity and a population structure consistent with the geographic separation of river basins (Faivre-Rampant *et al.*, 2016). *Ex situ* provenance trials have been conducted to study several characteristics, such as leaf functional traits (Guet *et al.*, 2015), biomass and bioenergy (Allwright *et al.*, 2016), and wood chemical properties (Gebreselassie *et al.*, 2017).

Genetic mapping of full-sib poplar pedigrees has identified genome regions or quantitative trait loci (QTL) controlling complex adaptive traits, such as growth (Rae *et al.*, 2008), bud phenology (Rohde *et al.*, 2011; Fabbrini *et al.*, 2012), disease resistance (Jorge *et al.*, 2005) and response to elevated carbon dioxide (CO₂) (Rae *et al.*,

2007) and cadmium (Iori *et al.*, 2016). A great breakthrough was the public release of the genome sequence of *P. trichocarpa*, the first among tree species (Tuskan *et al.*, 2006). These genomic resources are now widely applied thanks to technological advances and decreasing costs. Genome-wide association studies have been carried out on large collections of unrelated plants and have identified candidate genes associated with productive traits, such as biomass and wood quality in *P. nigra* (Allwright *et al.*, 2016) and *P. deltoides* (Fahrenkrog *et al.*, 2017).

Eucalypts are the world's most widely planted hardwood trees (Myburg *et al.*, 2014). *Eucalyptus* species and hybrids are of great interest as FGTs, mostly the subtropical *Eucalyptus grandis* W. Hill, *E. urophylla* S.T. Blake and *E. camaldulensis* Dehnh., and the temperate *E. globulus* Labill. and *E. nitens* Maiden. Hybrid eucalypts are the result of crosses among *E. grandis*, *E. urophylla*, *E. tereticornis* Sm., *E. camaldulensis* and *E. pellita* F. Müller (FAO, 1979a; Doughty, 2000). Eucalypts are native to Australia and adjacent islands and have high diversity and adaptability and rapid growth, and they can easily be propagated vegetatively (FAO, 1979a).

A marked genetic differentiation between populations is common in *Eucalyptus* species, whereas quantitative traits display clinal gradients associated with environmental factors. *E. camaldulensis* is the only species widespread across the Australian continent with a major ecological role. In this species, populations within river basins represent metapopulations with significant inner diversity. The neutral genetic diversity is defined by large-scale variation in latitude and moisture index (Butcher, McDonald and Bell, 2009), but the functional diversity displays differentiation patterns associated with local environments (Dillon *et al.*, 2014). The native genetic resources of *E. camaldulensis* should be considered as a panel of subspecies with high genetic diversity. *E. globulus* is a temperate species spread across South Australia and Tasmania. *In situ* genetic studies have found a genetic structure well correlated with geographic distribution, whereas the differentiation of quantitative phenotypic traits was driven by natural selection (Steane *et al.*, 2006). *Eucalyptus* has been extensively studied as a model for tree genetics; the genome sequence is publicly available, together with advanced biotechnological resources (Myburg *et al.*, 2014). Genome-wide analyses have been applied to high-density linkage maps for the identification of DNA markers associated with growth and wood traits (Silva-Junior and Grattapaglia, 2015).

Pinus radiata D. Don (radiata pine or Monterey pine) is native to North America and is the most planted softwood worldwide. It was introduced to Europe in the eighteenth century, then to Australia, and later to other continents, mainly in the southern hemisphere. *P. radiata* is widely planted as an exotic tree, but its native range is small and restricted to five populations of North America (Mead, 2013). As a consequence, its genetic diversity is lower than in other planted softwoods (Moran, Bell and Eldridge, 1988). The domestication and breeding of *P. radiata* started in Australia and New Zealand. Cultivated *P. radiata* germplasm mainly originates from the two northern provenances, Monterey and Año Nuevo, and represents a narrow fraction of the natural genetic diversity (Moran and Bell, 1987).

P. radiata can be vegetatively propagated by rooted cuttings, allowing the establishment of informative replicated experiments, accurate estimation of trait heritability, and selection of clonal varieties (Baltunis and Brawner, 2010). *Ex situ* studies have allowed significant progress in quantitative genetics, with the obtention of genetic linkage maps (Kuang *et al.*, 1999). Progeny tests and multisite common garden trials have investigated the quantitative genetics of key traits related to growth and form and have provided fundamental information for breeding (Baltunis and Brawner, 2010). Genomic research on *P. radiata* has made progress in the last decade. A full reference genome sequence is not yet available in this species, but transcriptome sequence data provide a large set of genome-wide single nucleotide polymorphism (SNP) markers useful for research and breeding (Telfer *et al.*, 2018).

Pseudotsuga menziesii (Mirb.) Franco (Douglas fir) is native to North America. Two varieties are known: *Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco (= var. *viridis* (Schwer.) Franco) (coastal Douglas fir), and *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco (interior, Rocky Mountain or blue Douglas fir). These varieties differ in growth rate and size at maturity, with the variety *menziesii* having more rapid growth and a larger size than the variety *glauca*. Further, the variety *glauca* grows at higher altitudes than the coastal variety. *P. menziesii* has a broad geographic range in North America and exhibits great genetic and adaptive differentiation associated with environmental and geographic clines (Chakraborty *et al.*, 2016). *In situ* studies, coupled with *ex situ* common

garden trials, have shown geographic patterns of genetic and phenotypic variation in the native range. Populations markedly differ in adaptive traits such as bud phenology and seedling emergence.

P. menziesii evolutionary adaptation to western North America is mainly shaped by winter temperatures and frost dates (St. Clair *et al.*, 2005). This species was introduced in Europe in 1827; it was planted in the United Kingdom of Great Britain and Northern Ireland it was planted initially for ornamental purposes and later for forestry. Thanks to its adaptive trait variability, *P. menziesii* has become an important planted species in temperate biomes of Europe, South America, South Africa, New Zealand and Australia. In Europe, it is one of the most successful introduced species, being well adapted to various climates and soils (Ducci *et al.*, 2003; San-Miguel-Ayán *et al.*, 2016). The germplasm introduced in Europe mainly represents the coastal variety and originates from a wide range of provenances, whereas the interior variety has limited presence (van Loo *et al.*, 2019). More than 50 provenance trials have been established in Europe for the evaluation of hundreds of provenances. Replicated trials have shown that stem growth traits display a significant effect of provenance origin, whereas phenology is dependent on the climate conditions of the growing site (Gould, Harrington and St. Clair, 2012). *P. menziesii* is one of the few conifers with recently developed genomic resources, including a reference genome sequence (Neale *et al.*, 2017).

Management of fast-growing tree genetic resources

Genetic resource management serves to ensure conditions in which the genetic diversity of tree species can evolve in response to an ever-changing environment, maintaining vitality of forests and resilience to pests and diseases. The management of FGT genetic resources is also the foundation for breeding and selection programmes (Bradshaw and Strauss, 2001). Human activities, deforestation, habitat fragmentation and climate change are major threats to the integrity of genetic resources. Uncontrolled movement of forest reproductive material (FRM) and introduction of exotic species are additional causes of decline (Amaral, Thomson and Yanchuk, 2004). Static (short-term) and dynamic (long-term) approaches for conservation of genetic resources are complementary and can be used in combination (St. Clair and Hove, 2011). Dynamic gene conservation aims to maintain the evolutionary processes of tree populations to safeguard their adaptive potential. Restoration of degraded ecosystems is a strategy of dynamic conservation that enhances and accelerates natural processes of regeneration (Rotach, 2001; Vietto *et al.*, 2008). Tree stands can be established outside the native range of the species (dynamic *ex situ* conservation), according to climate-change predictions and supported by the characterization of plant material in previous provenance trials. The planted *ex situ* germplasm should represent the genetic diversity of the original population, and the stands must be large enough to ensure a minimum viable population size (FAO, 1992). In response to climate change, tree species have to adapt *in situ* or migrate to more suitable environments (range shift) (Hamrick, 2004; Marchi and Ducci, 2018). Marginal populations may be crucial for adaptation to future environmental conditions.

Forest genetic resources dynamically change, and genetic monitoring has been recently introduced to quantify the temporal changes in genetic variation and in the structure of populations. This approach should focus on keystone tree species and on rare or endangered tree species (Aravanopoulos, 2016). Dynamic gene conservation strategies concentrate on gene conservation units, which refer to a stable tree population in specific environmental conditions, selected for its high potential for adaptive evolution (EUFGIS, n.d.). Static approaches of *ex situ* conservation have the objective of preserving the current genetic diversity of a species in germplasm collections. Clonal archives (e.g. poplars, willows [*Salix* L.], elms [*Ulmus* L.], eucalypts [*Eucalyptus* L'Hér], casuarinas [*Casuarina* L.], paulownias [*Paulownia* Siebold & Zucc.] and *Pinus radiata*), seed orchards (e.g. alders [*Alnus* Mill.], locusts [*Robinia* L.], *Pinus taeda* L. and *Pseudotsuga menziesii*) and seed banks in cold storage (e.g. poplars, locusts and eucalypts) are used in conservation programmes and support plant breeding. For most broadleaved trees, seed banks are considered a short-term conservation strategy, but other species, such as species of pines and locusts, have orthodox seeds that maintain a high germination rate over many years of storage. Some forest species with recalcitrant seeds require frequent regeneration or advanced techniques such as tissue culture and cryo-conservation (Willan, 1985; Engelman, 2004; Pritchard *et al.*, 2014).

Long-term conservation of ecosystems at the pan-European level, including native populations of FGTs, is ensured by Council Directive 92/43/CEE “Habitat” (Ministero della Transizione Ecologica, 2021). In this context, the “Natura 2000” ecological network has been established to ensure the preservation and long-term survival of threatened species and habitats. It is the largest coordinated network of protected areas worldwide and covers 27 European Union countries (European Commission, n.d.). To promote a European conservation strategy, a European Forest Genetic Resources Programme (EUFORGEN) was established in 1994, with considerable efforts to conserve forest genetic diversity (de Vries *et al.*, 2015). Currently, the global conservation of genetic resources is addressed by the European Union programme GenRes Bridge, which aims “to strengthen conservation and sustainable use of genetic resources by accelerating collaborative efforts and widening capacities in plant, forest and animal domains” (GenRes Bridge, n.d.). Within EUFORGEN, priority is given to the dynamic *in situ* conservation of forest genetic resources. A pan-European network of selected genetic conservation units (Koskela *et al.*, 2013), with the European Information System on Forest Genetic Resources (EUFGIS) (Kelleher *et al.*, 2015), has been created to conserve the adaptive genetic diversity of various tree species and to promote links among national forest genetic resources conservation programmes. The EUFGIS database (available at <http://portal.eufgis.org/>) contains information on 3 210 conservation units and 107 tree species in 35 European countries. Several FGT species are listed in this information system, and technical guidelines for genetic conservation and use of some of them are available at <https://www.euforgen.org/publications/technical-guidelines/>.

Beside the conservation issue, several attempts have been made to share plant genetic resources and their benefits. In 2010, the Tenth Conference of the Parties to the Convention on Biological Diversity (CBD) adopted the Nagoya Protocol on Access and Benefit Sharing, an “international agreement which aims at sharing the benefits arising from the utilization of genetic resources in a fair and equitable way” (SCBD, 2011). The protocol requires that users of genetic resources and associated traditional knowledge from other countries (for research and development purposes) must receive permission and the terms and conditions of the exchange in advance. 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.

Selection and breeding of fast-growing trees

Forest tree breeding has been developed since the beginning of the last century. It mimics natural selection through recombination and selection pressure, but with two main differences: (1) artificial selection is directed, focusing on socioeconomic needs and adaptation requirements, and (2) the selection process is faster. Forest tree breeding is mainly concerned with species of economic importance, for which artificial regeneration through planting or direct sowing is a common practice. Several FGT species have breeding programmes geared towards the selection and approval of clones. Nevertheless, in central and northern Europe, clonal forestry is viewed critically because genetic diversity is considered a higher priority. The spectrum of breeding methods applied to FGT species ranges from traditional hybrid breeding to cultivar development supported by molecular genetic studies. The development and status of breeding activities in some of these species are summarized below.

Poplar breeding began in 1914 in the Royal Botanical Gardens, Kew, United Kingdom of Great Britain and Northern Ireland (Stanton, Serapiglia and Smart, 2014). In the 1990s, breeding programmes were restructured in two directions: long term and short term (Kang, Lascoux and Gullberg, 1996). Long-term breeding aims to preserve genetic diversity to ensure adaptability. Short-term breeding, on the other hand, aims at the rapid selection of clones as commercial varieties (Bisoffi and Gullberg, 1996). The success of poplar breeding is measured by how easily interspecific hybrids with high vigour (*P. ×canadensis* Moench; *P. ×generosa* A. Henry; *P. ×wettsteinii* Hämet-Ahti) and easy vegetative propagation can be obtained (Figure 3). The genetically superior quality of poplar clones allows immediate gains in productivity but can also result in serious losses, as in the case of the *Marssonina brunnea* (Ellis & Everh.) Magn. pathogen on poplar plantations in Europe (Zsuffa *et al.*, 1993).

Currently, the main poplar breeding objectives are survival and growth, disease and insect resistance, adaptability, crown architecture and wood quality. In short-rotation forestry (SRF), there are additional breeding goals: rapid juvenile growth, sprouting capacity after coppice and density tolerance (Lieseback, Schneck and Wolf, 2012). Breeding objectives are distinct from traits evaluated as selection criteria. A frequent approach in long-term breeding includes first-generation interspecific hybridization, combined with reciprocal recurrent selection of the parental species (Box 1). Other breeding strategies (backcrossing, multiple species hybridization, polyploidy and somaclonal variation) are not frequently applied in long-term breeding but are used in short-term programmes (Stanton, Neale and Li, 2010). Poplar breeding can be accelerated by genomic resources (Tuskan *et al.*, 2006), high-throughput genotyping (Levy and Myers 2016) and automated phenotyping (Ludovisi *et al.*, 2017). The extensive knowledge on poplar genetics has been poorly applied by marker-assisted selection (MAS), but recent approaches of genomic selection allow the prediction of breeding value using genome-wide DNA polymorphisms and could greatly accelerate genetic gain in poplar breeding (Alves *et al.*, 2020; Pégard *et al.*, 2020). Genetic transformation has been applied to improve wood quality (Boerjan *et al.*, 1997), to confer herbicide resistance (Meilan *et al.*, 2002), and to enhance phytoremediation capacity (Doty, 2008). Validating gene function is a fundamental technique, but the commercial use of genetically modified poplars is still challenging due to governmental regulations and societal perceptions (Strauss *et al.*, 2004). Genome editing by CRISPR-Cas technology is the new frontier of plant genetic improvement, but its application to forest trees has been limited because of the high heterozygosity (Zhu, Li and Gao, 2020). Recent research has demonstrated the efficiency of CRISPR-Cas to obtain modified phenotypes (i.e. altered cell wall composition) by inactivation of genes (Takata *et al.*, 2019). Given the societal scepticism towards transgenic plants, genome editing is promising as it does not require the integration of transgenic DNA.

Willow (*Salix* L.) breeding began in Sweden with hybridization (Heribert-Nilsson, 1918) and cytological studies (Hakansson, 1938). Twelve species and hybrids are included in willow breeding for biomass and wood production (Stanton, Serapiglia and Smart, 2014). Most of the commercial willows come from the United Kingdom of Great Britain and Northern Ireland and Sweden, and the largest germplasm collection, with 1 500 accessions, is conserved at Rothamsted, United Kingdom (FAO, 1979b). In addition to increasing biomass production, the improvement of resistance to leaf rust, in connection with molecular genetics, is an important target of willow breeding (Hanley *et al.*, 2011). In Sweden, willow breeding restarted in 1978 with the selection of vigorous individuals in natural stands and is mainly based on the species *Salix viminalis* L. and *S. dasyclados* Wimm. The Swedish breeding programme is closely linked to molecular genetics and ecophysiological research at Swedish Uppsala University (Weih *et al.*, 2008), where a collection of 600 accessions has been established as the basis for recurrent selection breeding (Gullberg, 1993). This breeding programme is geared towards increasing yield, rust resistance, insect tolerance and frost hardiness, with the objective of regularly deploying new varieties (Gebhardt, 2012). Willow varieties adapted to warm and dry climate conditions have been recently selected (Salix Energy Europa AB, 2016). In Argentina, willow breeding began in 1950 (Ragonese and Rial Alberti, 1958). Currently, the breeding programme continues with the development of hybrids, mainly *S. matsudana* Koidz. × *S. alba* L.; selection focuses on disease tolerance, adaptation, higher yield and quality of wood for the paper and sawmill industries (Cerrillo *et al.*, 2016). There is also a focus on the conservation of *S. humboldtiana* Willd., the only native species (Gallo *et al.*, 2020). The selection of five improved clones of *S. viminalis* L. for basketry was recently completed, to be applied in plantations in Delta del Paraná, Argentina (Cerrillo, 2021).

The most intensive breeding of *Robinia pseudoacacia* L. (black locust) outside its natural range has been carried out in Hungary, where selection began in 1930 (Fleischmann, 1933). From 1951, black locust improvement was further intensified (Keresztesi, 1983; Rédei, Osváth-Bujtás and Veperdi, 2008). The aim of the Hungarian breeding programme was to improve wood quality and growth performance. The best stands across the country were selected and approved as seed stands that produce most of the propagation material (Rédei, 2003). Furthermore, particularly vigorous trees were selected from these stands and the vegetatively propagated (root cuttings, tissue culture) clones or clone mixtures were tested in field trials. The best clones and clone mixtures were approved as varieties and propagated for cultivation (Keresztesi, 1983). In recent years, clones for biomass production in SRF have been selected and deployed (Rédei, 2003). Parallel efforts have been made to improve

black locust in the United States of America. Clones of *R. pseudoacacia* were selected in 1938, and field trials were carried out on this material between 1948 and 1965 (Bongarten, 1992). This programme resulted in two seed orchards and the approval of three clones for commercial distribution. Other programmes were based on progeny tests of *R. pseudoacacia* plus trees (Liesebach and Schneck, 2018).

Eucalypts are now grown in over 100 countries for biomass and solid wood production, pulp and paper, charcoal for the steel industry and biochemicals. In Brazil, eucalypt breeding started in 1941 with species and provenance testing (de Oliveira Castro *et al.*, 2016). Initially, planting was performed using seeds from non-selected stands, with low productivity and susceptibility to pathogens. To minimize these issues, different species were crossed to produce hybrids with the objective of improving productivity and wood properties for industry plantations. In the mid-1970s, research on quantitative genetics gained strength, and the breeding of eucalypts focused mainly on clonal selection to replicate superior genotypes. Genetic improvement involves three selection stages (Rezende, de Resende and de Assis, 2014): (1) selecting parents for hybrid recombination ability; (2) selecting candidate clones among the hybrid offspring based on field progeny tests; and (3) selecting operational clones based on clonal field trials. Currently, nearly 50 percent of eucalypt forests in Brazil are clonal (Rezende de Resende and de Assis, 2014). Nowadays, genomics tools are implemented in the breeding of eucalypts to efficiently improve productive traits such as diameter growth and wood quality (Resende *et al.*, 2012; Müller *et al.*, 2017).

Breeding of *Pseudotsuga menziesii* in western North America dates back to the 1950s and has been summarized by Howe *et al.* (2006), including the approach to breeding zones, breeding cycles and methods of deployment. Recently, Jayawickrama and Ye (2020) reported the status of the large and intensive second-cycle breeding and testing programme in the United States of America. In Europe, genetic improvement of *P. menziesii* began as soon as information on intraspecific variability was available. A second phase started in the 1960s and 1970s with the phenotypic selection of superior trees in the best stands. Currently, breeding of *P. menziesii* in Europe takes advantage of the knowledge provided by the existing network of provenance and progeny tests (Bastien *et al.*, 2013). Genomic and phenotypic data can be combined to predict plant performance and could be further developed into genomic selection of *P. menziesii*, with better genetic gain for late-expressed and low-heritability traits (Ratcliffe *et al.*, 2019; Thistlethwaite *et al.*, 2019).

Breeding of *Pinus radiata* began in the 1950s in New Zealand and Australia, with the first seed orchards (Wu *et al.*, 2007). Successful breeding of radiata pine is due to a combination of favourable conditions: early introduction of germplasm came from the better provenances (Año Nuevo and Monterey), and selection in local environments resulted in landraces adapted to the new habitat. The main objectives of breeding are fast growth, stem straightness, wood properties and resistance to diseases (Burdon, 2001). Mass selection was the first breeding strategy, with the phenotypic selection of superior trees; it was applied in New Zealand and Australia prior to the availability of seed orchards. In the early stages, seed orchards produced open-pollinated seeds with low genetic improvement (Burdon, Carson and Shelbourne, 2008). Later, seed orchards were established based on progeny tests, and improved, open-pollinated seed is currently used in most plantations (Mead, 2013). Control-pollinated orchards were set up in the 1990s and almost doubled the genetic gain (Carson, 1986; Burdon, Carson and Shelbourne, 2008). Recent developments of nursery cuttings, micropropagation and somatic embryogenesis have provided new ways for the deployment of clonal plant material (Carson and Carson, 2011). Newly selected clones have allowed high genetic gains in growth and wood traits (Mead, 2013). Selection and genomic prediction could be further applied in radiata pine to improve the efficiency of selection for traits with low heritability (Klápště *et al.*, 2020).

Fast-growing tree reproductive material

The distribution of FRM is regulated to varying degrees (Stanton, Serapiglia and Smart, 2014). Some FRM is not traded, meaning that private forest companies can breed and produce reproductive material for their own forests. This also applies to cooperatives, as in the case of *Pseudotsuga menziesii* in the United States of America (Jayawickrama and Ye, 2020). At the international level, the Organisation for Economic Co-operation and

Development (OECD) Scheme for the Certification of Forest Reproductive Material Moving in International Trade (OECD, 2019) is open to OECD members (Table 5) and United Nations member states. The scheme was established in 1967 and is regularly revised. Under the OECD scheme, FRM may be produced and traded only with registered basic material. The OECD scheme includes four categories of FRM that derive from six types of approved basic material (Table 5 and Table 6). The scheme specifies minimum requirements, but each country can add further requisites in specific cases. There are no restrictions in international trade for the tree species included in the OECD scheme.

The legal framework for production and marketing of FRM in the European Union is Council Directive 1999/105/EC, which applies to all European Union member states and is harmonized with the OECD scheme. The requirements of this directive fall into four FRM categories (Tables 6 and Table 7). The directive sets rules for the approval of basic forest material and for the production and marketing of FRM. It also prescribes a system for registration, labelling and control to identify FRM from collection to the market (Konnert *et al.*, 2015). The directive has been implemented into national law by all 27 European Union member states (Table 5), and its objectives are to:

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

The directive provides a common set of minimum requirements but allows European Union member states to enforce additional and more stringent requirements, except for marketing. According to the directive, forest seed and planting stocks produced in seven non-European Union countries (Canada, Switzerland, Norway, Serbia, Türkiye, the United Kingdom of Great Britain and Northern Ireland and the United States of America) and officially certified under the OECD scheme are considered equivalent to seed and planting stocks complying with Council Directive 1999/105/EC. Supplementary third countries, such as Serbia and the United Kingdom of Great Britain and Northern Ireland, have adopted similar rules. Türkiye has also adopted the Council directive, with all definitions of FRM categories. The directive's scope is limited to 47 species and to artificial hybrids important for forestry purposes. Some member states have not approved FRM for tree species without national economic importance, but the cultivation and distribution of FRM by national forest seed and plant companies are allowed.

Neither the European Union directive nor the OECD scheme include requirements on the end use of FRM, but states are free to determine requirements in their national or regional legislation (Liesebach, 2020). The European Union has established the online database FOREMATIS (Forest Reproductive Material Information System) on approved basic material, with a search tool for forest breeders, forest nurseries, experts and the general public (available at <https://ec.europa.eu/forematis/>). Willows do not fall under the European Union directive or national law and may be freely propagated and marketed, provided that there is no plant variety protection. An international register of poplar clones, with 358 entries, has been established by the IPC and is frequently updated (available at www.fao.org/forestry/ipc/69637/en/).

An important aspect of FRM trade is protection against the introduction of pathogens and pests, an increasing risk due to market globalization and climate change. It is therefore necessary to adopt measures against phytosanitary risks, subject to international agreements and international conventions such as the International Plant Protection Convention (the treaty was originally signed in 1951 and revised in 1997). For European Union member states, Regulation 2016/2031 recently came into force (European Union, 2016), replacing Directive 2000/29/EC. This regulation poses some limitations to the free trade of FRM.

Table 5. European Union member states and the Organisation for Economic Co-operation and Development Scheme for the Certification of Forest Reproductive Material Moving in International Trade

Continent	Country (ISO 3166)	OECD scheme	Council Directive 1999/105/EC
Africa	BF, KE, MG, RW, UG	X	
North America	CA, US	X	
Asia	TR	X	
Europe	AT, BE, BG, DK, DE, FI, FR, IE, IT, HR, HU, NL, PT, RO, SK, ES, SE, SI	X	X
	CH, NO, GB, RS	X	
	EE, GR, LV, LT, LU, MT, PL, CZ, CY		X

Notes: OECD = Organisation for Economic Co-operation and Development. A key to country names is available at <https://www.iso.org/obp/ui/#search>. Sources are given in Table 7.

Table 6. Categories of forest reproductive material and origin of breeding material

Origin of breeding material	Categories of forest reproductive material			
	Source-identified	Selected	Qualified	Tested
Seed source	X			
Stand	X	X		X
Seed orchard			X	X
Parents of family/ies			X	X
Clone			X	X
Clonal mixture			X	X

Note: Sources are given in Table 7.

Table 7. Definitions of the four categories of forest reproductive material

Category	OECD scheme ⁱ	Council Directive 1999/105/EC ⁱⁱ
Source-identified	This is the minimum standard permitted. The location and altitude of the place(s) from which reproductive material is collected must be recorded; little or no phenotypic selection has taken place	Reproductive material derived from basic material, which can be either a seed source or stand located within a single region of provenance and which meets the requirements of Annex II ⁱⁱ
Selected	The material must be phenotypically selected at the population level	Reproductive material derived from basic material, which shall be a stand located within a single region of provenance, which has been phenotypically selected at the population level and which meets the requirements of Annex III ⁱⁱ
Qualified	The components of the basic material have been selected at the individual level; evaluation may not have been undertaken or completed	Reproductive material derived from basic material which shall be seed orchards, parents of families, clones or clonal mixtures, the components of which have been phenotypically selected at the individual level, and which meets the requirements of Annex IV. ⁱⁱ Testing need not necessarily have been undertaken or completed
Tested	The superiority of the reproductive material must have been demonstrated by comparative testing or an estimate of its superiority calculated from the genetic evaluation of the components of the basic material	Reproductive material derived from basic material which shall consist of stands, seed orchards, parents of families, clones or clonal mixtures. The superiority of the reproductive material must have been demonstrated by comparative testing or an estimate of the superiority of the reproductive material calculated from the genetic evaluation of the components of the basic material. The material shall meet the requirements of Annex V ⁱⁱ

Notes: Sources of tables 5-6-7:

ⁱ OECD (Organisation for Economic Co-operation and Development). 2019. *OECD scheme for the certification of forest reproductive material moving in international trade*. OECD Forest Seed and Plant Scheme. Paris. www.oecd.org/agriculture/forest/documents/forest-scheme-rules-and-regulations.pdf

ⁱⁱ Council Directive 1999/105/EC of 22 December 1999 on the marketing of forest reproductive material. <http://extwprlegs1.fao.org/docs/pdf/eur34525.pdf>

What do we need?

Forest trees are poorly domesticated, but FGT species are an exception as methods from agriculture are used on a large scale. The present challenge is to increase FGT wood production without eroding long-term adaptive potential or impairing the production capacity. Natural populations of forest trees represent a reservoir of genetic resources for FGTs. *In situ* and *ex situ* studies of wild germplasm are fundamental for characterizing the genetic and adaptive diversity of FGTs. *Ex situ* collections and field trials should be better connected with breeding and conservation programmes. Long-term field trials in replicated environments provide vital information on plant adaptability and allow for the monitoring of the impacts of climate change, but such research infrastructures lack support for long-term management and monitoring.

Fast-growing tree species are widely planted worldwide, and activities to explore and characterize the natural genetic resources of FGTs need to be better connected in an international network. Climate change has an

impact on the integrity of FGT genetic resources and represents a challenge for their future adaptability. Genetic resources are also exposed to various threats: deforestation and habitat fragmentation, uncontrolled movement of FRM, introduction of exotic pests and human activities. It is therefore necessary to sustain the conservation of genetic resources *in situ* and expand *ex situ* collections with new germplasm.

Forest genetic resources dynamically change in response to strong pressures, and it is necessary to implement genetic monitoring on gene conservation units for dynamic *in situ* conservation. The existing networks for conservation of forest tree genetic resources are managed at the local level and need to be more coordinated worldwide. To support the sustainable use of FGTs, the different governments need appropriate policies and regulation frameworks.

Fast-growing trees are the most domesticated of forest trees, and genetic improvement has been typically designed to increase yield, wood quality and pest resistance. Present breeding programmes should match the future changes in environmental conditions and market demand, and new breeding objectives should include environmental adaptability and tolerance to emerging pests. The clonality and narrow genetic diversity of highly selected FGTs represent a vulnerability factor, and continuous infusion of wild germplasm into breeding programmes is necessary to support the resilience of plantations.

Hybridization among species continues to be a major way of genetically improving some FGTs, such as poplars and eucalypts. Forest tree genomics and phenotype predicting models could considerably accelerate tree improvement, but implementation of genomic selection in operational breeding requires a complex and multidisciplinary approach. Genetic improvement of tree species is a long-term business, which needs continuity in breeding programmes.

Currently, trading of FRM is largely unhindered, but some countries only allow local FRM for plantations. These restrictions need to be adjusted to use FGT plant material better adapted to climate change. The area of deployment should be recorded by authorities to allow for long-term monitoring of tree adaptive response. Reproductive material of FGT species should be marketed worldwide according to uniform rules.

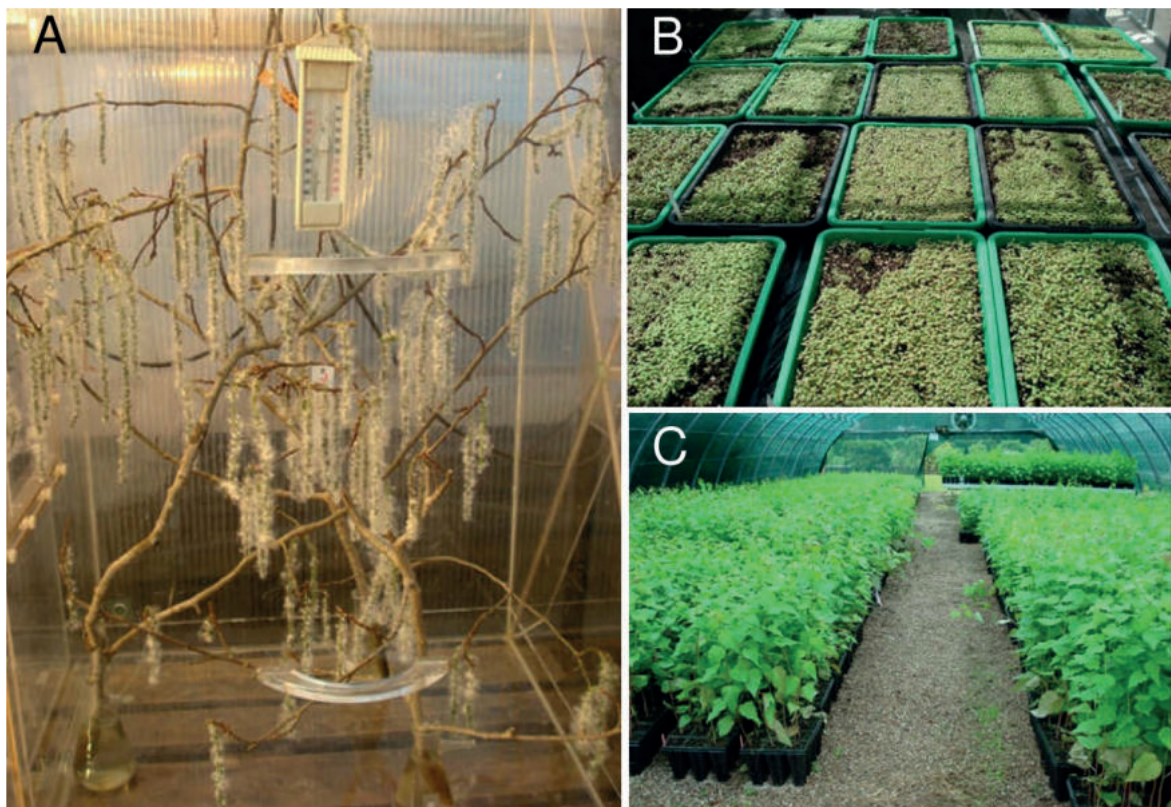
Take-home messages

- Natural populations of FGTs represent a reservoir of genetic resources and are worthy of thorough *in situ* characterization and conservation.
- Germplasm collections and common gardens support conservation strategies and breeding but lack adequate investments for long-term maintenance and monitoring.
- Dynamic gene conservation of FGTs *in situ* requires the definition of gene conservation units, the implementation of genetic monitoring and better international coordination.
- Breeding programmes have selected highly productive FGTs for intensive cultivation, and new breeding objectives are required in response to climate change and emerging pests.
- Interspecific hybrids will continue to be the main road for the improvement of some FGTs, and genomics, phenomics and modelling will be implemented in future genetic improvement programmes.
- Trade and deployment of FRM at a global scale would benefit from a wider participation of countries in the OECD scheme.

Figure 2. Natural population of *Populus nigra* along the Paglia River, Acquapendente, Italy



Figure 3. *Populus ×wettsteinii* interspecific breeding: A) release of seeds from female catkins after controlled crossing; B) full-sib progenies in germination trays; C) transplanted seedlings in the greenhouse

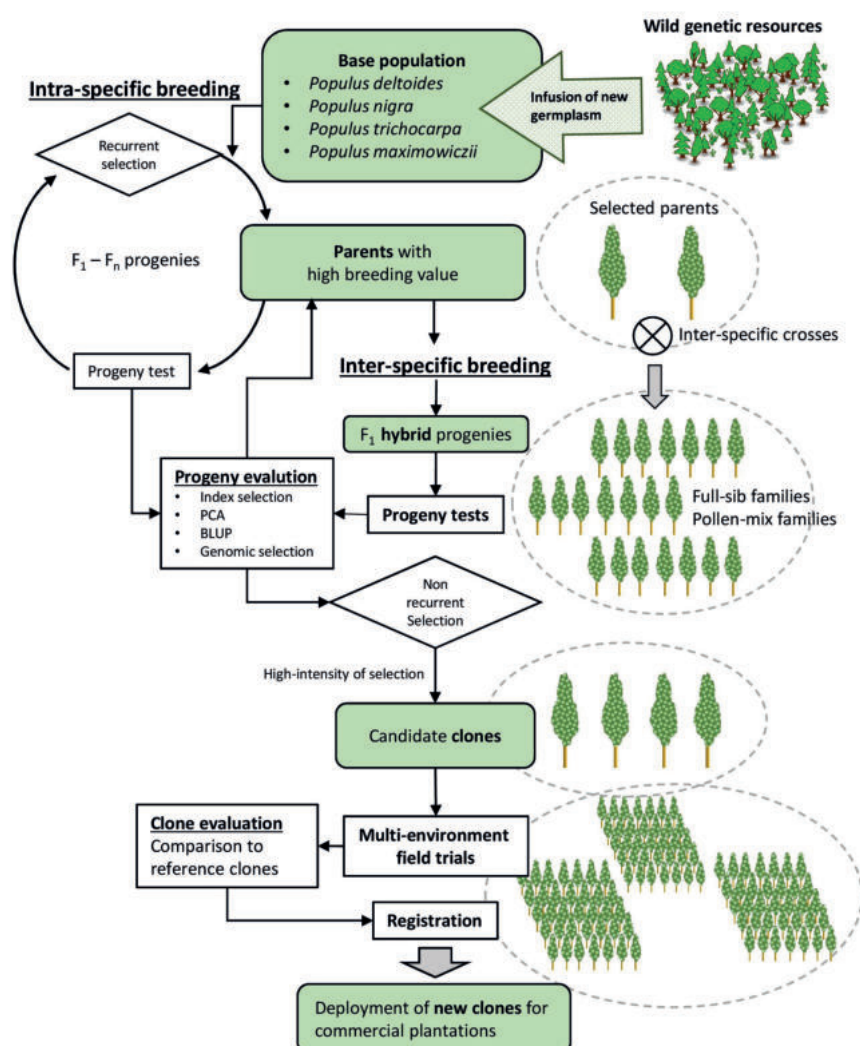


Box 1. OVERVIEW OF POPLAR BREEDING FOR HYBRID CLONES

Base plant material (seeds or cuttings) is sampled from wild populations considered to be representative of the genetic and environmental diversity of each species and is grown in *ex situ* collections. Germplasm collection over a latitudinal gradient is important to capture the variation of adaptive traits. The continuous infusion of new germplasm is necessary to avoid relatedness and loss of genetic variability. Recurrent intraspecific breeding of two or more parental species is then conducted, based on the performance of intraspecific progeny tests. Parents with high breeding value are selected and crossed to obtain F_1 interspecific hybrids, which are tested in replicated field trials. Linear models integrate data from several traits to achieve a multitrait evaluation of F_1 progenies using the selection index method, principal component analysis (PCA) and best linear unbiased prediction (BLUP). Genomic data, phenomics and phenotype prediction can be implemented in poplar breeding to accelerate selection steps (genomic selection). Progeny tests of hybrid families may influence the intraspecific recurrent selection to obtain parental clones with high interspecific combination ability. The hybrid clones are screened with high-intensity selection to identify a small set of candidate clones for multi-environmental field trials. This evaluation is performed on diverse sites over multiple years, with continuous comparison to local reference commercial clones. The superior clones must be accepted for registration (depending on country regulations) and are then deployed in operational plantations. Figure 3 presents a simplified breeding scheme for poplar hybrid clones.

Figure 4. Breeding scheme for poplar hybrids

Source: Authors' own elaboration.



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