



Utilization and transfer of forest genetic resources: A global review



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ABSTRACT

Over the last 200 years, genetic resources of forest trees have been increasingly transferred, within and outside of species' native distribution ranges, for forestry and for research and development (R&D). Transferred germplasm has been deployed to grow trees for numerous purposes, ranging from the production of wood and non-wood products to the provision of ecosystem services such as the restoration of forests for biodiversity conservation. The oldest form of R&D, provenance trials, revealed early on that seed origin has a major influence on the performance of planted trees. International provenance trials have been essential for selecting seed sources for reforestation and for improving tree germplasm through breeding. Many tree breeding programmes were initiated in the 1950s, but as one round of testing and selection typically takes decades, the most advanced of them are only in their third cycle. Recent advances in forest genomics have increased the understanding of the genetic basis of different traits, but it is unlikely that molecular marker-assisted approaches will quickly replace traditional tree breeding methods. Furthermore, provenance trials and progeny tests are still needed to complement new research approaches. Currently, seed of boreal and temperate trees for reforestation purposes are largely obtained from improved sources. The situation is similar for fast growing tropical and subtropical trees grown in plantations, but in the case of tropical hardwoods and many agroforestry trees, only limited tested or improved seed sources are available. Transfers of tree germplasm involve some risks of spreading pests and diseases, of introducing invasive tree species and of polluting the genetic make-up of already present tree populations. Many of these risks have been underestimated in the past, but they are now better understood and managed. Relatively few tree species used for forestry have become invasive, and the risk of spreading pests and diseases while transferring seed is considerably lower than when moving live plants. The implementation of the Nagoya Protocol on access to genetic resources and benefit sharing (ABS) may significantly change current transfer practices in the forestry sector by increasing transaction costs and the time needed to lawfully obtain forest genetic resources for R&D purposes. Many countries are likely to struggle to establish a well-functioning ABS regulatory system, slowing down the process of obtaining the necessary documentation for exchange. This is unfortunate, as climate change, outbreaks of pests and diseases, and continual pressure to support productivity, increase the need for transferring tree germplasm and accelerating R&D.

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1. Introduction

Genetic resources of forest trees have been used and transferred by humans for millennia. The ancient Greeks and Romans played a significant role in spreading *Castanea sativa* and its cultivation from

the Eastern Mediterranean region (including Anatolia and the Caucasus) to other parts of Europe (Conedera et al., 2004). In Africa, temple art at Deir El Bahari in Egypt dating from around 1500 BC shows potted *Boswellia* sp. seedlings being loaded onto ships for transport from the Land of Punt (present day Somalia) to Egypt (see Harlan (1975) and references therein). *Tectona grandis* was introduced from Laos to the island of Java in Indonesia by Hindu travellers between the 14th and 16th centuries, if not earlier, and from North India to Africa by the Germans at the end of the 19th century (Verhaegen et al., 2010). In the 18th century, seeds of *Pinus sylvestris*, *Picea abies*, *Larix decidua* and *Quercus* spp. were widely traded across European countries (Tulstrup, 1959). Exploration by Europeans in Australia and North America in the 19th century also resulted in international transfers of tree germplasm (i.e., seed, cuttings or other propagating parts of a tree) for forestry purposes, and such exchange continues to this day (Griffin et al., 2011).

In addition to being driven by the uses of various species, the transfer of tree germplasm has been influenced by the prevailing mind sets of different historical and political eras (Carruthers et al., 2011). During the mid- to late-colonial period from the 19th century to the mid-20th century, tree germplasm was transferred to “improve” both the aesthetic value of landscapes and their economic productivity. The economic aspects were further emphasized during the period of post-colonial national development in many countries over much of the 20th century, during which time tree germplasm was transferred for establishing large-scale plantations to supply raw material for industrial modernization. Since the 1980s, tree germplasm has been increasingly transferred under the banner of sustainable development to improve the livelihoods and environments of smallholders and local communities (Graudal and Lillesø, 2007).

Before proceeding further, a note on terminology is necessary. The movements of trees and other plants were categorised by Kull and Rangan (2008) into three processes, namely transfer, diffusion and dispersal. The first two of these they classified as human-mediated, defining “transfer” as transoceanic or other large-scale movements of germplasm, while with “diffusion” they referred to movements at national or local scales. With “dispersal”, Kull and Rangan (2008) referred to the movement of reproductive material by biotic and abiotic agents. We recognize the utility of this classification, but the border between “transfer” and “diffusion” is sometimes difficult to define. Therefore, in this paper we use the term “transfer” for all human-mediated movements of tree germplasm, regardless of geographical scale.

The transfer of tree germplasm has shaped the management, ecology and genetic diversity of forests, both planted and natural, in many parts of the world. Transferred germplasm has been used to grow trees for numerous purposes, ranging from the production of wood and non-wood products to the provision of ecosystem services including the restoration of forests for biodiversity conservation. This has brought economic and environmental benefits, has increased food security and alleviated poverty in many regions, and has created incentives for conserving forest genetic resources (Dawson et al., 2014, this special issue). In many countries, the transfer of tree germplasm has increased investments (at least in the short-term) in research and development (R&D). Furthermore, the establishment of research trials has promoted international collaboration and the sharing of information.

The transfer of tree germplasm has, however, also raised concerns, such as the potential for spreading pests and diseases, and that introduced tree species may become invasive. Over the last decades, research and debate on alien invasive species and their effects on biodiversity and livelihoods have expanded to such an extent that Carruthers et al. (2011) considered ‘invasion biology’ as the newest ethos in the history of plant introductions. Climate change is likely to alter the suitable distribution range of many tree

species, while their natural dispersal dynamics are often limited by natural barriers or human activities. This has led to a debate on assisted migration (i.e., the intentional movement of species within or outside their historical ranges to mitigate observed or predicted biodiversity losses as a result of climate change) that is closely linked to the debate on invasive species (e.g. Hewitt et al., 2011; Alfaro et al., 2014, this special issue). Although such debate has often been subjective, it has increased awareness of the necessity of evaluating risks and benefits more carefully.

In 2010, the tenth 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 arrangements are known by their acronym ABS). This agreement will enter into force on 12 October 2014. The implementation of the Nagoya Protocol is left to individual Parties (i.e., national governments), which, unfortunately, have had a poor track record in implementing earlier ABS measures (CBD, 2014). The “utilization of genetic resources” is defined rather narrowly in the Nagoya Protocol, meaning “to conduct research and development on the genetic and/or biochemical composition of genetic resources, including through the application of biotechnology” (CBD, 2011). The protocol does not apply therefore to the use of genetic resources for purely production purposes, such as raising seedlings and planting them for forestry in the way that it does to R&D.

In this article, we first provide an overview of the past human-mediated transfer of forest genetic resources since the beginning of provenance research, focusing on examples of tree species which are important in forestry around the world, and which provide both wood and non-wood products. These examples include: (1) temperate and boreal trees in the northern hemisphere, (2) fast-growing tropical and subtropical plantation trees, (3) high-value tropical hardwoods; and (4) agroforestry trees. We then summarize past experiences in utilizing the genetic resources of these trees, both for production and R&D purposes (i.e., we use a broader definition of “utilization” than that of the Nagoya Protocol), and the associated concerns. Finally, we discuss future challenges related to germplasm utilization and transfer in the forestry sector, including the implications of the Nagoya Protocol. The findings and conclusions of this paper draw on an earlier report we prepared for the Food and Agriculture Organization of the United Nations (FAO) on the same topic (Koskela et al., 2010), as well as on relevant new literature and on our collective experience on the conservation and use of forest genetic resources.

2. Transfer of forest genetic resources: an historical overview

2.1. Temperate and boreal trees in the northern hemisphere

By 1850, deforestation had reduced average forest cover in Europe to an estimated 20% of land (Kaplan et al., 2009). Already in the late 18th century, several European countries had started large-scale reforestation efforts to stop this forest decline and the continent’s forest cover subsequently started to increase during the 19th and 20th centuries (Mather, 2001). The transition from deforestation to reforestation created a strong demand for forest tree seed. In many countries, however, the remaining forests could not meet the high demand and seed had to be sourced from other nations. As a result, large quantities of *L. decidua*, *P. abies*, *P. sylvestris* and *Quercus* spp. seed were transferred across Western and Central Europe throughout the 19th century and into the early 20th century (Tulstrup, 1959). The use of tree species introduced into Europe also played an important role in these historical reforestation efforts (e.g., Kjaer et al., 2014).

High demand for seed created an interest in the role of seed origin in reforestation efforts. Provenance research started with temperate and boreal trees in the mid-18th century when the first field tests of different *P. sylvestris* seed sources were established in Europe (Langlet, 1971). By the late 18th and early 19th centuries, provenance research had demonstrated that seed source has a major influence on the performance of planted trees (König, 2005). Furthermore, the first basic principles for introducing tree species and provenances from North America to Germany, emphasizing the matching of climatic and other site conditions, were published in 1787 (Langlet, 1971). Increased knowledge on various species and provenances slowly started to shape the nature of the demand for tree seed. Provenances with specific phenotypic traits (e.g., good stem form and late flushing), such as *Quercus robur* from Slavonia (Sabadi, 2003) and *P. abies* from Westerhof (Giertych, 2007), became sought after and these were widely transported across Europe. The selection of seed sources during this early period was, however, not always undertaken systematically. Some reforestation efforts failed as a result, and several countries attempted to restrict the use of imported seed in the late 19th and early 20th centuries (König, 2005). In the 19th century, more systematic exploration efforts were also extended to North America, and large quantities of seed of many trees from that region were shipped to other areas. Interestingly, several North American tree species were tested for forestry in Europe before they were assessed for this purpose in their home region (e.g., Samuel, 2007).

During the 20th century, the transfer of tree germplasm for R&D purposes increased further when several international provenance trials were established for temperate and boreal species under the auspices of the International Union of Forest Research Organizations (IUFRO) (see König, 2005). A series of IUFRO provenance trials was established for *P. sylvestris* (in 1907, 1938–39 and 1982) and *P. abies* (in 1938 and 1972), for example. The second IUFRO trial of *P. abies*, which was planted in Europe and Canada, is probably one of the largest trials ever established, involving 1,100 provenances (König, 2005). The number of provenances tested in these trials was, however, usually much lower, ranging from 20 to 50. Provenance trials were also established for several other European trees, such as *Abies alba*, *L. decidua*, *Quercus petraea* and *Q. robur*, as well as for North American species including *Abies grandis*, *Picea sitchensis* and *Pseudotsuga menziesii*. Many of these trials led to the identification of provenances that were superior to local seed sources (e.g., Madsen, 1995; Eriksson, 2010). The early reforestation and R&D efforts contributed significantly to the introduction of *P. sylvestris* and *P. abies* to 13 and 11 new countries, respectively, in Europe and other regions (Table 1).

In Canada, initial provenance trials of native trees were established for *Picea* spp. in the 1930s and 1940s, and for *Pinus banksiana*, *Pinus resinosa* and *P. menziesii* in the 1950s (Anon, 1997; Orr-Ewing, 1962). In the USA, one of the earliest provenance trials, established in 1926, was for *Pinus taeda* (Rogers and Ledig, 1996). One of the largest provenance trials established in North America included 140 seed sources of *Pinus contorta* planted in 60 locations in British Columbia, Canada (Wang et al., 2010). Other tree species received less attention in the Pacific Northwest, but some provenance research was also undertaken on *Chamaecyparis lawsoniana*, *P. sitchensis*, *Pinus lambertiana*, *Pinus monticola*, *Larix occidentalis*, *Thuja plicata* and *Tsuga heterophylla*.

P. taeda and *P. menziesii* have been introduced to 22 and 27 countries, respectively, beyond their native range (Table 1), making them some of the most widely planted North American temperate tree species in other continents, together with *Pinus radiata*, which is an exceptional case in several regards. The natural distribution of *P. radiata* is limited to a handful of remaining populations in Mexico and the USA where it has no role in commercial forestry (Rogers, 2004). The species was introduced into Australia in the

1850s for ornamental plantings and R&D work started there one hundred years later, resulting in significantly improved germplasm (Wu et al., 2007). Today, *P. radiata* is widely planted in diverse countries including Chile and New Zealand, in addition to Australia (Rogers, 2004).

2.2. Fast-growing tropical and subtropical plantation trees

Germplasm transfer of currently widely-used tropical and subtropical plantation trees such as *Acacia*, *Eucalyptus* and *Pinus* spp. started soon after their native ranges were colonised by Europeans (Bennett, 2011). The development of their historical transfer patterns is similar to that of the temperate and boreal species: large-scale tree planting efforts first created demand for germplasm transfer for production purposes and, later, germplasm was also transferred increasingly for R&D.

By the 19th century, collection and export of *Acacia* and *Eucalyptus* spp. seed from Australia was well organized. During the same century, eucalypts, including *E. camaldulensis*, *E. globulus* and *E. tereticornis*, were widely planted throughout the temperate and Mediterranean-like climatic regions of the world (FAO, 1979; Freeman et al., 2007). Acacias such as *A. saligna*, *A. cyclops* and *A. longifolia* were similarly exported to southern Africa (Carruthers et al., 2011). Exploration, collection and assessment of these species and the transfer of their germplasm for production purposes were intensified in the 20th century, and more systematic R&D work was initiated around 50 years ago. *Eucalyptus camaldulensis* and *E. globulus*, for example, have been introduced from Australia to 91 and 37 countries, respectively (Table 1). Of the more than 600 *Eucalyptus* species, just nine cover 90% of the planted eucalypt area globally: *E. camaldulensis*, *E. dunnii*, *E. grandis*, *E. globulus*, *E. nitens*, *E. pellita*, *E. saligna*, *E. tereticornis* and *E. urophylla* (Harwood, 2011). Of the 1,012 Australian *Acacia* species, it is estimated that 386 have been introduced by humans outside Australia (Richardson et al., 2011), though R&D efforts in the last decades have largely focused on just a few tropical species, most notably *A. mangium* and *A. crassicarpa*. Today, *A. mangium* is estimated to be planted in 25 countries outside its native range (Table 1).

In addition to *Acacia* and *Eucalyptus* species, the germplasm of several fast-growing pines, predominantly from Central America, Mexico and the southern United States, has been transferred for establishing plantations throughout the tropics and subtropics. In Mexico, one of the first collections of *Pinus patula* seed was carried out in the early 20th century and the material was transferred to South Africa for establishing the first pine plantations in the country (Butterfield, 1990). The South African plantations then served for many years as a seed source for other countries in southern Africa (Butterfield, 1990; Poynton, 1977). More systematic exploration and collection of pine germplasm was done in Central America and Mexico between the late 1950s and the early 1970s, focusing on *Pinus caribaea*, *Pinus maximinoi*, *Pinus oocarpa*, *Pinus greggii*, *Pinus tecunumanii* and *P. patula*. Subsequently, *P. caribaea* and *P. oocarpa*, for example, have been introduced to 79 and 34 countries, respectively (Table 1).

2.3. High-value tropical hardwoods

The past germplasm transfer patterns of tropical hardwoods are more diverse when compared to the above-discussed categories of species. Some tropical hardwoods were introduced for production purposes outside their natural ranges several hundred years ago, long before systematic R&D efforts started. More recently, however, germplasm of several tropical hardwoods was first transferred for R&D, and the results of this work then created interest and demand for further transferring germplasm for production purposes.

Table 1
Natural and introduced distribution of selected tree species (according to CAB International, 2014).

Species	Natural distribution by region (number of countries)	Total number of countries within natural distribution	Introduced distribution by region (number of countries)	Total number of countries within introduced distribution
<i>Acacia mangium</i>	Asia (1); Oceania (2)	3	Asia (9); Africa (7); Caribbean (1); Central America (2); North America (1); South America (1); Oceania (4)	25
<i>Azadirachta indica</i>	Asia (10)	10	Asia (5); Africa (50); Caribbean (16); North America (2); South America (12); Oceania (6)	91
<i>Casuarina equisetifolia</i>	Asia (10); Oceania (14)	24	Europe (5); Asia (14); Africa (46); Caribbean (29); Central America (4); North America (2); South America (6); Oceania (4)	110
<i>Eucalyptus camaldulensis</i>	Oceania (1)	1	Europe (8); Asia (25); Africa (37); Caribbean (2); Central America (6); North America (2); South America (9); Oceania (2)	91
<i>Eucalyptus globulus</i>	Oceania (1)	1	Europe (5); Asia (5); Africa (12); Caribbean (1); Central America (1); North America (2); South America (10); Oceania (1)	37
<i>Picea abies</i>	Europe (24)	24	Europe (6); Asia (1); Africa (1); North America (2); Oceania (1)	11
<i>Pinus caribaea</i> var. <i>hondurensis</i>	Caribbean (3); Central America (5); North America (1)	9	Asia (15); Africa (28); Caribbean (9); Central America (2); North America (2); South America (10); Oceania (13)	79
<i>Pinus oocarpa</i>	Central America (5); North America (1)	6	Asia (2); Africa (14); Caribbean (3); Central America (2); South America (8); Oceania (5)	34
<i>Pinus sylvestris</i>	Europe (31); Asia (8)	39	Europe (7); Asia (2); North America (3); Oceania (1)	13
<i>Pinus taeda</i>	North America (1)	1	Asia (7); Africa (7); South America (6); Oceania (2)	22
<i>Pseudotsuga menziesii</i>	North America (3)	3	Europe (26); Oceania (1)	27
<i>Tectona grandis</i>	Asia (5)	5	Asia (16); Africa (24); Caribbean (4); Central America (6); North America (2); South America (9); Oceania (4)	65

Tectona grandis is a well-known example of the first category of tropical hardwoods. The large-scale transfer of its germplasm from Asia to other continents started more than one hundred years ago. Today, the species is estimated to be planted in a total of 65 countries outside of its native range (Table 1). Transferred germplasm of *T. grandis* originated from multiple sources and this contributed to the development of landraces in Africa and Central America. The origins of these landraces are poorly understood, but historical records and genetic studies have shed some light on the possible routes of introduction, and the likely sources of germplasm. In Africa, it appears that *T. grandis* was first introduced to Tanzania at the end of the 19th century, and from there to other countries in East and (later) West Africa. The African landraces are reported to originate from multiple and rather diverse seed sources in India, Myanmar and possibly Java (Wood, 1967). These landraces have a relatively high level of genetic diversity (Kjaer and Siegismund, 1996). No clear genetic relationship with *T. grandis* populations in South India has been found (Fofana et al., 2008), but Verhaegen et al. (2010) indicated that North India may have been an important seed source for many African introductions. Several other studies on the genetic diversity of *T. grandis* (e.g., Kertadikara and Prat, 1995; Shrestha et al., 2005; Sreekanth et al., 2012) have also increased our understanding of the African landraces, but they have not been able to reveal their exact origins. In Central America, the first introductions of *T. grandis* occurred in Trinidad, where the seed probably originated from Myanmar and India (Keogh, 1980). In the early 20th century, *T. grandis* was also planted in Panama using a small seed lot presumed to originate from India (Keogh, 1980). Subsequently, seed were collected from these first plantations in Trinidad and Panama for further introductions in Central America; such collections acted as bottlenecks, reducing the genetic diversity of *T. grandis* germplasm in the region (e.g., Kjaer and Siegismund, 1996).

Systematic R&D on *T. grandis* started long after the species was introduced from Asia to other regions. According to Mathauda (1954), one of the first provenance trials for the species was established in India in 1930. It was not until the early 1970s, however, that the first series of international provenance trials was established. A total of 75 provenances, including many African and Latin

American landraces, were collected between 1971 and 1973 and distributed for 48 trials established in India, Southeast Asia and West Africa, as well as in Central and South America (Keiding et al., 1986). These provenance trials continue to provide valuable information on the performance and traits of *T. grandis* seed sources for plantation and improvement programmes (Kjaer et al., 1995).

Khaya senegalensis offers an example of the second above-mentioned category of tropical hardwoods. For centuries, the species was exploited for various purposes within its natural distribution range in West and Central Africa (Karan et al., 2012), before introduction to other regions started a few decades ago. In the late 1960s, *K. senegalensis* germplasm from 24 seed sources, spanning 11 of the 19 African countries where the species occurs naturally, was transferred to Australia for R&D (Nikles, 2006; Nikles et al., 2008). Later, *K. senegalensis* was established in Asia and tropical America. There is continued interest especially in Australia to transfer more germplasm for further R&D (Fremlin, 2011; Karan et al., 2012). Other examples where tropical hardwood germplasm transfer has increased following initial R&D include *Swietenia macrophylla* and *Cedrela odorata*, the most important native hardwoods of Central America. Since 1980, the demand for seed of these two species and other native trees has increased considerably in Central America, after R&D efforts spearheaded by the Tropical Agricultural Research and Higher Education Centre (CATIE) and other research institutes. This research demonstrated the potential of these species to provide high quality timber from a relatively short rotation. Today, *S. macrophylla* and *C. odorata* are also planted widely in other regions, such as Africa and Asia.

There are many other emerging high-value tropical hardwoods for which R&D has been intensified recently (e.g., Ichols and Vanclay, 2012; Camcore, 2011; Midgley et al., 2010). These include *Milicia excelsa* in Africa, *Pachira quinata* and *Terminalia amazonia* in the tropical Americas, *Ochroma pyramidale*, *Endospermum medullosum* and *Santalum* spp. in the Pacific, and *Dipterocarpus* spp. in Southeast Asia. These species have often been unsustainably harvested from natural forests, but efforts are now being made to conserve their genetic resources and to develop plantation-based industries (e.g., Thomson, 2006; Camcore, 2011; Doran et al., 2012).

2.4. Agroforestry trees

Rural communities in parts of the tropics have planted trees within their farming systems for millennia. In the process, tree germplasm was sometimes widely exchanged, especially of food trees, as best exemplified by the ancient transfers of tree crops such as *Theobroma cacao* and *Bactris gasipaes* in South and Central America (Lentz, 2000; Clement et al., 2010; Powis et al., 2011). Throughout the colonial period, many other transfers of tree commodity crop germplasm took place, including of *T. cacao* and *Coffea arabica*, both important species in the past and still in the present (see Dawson et al., 2014, this special issue). In the case of *C. arabica*, modern cultivars are derived from two base populations known as Typica and Bourbon that were transported from East Africa throughout the tropics in the early 1700s. *Theobroma cacao* was introduced into Indonesia by the Dutch from Venezuelan sources in 1560 and by the Spanish into the Philippines in around 1600. The French introduced *T. cacao* to multiple locations from the middle of the 17th century onwards, and the patterns of transfer and introduction thereafter were complex. Forastero *T. cacao* trees were apparently established from Brazilian sources on islands off the coast of continental West Africa from the 1820s onwards, before being transported to the mainland (see Mohan Jain and Priyadarshan (2009) for references to both coffee and cacao germplasm transfers in the colonial period).

The steps involved in the past global distribution of other important agroforestry trees for small-scale farmers are generally less well understood, until documentation improved in the last few decades. Transfers prior to then were often clearly extensive, however, as evinced by the exotic nature of many of the tree species currently grown by smallholders. This was illustrated by Koskela et al. (2010), who undertook a review of the known indigenous and exotic distributions of 120 tree species important for smallholder agroforestry planting using the Agroforestry Database (AFTD, 2014). On average, the 120 tree species surveyed had been distributed to 21 countries beyond their native ranges (Koskela et al., 2010). *Casuarina equisetifolia*, mainly used for timber, is believed to be the most widely distributed agroforestry tree species, introduced to 110 countries outside its native range (Table 1). Other widely distributed agroforestry tree species include *Azadirachta indica*, *Mangifera indica* and *Leucaena diversifolia*, providing medicine, fruit and fodder, respectively (Koskela et al., 2010).

Although in more recent times the documentation of germplasm transfers of agroforestry trees to support tropical agricultural practices has improved, much information, especially on the origin of provenances and if any selection was undertaken, frequently still remains unknown. This reflects a lack of attention by agricultural development specialists to the quality aspects of tree germplasm supply for smallholders (Graudal and Lillesø, 2007). As a consequence, many current sources of planting material used widely by smallholders are of undefined (but almost certainly sub-optimal) performance (see also Dawson et al., 2014, this special issue).

3. Utilization of forest genetic resources

3.1. Research and development

With a few exceptions, forest genetic resources have been utilized extensively in systematic R&D only for about 100 years. The oldest form of R&D is the testing of tree species and their provenances for different uses and under different environmental conditions. The main purpose of provenance research has been, and still is, the identification of well-growing and sufficiently-adapted tree populations to serve as seed sources for reforestation (König, 2005). Such research has shown that most tree species have a high

degree of phenotypic plasticity (i.e., large variation in phenotype under different environmental conditions, e.g., Rehfeldt et al., 2002) and that this varies between provenances (e.g., Aitken et al., 2008). Since the 1990s, provenance trials have also demonstrated their value for studying the impacts of climate change on tree growth (e.g., Mátyás, 1994, 1996).

Many old provenance trials still exist and continue to provide valuable information for R&D. Due to the long timeframe (often in decades) to reach recommendations, however, it has been challenging for many countries and research organizations to maintain trials, and to continue measuring them. Unfortunately, several important trials have been abandoned and some collected data lost. Furthermore, there are old trial data sets sometimes dating back decades that have not yet been thoroughly analysed and published (FAO, 2014). As provenance trials are costly to establish and maintain, new approaches, such as short-term common garden tests in nurseries and molecular analyses in laboratories, are increasingly used for testing provenances (FAO, 2014). However, while usefully complementary, these approaches cannot fully substitute for provenance trials, which are still needed for studying long-term growth performance, including the plastic and adaptive responses of tree populations to climate change (see Alfaro et al., 2014, this special issue).

In addition to maintaining old provenance trials, it is necessary to invest in establishing new ones. Some existing provenance trials may suffer from problems related to sampling and test sites, for example (König, 2005). The provenances sampled for trials may not cover adequately the whole distribution range of a species, and some provenances may be inadequately represented by genetic material that has been collected from a few trees only. Often, existing trials have not been established in marginal sites that would be particularly useful for analysing climate change-related tree responses. Furthermore, many trials were established long before climate change became a research topic and the traits that were or are being measured may not be the most important ones in this context (Alfaro et al., 2014, this special issue).

The results of provenance research have been crucial for tree breeding programmes, which mostly aim at gradual improvement of breeding populations rather than the development of new varieties (there are some exceptions, such as the breeding of eucalypts and poplars). Tree breeding was initiated in a few European countries in the 1930s (Hitt, 1952), and by the 1950s many countries across the world had established tree breeding programmes that currently include around 700 tree species (according to FAO, 2014). Tree breeding is a rather slow process, as one cycle of testing and selection may take decades, rather than the months or year required in the breeding of most agricultural crops. The oldest tree breeding programmes are now 50–70 years old, and the most advanced of them are only in their third cycle of testing and selection (Neale and Kremer, 2011). Traditional tree breeding is based on the phenotypic selection of individuals (plus trees), testing their progeny and then selecting again the best individuals for the establishment of seed orchards and further breeding. Testing is usually focused on growth, wood properties, resistance or tolerance to pests and diseases, and other traits of commercial interest. More recently, climate change-related traits such as plasticity and drought tolerance have been increasingly considered by breeding programmes (FAO, 2014). Molecular marker-assisted selection (MAS) has raised hopes to reduce the time and money needed for tree breeding, but the polygenic architecture of the traits and the variable expression of quantitative trait loci across environments mean that progress remains difficult when applying MAS to forest trees (Neale and Kremer, 2011).

Tree breeding is mainly carried out by research institutes, cooperatives and public and private companies. The level of engagement of different tree breeding programmes in international

collaboration and germplasm transfer varies considerably, depending on the way they have organized their work and the availability of financial resources. In Australia, New Zealand and the United States, a number of breeding cooperatives were formed early to pool the resources of collaborators through joint breeding programmes for a number of tree species. The International Tree Breeding and Conservation Program (Camcore), established in 1980, is a notable example largely funded by the private sector that now has a global membership. Camcore's early work focused on Mesoamerican pines but now it convenes breeding programmes for both conifers and broadleaves, and it has had a major role in transferring tree germplasm for breeding purposes. From the 1980s, it undertook range-wide seed collections of 191 provenances of six Mesoamerican pines (*P. tecunumanii*, *P. oocarpa*, *P. caribaea*, *P. maximinoi*, *P. patula* and *P. greggii*) (Dvorak et al., 1996) and it has established provenance or progeny trials at 823 locations in ten countries. Tree improvement programmes based on the Camcore material for *Pinus chiapensis*, *P. greggii*, *P. maximinoi*, *P. oocarpa* and *P. tecunumanii* are at the stage where second and third-generation field trials have been established (Camcore Annual Report, 2012).

In Europe, national research institutions operated 15–20 separate breeding programmes often on the same species until 1990 (Pâques, 2013). This changed dramatically in the 1990s when budgets of many research institutes were cut and the interest of policymakers in tree breeding decreased. As a result, tree breeding programmes in Europe were forced to change their operating practices and to seek greater synergies through increased international collaboration and coordination, sharing responsibilities and targeting fewer tree species. During the past 20 years, a number of projects, and especially the TreeBreedex project (2006–2010), have supported the transformation of European tree breeding into a collaborative effort, carried out by a network of national institutions sharing their research facilities, breeding material and field tests (Pâques, 2013). This new *modus operandi* now resembles the way tree breeding has been carried out elsewhere for decades.

During the past decade or so, genetic analysis of forest tree populations with molecular markers has strengthened R&D efforts and has increased the transfer of DNA samples. Range-wide genetic surveys were initiated for temperate tree species (e.g., Petit et al., 2002; Magri et al., 2006) and they are now increasingly also conducted for tropical species (e.g., Jamnadass et al., 2009; Kadu et al., 2011). These studies have provided useful information on the geographic structure of genetic diversity, knowledge of importance for the management of natural tree populations and for the formulation of conservation strategies. Site-specific studies with molecular markers have also been essential to better understand ecological and genetic processes within tree populations (e.g., Lee et al., 2006), and the impacts of forest fragmentation and logging on them (e.g., Rymer et al., 2013; Wickneswari et al., 2014, this special issue). Genomic developments and new markers, such as those based on single nucleotide polymorphisms (SNPs), also offer possibilities to survey adaptive diversity within tree populations (Neale and Kremer, 2011). With the advent of new, 'next generation' sequencing technologies, genetic markers for almost any tree species can now be developed at low cost (van der Merwe et al., 2014; Russell et al., 2014).

3.2. Production and use of forest reproductive material

Tree seed crops often have high year-to-year variation, causing remarkable fluctuations in seed availability. This makes it desirable to maintain seed storage capacity and maximise seed harvest during most years. However, many tree species (e.g., around 70% in humid tropical forests; Sacandé et al., 2004) produce recalcitrant or intermediate seed which lack dormancy and which are sensitive

to both desiccation and low temperature (see Pritchard et al., 2014, this special issue). This makes it difficult or sometimes impossible to collect, transport, process and store these seed. For some tropical trees, the collection of naturally regenerated seedlings (wildlings) from forests is an alternative option for obtaining reproductive material. However, this can be time consuming and expensive, and the transplant success rate may be low. These problems have raised interest in vegetative propagation. The rooting of cuttings has been used for centuries in Japan for producing reproductive material of *Cryptomeria japonica* and today this is still the most frequently used method for vegetative propagation in forestry (Wilhelm, 2005). During the past two decades, micropropagation methods, such as microcuttings or somatic embryogenesis, have also been increasingly deployed (FAO, 2004).

The seed of temperate and boreal trees used for forestry in Europe and North America are largely obtained from selected seed stands and seed orchards. Within the European Union (28 countries), there are over 58,000 seed stands and nearly 1,700 seed orchards producing seed of about 40 tree species (European Commission, 2014). In Canada, there are 355 seed orchards producing improved seed for 28 species (Natural Resources Canada, 2012), while in the USA around 150 breeding programmes produce improved seed for more than 70 species (FAO, 2014). In Canada and the USA, the vast majority of seed orchards are run by cooperatives involving both private and public sectors, while in Europe seed orchards are often managed by government agencies or government-owned companies.

In the case of *Acacia* and *Eucalyptus* spp., until recently, bulk seed collected from natural stands was the major source of material for establishing plantations around the world. Today, new plantations of these species are being established using improved seed or by deploying clonal planting stock. Australia, Indonesia, Malaysia and Vietnam all produce significant amounts of genetically-improved seed of *A. mangium*. Seed orchard material is used extensively for eucalypts originating from southern Australia (notably *E. benthamii*, *E. dunnii*, *E. globulus* and *E. nitens*) as they are generally difficult to clonally propagate. The tropical eucalypts (including *E. camaldulensis*, *E. grandis*, *E. pellita*, *E. tereticornis* and *E. urophylla*) can be readily propagated by cuttings and this has allowed widespread deployment of clones of pure species and interspecific hybrids. Vegetative propagation of the tropical acacias is less widespread than for tropical eucalypts. In clonal propagation of *A. mangium*, for example, the ageing of clonal hedges leads to loss of vigour of planting stock. The *A. mangium* × *auriculiformis* hybrid, however, does not suffer this ageing problem and it is clonally propagated on a large scale in Vietnam.

Notwithstanding the increased availability of genetically improved material of *Acacia* and *Eucalyptus* species, significant quantities of wild seed are still exported from Australia for plantation establishment (Singh et al., 2013). Furthermore, the establishment of new breeding populations and the need to enrich the genetic diversity of existing ones has maintained the demand for collecting seed from natural stands of acacias and eucalypts. There are, however, logistical difficulties in collecting from some locations, particularly for those species with natural distributions outside of Australia. Some important source populations have been lost due to deforestation and urban encroachment in recent decades. This has encouraged breeding programmes to exchange their germplasm instead of investing in new seed collections from natural populations.

Seed from Central American and Mexican pines are now largely obtained from seed stands and seed orchards. The seed of *P. caribaea* are produced in commercial seed stands and seed orchards in several countries (e.g., Australia, Brazil and Venezuela) and are sold on the world market. In the case of *P. patula*, large-scale seed producers include South Africa and Zimbabwe, which have exten-

sive breeding and planting programmes. However, the collection of pine seed from natural populations also continues, with Honduras, for example, selling large quantities of bulk seed of *P. caribaea*, *P. maximinoi* and *P. tecunumanii*. The demand and supply of Central American and Mexican pine seed have greatly fluctuated over the past 30 years, depending on the establishment rate of new plantations and changes in seed production capacity, as new seed stands and seed orchards mature. Currently, the available world-wide seed production of *P. caribaea*, *P. greggii*, *P. oocarpa* and *P. patula* appears to be able to meet demand, but in the cases of *P. maximinoi* and *P. tecunumanii* demand exceeds supply.

For high value tropical hardwoods, the picture is rather different. There are few improved seed sources available and seed is mostly sourced from natural stands, plantations and even research trials. Usually, the available seed supply cannot meet the strong demand for plantation establishment. In the case of *T. grandis*, for example, Kjaer and Suangtho (1997) found that (fairly large) selected seed production areas in Thailand could only supply a small portion of the seed needed by nurseries, because of very low seed yield per tree. Low seed yield per tree is also a problem in clonal seed orchards of the species (Kaosa-ard et al., 1998; Nagarajan et al., 1996; Palupi and Owens, 1996; Varghese et al., 2008; Wellendorf and Kaosa-ard, 1988). This problem, combined with the low and sporadic germination of *T. grandis* seed, leads to a low multiplication factor. To overcome these difficulties, vegetative propagation methods were developed for *T. grandis* in the 1980s (e.g., Guptha et al., 1980; Kaosa-ard et al., 1987). These efforts have yielded positive results (Kaosa-ard et al., 1998) in opening new opportunities for large scale deployment of the best teak genetic resources, linking propagation work directly to testing and breeding programmes (Goh et al., 2007).

The seed production of many agroforestry trees is often informal and very few countries have included these species in their tree improvement programmes. Germplasm of exotic tree species, typically from introductions of unknown provenance and uncharacterised performance, is often collected by smallholders directly for their own planting. Lillesø et al. (2011), for example, identified five sources for farmers' tree planting material (farmland, natural forest, plantations, seed orchards and vegetative propagules) and indicated heavy reliance on the first source, with natural forest sources being underutilised. Farmers and local seed dealers often prefer to collect seed from previously introduced exotic trees in farmland rather than source externally because the transaction costs are lower, even when better-performing seed sources of the same trees may be available elsewhere (Lengkeek et al., 2005; Muriuki, 2005). In recent decades, there has been a greater focus on the cultivation of indigenous tree species in agroforestry systems, with the involvement of local people in carrying out genetic selection for tree characteristics of importance to them. One such approach, known as participatory domestication, has been developed in Africa on indigenous fruit trees (see Dawson et al., 2014, this special issue). The advantage of this approach is that genetic quality as a concept is explicitly considered, and local wild stands provide significant genetic variation that is a pool for selection (Tchoundjeu et al., 2006).

4. Concerns related to the transfer of tree germplasm

4.1. Phytosanitary aspects

The risk of spreading pests and diseases while transferring reproductive material is often considerable. Pests and diseases travel in different substrates and it is challenging to monitor the way they spread; for example, to reconstruct the exact pathways of their past movements. In Europe, Santini et al. (2013) recon-

structed the most probable pathways of alien invasive forest pathogen spread since 1800. They found that living plants (57% of all pathogen introductions) and wood (10%) were likely major vectors for introductions, while the share of any other pathway, such as bark, seed, soil and cuttings, was less than 10% over the last two centuries. According to the same authors, over the last few decades, the invasion rate of alien forest pathogens has increased exponentially in Europe, with soil recently becoming a major transfer substrate second to living plants. In the USA, a similar study attributed 69% of the introductions of non-native forest insects and pathogens since 1860 to the trade in living plants (Liebhold et al., 2012). These studies confirm the need for phytosanitary regulations and their careful implementation while transferring tree germplasm. However, they also show that the pathogen risk associated with transferring seed is considerably lower than the risk connected with transferring other materials such as living plants or wood. Living plants are mostly imported from other regions for ornamental purposes, rather than for forestry production.

A global review of 25 countries indicated around three times as many indigenous forest pests (a total of 344 insect, pathogen and other species reported) as introduced ones (101 species), and that most of the introduced pests (72 species) occurred only in planted forests (FAO, 2009). Many recently-emerged infectious diseases are caused by fungal and fungal-like pathogens such as *Fusarium circinatum*. This serious disease has caused widespread mortality of *P. radiata* in its natural range, is a serious problem in nurseries (Steenkamp et al., 2014), and hampers planting in South Africa (Mitchell et al., 2013). The transfer of conifer germplasm from affected regions to countries that are thus far free of this disease (e.g., Australia and New Zealand) is strictly controlled, meaning that further genetic infusions from natural stands into Australasian breeding populations cannot in practice occur.

Despite phytosanitary measures, a number of significant pest and disease outbreaks have occurred in Asia and Australasia during the last decade. In Australia, a recent (identified in 2010) introduction of *Puccinia psidii*, an exotic rust that threatens a broad range of native Myrtaceous genera (e.g., *Corymbia*, *Eucalyptus* and *Melaleuca*; Pegg et al., 2012), has spread rapidly in wild coastal forests and plantings. Some tree species have been found to have little resistance to the disease and work is being undertaken to determine which are most at risk; containing the disease is now thought to be impossible. In the humid tropics, *Ceratocystis* spp. diseases of acacias (Tarigana et al., 2011) have become widespread, particularly in Indonesia and Malaysia. *Acacia mangium*, the most important plantation species in many tropical lowland locations, appears to have very little resistance to *Ceratocystis*, and where disease occurs growers are often forced to plant other, less-productive tree species. In India and parts of Southeast Asia (notably Thailand), the Middle East and Africa, extensive damage to eucalypt plantations (particularly *E. tereticornis*, *E. camaldulensis* and hybrids involving these species) has been caused by a gall wasp, *Leptocybe invasa* (Kim et al., 2008). Again, this has forced growers to deploy alternative species and hybrids.

Restricting the spread of these diseases is a major challenge. In many parts of the world, this and invasiveness features (see Section 4.2) have led policymakers to focus their attention on the potential negative consequences of transferring tree germplasm. These risks partly explain why germplasm transfer is being increasingly controlled, in some cases even beyond the agreed phytosanitary regulations. Climate change is posing another challenge for containing the spread of pests and diseases. There is growing evidence that climate change is accelerating invasion by altering the environment for forest pests and diseases, by stressing tree populations that then become more sensitive to attack, and by facilitating the establishment of alien plant and animal species in

new areas (Dukes et al., 2009; Huang et al., 2011; Alfaro et al., 2014, this special issue).

4.2. Invasiveness of introduced tree species

Introduced tree species can sometimes become invasive of agricultural and natural ecosystems, and there has been much debate in the literature about this danger (e.g., Richardson et al., 2011). Many introduced tree species have been recognized as invasive only fairly recently, despite the long history of the transfer of tree germplasm. A global survey conducted by Richardson and Rejmánek (2011) found a total of 357 introduced tree species known to be invasive in some part of the world. The majority of species were introduced for horticulture, but some were introduced for forestry and agroforestry (Richardson and Rejmánek, 2011). Better-studied taxa, such as *Pinus* spp. and Australian *Acacia* spp., are considered as model groups in plant invasion ecology (Richardson, 2006; Richardson et al., 2011), but in many other cases little is known about invasiveness.

The case of Australian acacias illustrates the benefits and risks: an introduced species can be simultaneously a commercially important crop and, if it escapes from plantations, an invasive. Not all introduced tree species of invasive genera, however, turn out to be weedy in new environments. Of the 386 acacia species that have been transferred outside of Australia, only 23 are currently invasive (Richardson et al., 2011). Although they are relatively few, these invasive acacias have caused significant damage to natural ecosystems, especially in Mediterranean-type climatic regions (Gaertner et al., 2009). In South Africa, for example, nine Australian acacias are classified as 'major invaders' and another three are considered as 'emerging invaders' (Nel et al., 2004). In a review of tree invasions, Lamarque et al. (2011) noted that large propagule pressure is often an important factor for an introduced species to become invasive. A similar conclusion was made by Procheş et al. (2012), who reported that the number of experimental plantings strongly correlated with the invasive range size of certain pines in southern Africa. In northern Europe, Kjaer et al. (2014) observed that the few introduced tree species planted on a large scale were the ones that created invasiveness problems later.

The benefits and risks of introduced tree species change over time and include social aspects. This is illustrated by the introduction of several *Prosopis* species from Latin America to Africa, Australia, India and other tropical regions of the world at the end of the 19th century. These introductions were first considered very valuable sources of shade, fodder, fuel wood and other products (e.g., gums, honey and resins), as they were able to grow in extreme conditions (Felker, 2009). Later, in the 1960s, the first signs of infestation appeared and the negative impacts of *Prosopis* species in some areas came to be perceived to outweigh the positive effects (Shiferaw et al., 2004; Van Klinken and Campbell, 2001).

These examples show that the environmental risks related to the introduction of tree species have been underestimated in the past. However, awareness of these risks has grown in recent years, and the invasive potential of tree species is now considered more carefully before any new introductions.

4.3. Genetic pollution and hybridization

The risks of genetic pollution and hybridization are related to the transfer of tree germplasm to an area where the same or a related species already occurs. Hybridization and introgression are natural evolutionary processes (Arnold, 1992), but the term 'genetic pollution' usually refers to a situation where the mixing of gene pools, between different individuals of the same or related species, has been initiated by, or significantly influenced through,

human activity. If the seed source used is not local, then planted trees are likely to have a different genetic composition from wild stands, and crossing between them could lead to the dilution and loss of unique diversity in the wild. The subsequent breakdown of co-adapted gene complexes could lead to outbreeding depression (Ledig, 1992).

Genetic pollution has been reported for many forest trees. One of them is *Juglans hindsii*, which is known to have hybridized with many congeners imported for commercial purposes (Rhymer and Simberloff, 1996). Another well-known example is *Populus nigra*, which was once widespread but is now extirpated over large parts of Western Europe (Lefèvre et al., 2001). Its habitats have been considerably reduced by the past transformation of rivers to canals and its gene pool is threatened by the large-scale cultivation of hybrid poplars (Smulders et al., 2008). Other examples are *Platanus racemosa*, which is currently disappearing from its native range through introgression with *Platanus × acerifolia* (Rhymer and Simberloff, 1996), and the genetic pollution of native gene pools of eucalypts resulting from plantation establishments in Australia (Potts et al., 2004). Concerns have also been expressed that cultivated-wild tree hybridisation could result in traits introduced into cultivars through genetic modification (GM) being transferred into natural stands, with potentially significant evolutionary consequences in the wild (see Delplancke et al. (2012) for concerns regarding cultivated *Prunus dulcis* and wild *Prunus orientalis*).

The environmental risks associated with genetic pollution were largely ignored in the past and it is important not to overstate them now. Strong barriers to hybridisation exist between some related species, such as differences in flowering time or the poor fitness of hybrids, which reduce the risks. One approach to reduce the potentially negative impacts of cultivated-wild tree hybridisation is to deliberately isolate cultivated material or to plant exotic rather than indigenous trees around natural forests and woodlands (Potts et al., 2001). More research is required on the magnitude of outbreeding depression in tree species, as it remains a relatively understudied phenomenon, with evidence limited mostly to inter-specific hybrid segregants (Ellstrand, 2003; Edmands, 2007). The topic is discussed further in other papers of this special issue (Wickneswari et al., 2014; Thomas et al., 2014).

5. Implications of the Nagoya Protocol on the forestry sector

Fair and equitable sharing of the benefits arising out of the utilization of genetic resources is one of the three objectives of the CBD (CBD, 1992). Article 15 of the CBD enshrines the sovereign rights of national governments over their natural resources and gives them the authority to determine access to genetic resources. The CBD also encourages its Parties to facilitate access to genetic resources, based on mutually agreed terms (MAT) and subject to prior informed consent (PIC), by taking appropriate legislative, administrative and policy measures. To help the Parties in this process, the CBD adopted the so called Bonn Guidelines in 2002 (CBD, 2002). These voluntary guidelines recommend that each Party should designate a national ABS focal point, which should then make available information on competent national authorities and procedures for acquiring PIC and MAT through the CBD clearing-house mechanism. As of May 2014, only 57 of the 193 Parties to the CBD had implemented some ABS measures (CBD, 2014) and only 33 Parties had designated one or more competent national authorities for ABS.

The poor implementation record of the earlier CBD commitments on ABS partly explains why under the Nagoya Protocol it is required for Parties to implement appropriate legislative, administrative and policy measures, and to set up operational administrative structures and procedures for providing access to genetic

resources. The Nagoya Protocol also goes further than earlier ABS commitments in two important aspects (Halewood et al., 2013a). First, the Nagoya Protocol requires its member states to obtain PIC from indigenous and local communities prior to accessing genetic resources and associated traditional knowledge. Second, it also obliges the member countries to establish mechanisms for monitoring compliance with foreign ABS laws and agreements, and to facilitate their enforcement.

The Nagoya Protocol is based on a bilateral approach in which a provider and a user of genetic resources agree the MAT. However, this approach may produce disappointing results not only in ensuring fair and equitable sharing of benefits, but also in promoting R&D and biodiversity conservation. Winter (2013) argued that the bilateral approach is likely to prejudice both the horizontal (i.e., among states having the same genetic resource or among communities holding the same traditional knowledge) and vertical (i.e., between providers and users) dimensions of equity. In the first case, the most 'advanced' provider states or communities can promptly secure their benefits and establish their 'dominance' in the market. This could lead to the exclusion of other providers that have lower capacity to set up the necessary measures and structures. Furthermore, potential competition between providers may lead to the lowering of access conditions. In the second case, providers may lose benefits as it is often difficult to bilaterally monitor the long processes of R&D and commercialization. As a result, providers may start restricting legal access to genetic resources in order to minimize the assumed lost benefits (Winter, 2013).

To alleviate these concerns, the 'common pool' approach has been proposed as more suitable, especially for genetic resources used by the agriculture and forestry sectors (e.g., Halewood et al., 2013b; Winter, 2013). Under this concept, genetic resources are provided for common use and the R&D benefits are shared between providers and users. A special feature of common pools is that different stakeholders often act both as providers and users in contributing (resources or results) to the R&D process. Common pools, such as farmers' seed exchange systems or networks of collections or databases, can operate at local, national or international levels, and they are often regulated by participating actors rather than states (Winter, 2013). The International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA), which entered into force in September 2004, is a rare example of a common pool approach that has been given an international legal framework. However, the common pool approach is also not flawless; some actors may enjoy the common benefits without sharing their genetic resources or the results of their R&D work, if the rules of engagement are unclear or if they are not properly enforced (Halewood et al., 2013b).

The provisions of the Nagoya Protocol do not apply for those genetic resources that are covered by a specialized international ABS instrument such as the ITPGRFA, which was designed for major food crops and forages. This has led to discussion on whether the ITPGRFA could be extended to cover other plant species or, alternatively, whether one or more new sector-specific ABS instruments should be negotiated to cover the genetic resources of aquatic species, farm animals, forest trees and micro-organisms and invertebrates. Article 4 of the Nagoya Protocol allows the Parties to develop and implement specialized ABS agreements, provided that they are supportive of the CBD and the Nagoya Protocol. However, it takes years to develop such specialized ABS agreements. Therefore, once the Nagoya Protocol enters into force, it will set the ABS framework for the genetic resources of non-crop species including forest trees.

The direct impacts of the Nagoya Protocol on the forestry sector's R&D work are likely to be immediate and significant. The first problem is the entry into force of the Protocol before all signatory countries have created a fully functional ABS regulatory system.

This will slow down, or even block, the process of obtaining PIC and negotiating MAT with certain nations. Countries are expected to designate one or more competent national authorities to provide PIC in a transparent and cost-effective manner, and to establish clear rules and procedures for negotiating MAT. This means that the state will play a central role in the ABS process and that the competent national authority is likely to be a ministry or a state-funded agency. Depending on the importance of forests and the forestry sector in a given country, the state authority responsible may be the ministry for the environment, for agriculture, for forestry, or for natural resources. In some countries, the responsibility for forests and forestry is shared between ministries; the ministry of the environment may be charged with the conservation of forest biodiversity, and the ministry of agriculture with forestry production, including the management of forest genetic resources. This makes it possible that competing interests among different ministries and their agencies further delay the establishment of a functional ABS system. Furthermore, as some countries are likely to favour a very centralized approach and designate only a single national authority for all ABS arrangements regardless of sector, this increases the risk that ABS issues related to forest genetic resources are tasked to an agency with limited competence in forestry. On the other hand, such centralization can bring benefits, such as in increasing awareness of the necessary steps to obtain PIC and in bringing clarity to legal processes (Louafi and Schloen, 2013).

Once a functional ABS system has been established at the national level, the Nagoya Protocol is likely to bring further changes to previous exchange practices in the forestry sector that have often been rather informal. The ABS system will add a new layer of administration and increase the transaction costs and time needed to obtain forest genetic resources for R&D purposes. Both providers and users of forest genetic resources will need to take this into account in future R&D projects, and start to build their legal and technical capacity. A hypothetical example of establishing a new range-wide provenance trial for a tree species illustrates the future challenges in compliance. A typical multi-locational provenance trial may involve obtaining seed from, say, 10 countries and establishing the trial in each of the same nations. Each country should then provide 9 PICs as a provider, and agree 9 MATs as a provider and another 9 as a user. It may take several months, if not years, for the project coordinator of such a trial to arrange the necessary documentation.

Louafi and Schloen (2013) pointed out that transaction costs should not exceed the expected monetary and non-monetary benefits for a user of genetic resources, and that the expected benefits for a provider should be higher than the costs of running an ABS regulatory system. It is difficult to contemplate how in future these conditions will be seen to be met in the forestry sector for many multi-locational provenance trials where benefits are often, at least initially, intangible. Furthermore, when DNA samples of tree populations are exchanged for range-wide genetic diversity assessments, the results bring no direct monetary benefits though they contribute to conservation and management. At issue, then, is how to quantify this value. High transaction costs may therefore severely affect R&D work in the forestry sector, where budgets mostly rely on limited public and private funding. Delays in establishing fully functional and transparent national ABS regulatory systems could also create an incentive to circumvent the law by claiming that R&D material is being transferred solely for production purposes.

6. Conclusions

Over the past two centuries, forest genetic resources have been increasingly transferred by humans for production and R&D purposes. The historical transfer pattern of most boreal and temperate

tree species, and of fast growing tropical and subtropical ones, is rather similar: germplasm was first transferred for reforestation and plantation establishment, before systematic R&D started later, during the 20th century. The early transfers of some tropical hardwoods also followed this pattern, but in recent decades germplasm of several tropical hardwoods has been first transferred for R&D and then deployed for establishing plantations. The transfer patterns of tree species used for agroforestry are more mixed and are less well documented. Overall, advances in R&D work in the forestry sector in different parts of the world have shifted germplasm demand toward species and provenances expected to perform well at specific sites for particular functions, bringing significant productivity benefits.

Provenance trials have been the backbone of R&D work on forest genetic resources. However, their contributions to the development of the forestry sector are not always well acknowledged and they are often considered too expensive to establish and maintain. A change in attitude by budgetary authorities, in which provenance trials are treated as a valuable asset and are maintained accordingly, is required. New research approaches, such as short-term common garden tests, provide results earlier and can therefore complement provenance trials. However, provenance research is still needed in some form for all planted tree species (FAO, 2014). Recent advances in forest genomics have increased our understanding of the genetic basis of adaptive and other traits, but it is unlikely that molecular marker-assisted approaches will quickly replace traditional tree breeding. Furthermore, provenance trials and progeny tests are complementary with genomic research, as it is necessary to link genomic and phenotypic data.

During the period 2005–2010, the global area of planted forests increased by 4.2 million hectares per year and reached 7% of total global forest area (FAO, 2010). This indicates that the demand for tree germplasm transfer remains high and it is likely to further increase in the near future. Globally, seed production of boreal and temperate trees, and of fast growing tropical and subtropical trees, often seems to meet or exceed demand for tree planting. The germplasm of many of these tree species is largely obtained from improved seed sources. In the case of tropical hardwoods, however, global demand is generally higher than supply from tested or improved seed sources, and seed is collected instead from untested and poorly documented sources. The seed of agroforestry trees are often harvested and deployed locally, making it difficult to evaluate the global situation.

Many countries still encounter problems related to the quantity and quality of forest reproductive material (FAO, 2014). This is often due to the lack of well-functioning national seed production and delivery systems that would reach all the diverse users of tree germplasm. Long-term investments in establishing and maintaining these systems are essential inputs to the development of the forestry sector, especially in developing countries. Governments and their agencies should develop regulatory frameworks, guidelines and training programmes to enable more active participation of the private sector in seed production and distribution (Graudal and Lillesø, 2007).

Transfers of tree germplasm involve some risks of spreading pests and diseases, of introducing invasive tree species and of polluting the genetic make-up of existing tree populations. Many of these risks have been underestimated in the past, but they are now increasingly analysed, and measures are being taken to minimize them while transferring germplasm. Risks should be considered in the context of the large benefits that people receive worldwide from transferred tree germplasm (these benefits need better measuring; Dawson et al., 2014, this special issue). Reconstructions of the historical movements of forest pathogens indicate that the risk of spreading pests and diseases while transferring seed is considerably lower than when moving living plants and other substrates (Liebhold et al., 2012; Santini et al., 2013).

Today, while phytosanitary regulations are rightly in place to control the transfer of tree germplasm, they are in our view unfortunately sometimes applied beyond their original purpose, limiting R&D activities. Of the nearly 360 tree species invasive in some part of the world (Richardson and Rejmánek, 2011), most have been introduced for horticultural purposes. However, several tree species used for forestry have also become invasive, so there is a need to consider weediness potential carefully. Although germplasm transfers can cause genetic pollution, hybridisation and introgression between new and existing stock also create opportunities, as novel genetic combinations can enhance the adaptation of tree populations to climate change (see Alfaro et al., 2014, this special issue).

With the implementation of the Nagoya Protocol, it is expected that current practices for transferring tree germplasm for R&D purposes will change, increasing transaction costs. Many countries are likely to struggle to establish a well-functioning national ABS regulatory system. This will likely slow down and sometimes will block the transfer of tree germplasm for R&D. Such a situation is unfortunate, as climate change, outbreaks of pests and diseases, and other ongoing productivity challenges, all increase the need for transferring tree germplasm to accelerate R&D. The continued need for germplasm transfers for research is well recognized by scientists and research institutes, who are pressing their governments to minimize the bureaucracy and costs related to the implementation of the Nagoya Protocol. Needs and options for specialized ABS arrangements for forest genetic resources to address concerns related to the Nagoya Protocol are also being explored by policymakers, in the context of FAO's Commission on Genetic Resources for Food and Agriculture.

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References

- AFTD, 2014. The Agroforestry Database. <www.worldagroforestry.org/resources/databases/agroforestry>. (accessed 15.07.14).
- Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol. Appl.* 1, 95–111.
- Alfaro, R., Fady, F., Vendramin, G.G., Dawson, I., Fleming, R.A., Sáenz-Romero, C., et al., 2014. Role of forest genetic resources in responding to biotic and abiotic factors in the context of anthropogenic climate change. *For. Ecol. Manage.* 333, 76–87.
- Anon, 1997. A Compendium of Experimental Sites and Scientific Investigations in the Petawawa Research Forest. Canadian Forest Service, Petawawa, Canada.
- Arnold, M.L., 1992. Natural hybridization as an evolutionary process. *Ann. Rev. Ecol. Syst.* 23, 237–261.
- Bennett, B.M., 2011. A global history of Australian trees. *J. Hist. Biol.* 44, 125–145.
- Butterfield, M.K., 1990. Isoenzyme variation in a South African and a Mexican population of *Pinus patula* Schiede & Deppe. M.Sc. Thesis, Department of Genetics, University of Natal, Natal, South Africa, p. 97.
- CAB International, 2014. *Forestry Compendium*. CAB International, Wallingford, UK.
- Camcore Annual Report, 2011. College of Natural Resources. NC State University, Raleigh, NC, USA, p. 54.
- Camcore Annual Report, 2012. College of Natural Resources. NC State University, Raleigh, NC, USA, p. 54.
- Carruthers, J., Robin, L., Hattingh, J.P., Kull, C.A., Rangan, H., Wilgen, B.W.V., 2011. A native at home and abroad: the history, politics, ethics and aesthetics of acacias. *Divers. Distrib.* 17, 810–821.
- CBD, 1992. Convention on Biological Diversity. United Nations, New York, USA.
- CBD, 2002. Bonn Guidelines on Access to Genetic Resources and Fair and Equitable Sharing of the Benefits Arising out of their Utilization. Secretariat of the Convention on Biological Diversity, Montreal, Canada.
- CBD, 2011. Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from Their Utilization to the Convention on Biological Diversity. Text and Annex. Secretariat of the Convention on Biological Diversity, Montreal, Canada.

- CBD, 2014. Database on ABS Measures. Secretariat of the Convention on Biological Diversity, Montreal. <www.cbd.int/abs/measures/>. (accessed 22.05.14).
- Clement, C.R., de Cristo-Araújo, M., d'Eeckenbrugge, G.C., Pereira, A.A., Picanço-Rodrigues, D., 2010. Origin and domestication of native Amazonian crops. *Diversity* 2, 72–106.
- Conedera, M., Krebs, P., Tinner, W., Pradella, M., Torriani, D., 2004. The cultivation of *Castanea sativa* (Mill.) in Europe, from its origin to its diffusion on a continental scale. *Veg. Hist. Archaeobot.* 13, 161–179.
- Dawson, I.K., Leakey, R., Clement, C.R., Weber, J.C., Cornelius, J.P., Roshetko, J.M., et al., 2014. The management of tree genetic resources and the livelihoods of rural communities in the tropics: non-timber forest products, smallholder agroforestry practices and tree commodity crops. *For. Ecol. Manage.* 333, 9–21.
- Delplancke, M., Alvarez, N., Espindola, A., Joly, H., Benoit, L., Brouck, E., Arrigo, N., 2012. Gene flow among wild and domesticated almond species: insights from chloroplast and nuclear markers. *Evol. Appl.* 5, 317–329.
- Doran, J., Bush, D., Page, T., Glencross, K., Sethy, M., Viji, I., 2012. Variation in growth traits and wood density in whitewood (*Endospermum medullosum*): a major timber species in Vanuatu. *Int. Forest Rev.* 14, 476–485.
- Dukes, J.S., Pontius, J., Orwig, D., Garnas, J.R., et al., 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: what can we predict? *Can. J. Forest Res.* 39, 231–248.
- Dvorak, W.S., Donahue, J.K., Hodge, G.R., 1996. Fifteen years of ex situ gene conservation of Mexican and Central American forest species by the CAMCORE cooperative. *Forest Genetic Resources*. No. 24. FAO, Rome, Italy.
- Edmands, S., 2007. Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. *Mol. Ecol.* 16, 463–475.
- Ellstrand, N.C., 2003. *Dangerous Liaisons? When Cultivated Plants Mate With Their Wild Relatives*. John Hopkins University Press, Baltimore, Maryland, USA.
- Eriksson, G., 2010. *Picea abies*: Recent Genetic Research. Department of Plant Biology and Forest Genetics, SLU, Uppsala, Sweden.
- European Commission, 2014. The Community List of Forest Reproductive Material. <http://www.ec.europa.eu/food/plant/plant_propagation_material/eu_marketing_requirements/forest_material_en.htm>. (accessed 20.05.2014).
- FAO, 1979. Eucalypts for Planting. FAO Forestry Series No. 11. Food and Agriculture Organization of the United Nations, Rome, Italy.
- FAO, 2004. Preliminary Review of Biotechnology in Forestry, Including Genetic Modification. Forest Genetic Resources Working Paper FGR/59E. Food and Agriculture Organization of the United Nations, Rome, Italy.
- FAO, 2009. Global Review of Forest Pests and Diseases. FAO Forestry Paper 156. Food and Agriculture Organization of the United Nations, Rome, Italy.
- FAO, 2010. Global Forest Resources Assessment 2010. Food and Agriculture Organization of the United Nations, Rome.
- FAO, 2014. The State of the World's Forest Genetic Resources. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Felker, P., 2009. Unusual physiological properties of the arid adapted tree legume *Prosopis* and their applications in developing countries. In: De la Barrera, E., Smith, W.K. (Eds.), *Perspectives in Biophysical Plant Ecophysiology: A Tribute to Park S. Nobel*. Universidad Nacional Autónoma de México, Mexico City, Mexico, pp. 221–255.
- Fofana, I.J., Lidah, Y.J., Diarrassouba, N., N'guetta, S.P.A., Sangare, A., Verhaegen, D., 2008. Genetic structure and conservation of Teak (*Tectona grandis*) plantations in Côte d'Ivoire, revealed by site specific recombination (SSR). *Trop. Conserv. Sci.* 1, 279–292.
- Freeman, J.S., Marques, C.M.P., Carocha, V., Borralho, N., Potts, B.M., Vaillancourt, R.E., 2007. Origins and diversity of the Portuguese landrace of *Eucalyptus globulus*. *Ann. Forest Sci.* 64, 639–647.
- Fremelin, R., 2011. Collecting widely to identify the best provenances. *Aust. Forest Grower* 34 (4), 39–40.
- Gaertner, M., Den Breeÿen, A., Hui, C., Richardson, D.M., 2009. Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Prog. Phys. Geogr.* 33, 319–338.
- Giertych, M., 2007. Provenance variation and inheritance. In: Tjoelker, M.G., Boratynski, A., Bugala, W. (Eds.), *Biology and Ecology of Norway Spruce*. Springer, Dordrecht, The Netherlands, pp. 115–146.
- Goh, D.K.S., Chaix, G., Baillères, Monteuis, O., 2007. Mass production and quality control of teak clones for tropical plantations: the Yayasan Sabah Group and CIRAD joint project as a case study. *Bois Forest Tropiq* 293, 65–77.
- Graudal, L., Lillestøl, J.-P.B., 2007. Experiences and future prospects for tree seed supply in agricultural development support: – based on lessons learnt in Danida supported programmes 1965–2005. Denmark Ministry of Foreign Affairs, Danida, Copenhagen.
- Griffin, A.R., Midgley, S.J., Bush, D., Cunningham, P.J., Rinaudo, A.T., 2011. Global uses of Australian acacias – recent trends and future prospects. *Divers. Distrib.* 17, 837–847.
- Guptha, P.K., Nadgir, A.I., Mascarenhas, A.F., Jaganathan, V., 1980. Tissue culture of forest trees: clonal multiplication of *Tectona grandis* (teak) by tissue culture. *Plant Sci. Lett.* 17, 259–268.
- Halewood, M., Andrieux, E., Crisnon, L., Gapusi, J.R., Mulumba, J.W., Koffi, E.K., Dorji, T.Y., Bhatta, M.R., Balma, D., 2013a. Implementing 'mutually supportive' access and benefits sharing mechanisms under the Plant Treaty, Convention on Biological Diversity, and Nagoya Protocol. *Law, Environ. Dev. J.* 9, 68–96.
- Halewood, M., López Noriega, I., Louafi, S., 2013b. The global crop commons and access and benefit-sharing laws: examining the limits if international policy support for the collective pooling and management of plant genetic resources. In: Halewood, M., López Noriega, I., Louafi, S. (Eds.), *Crop Genetic Resources as a Global Commons: Challenges in International Law and Governance*. Routledge, Abingdon, UK, pp. 1–36.
- Harlan, J.R., 1975. *Crops and Man*. The American Society of Agronomy and the Crop Science Society of America Madison, Wisconsin, USA.
- Harwood, C., 2011. Introductions: doing it right. In: Walker, J. (Ed.), *Developing a Eucalypt Resource. Learning from Australia and Elsewhere*. Wood Technology Research Centre, University of Canterbury, Canterbury, New Zealand, pp. 43–54.
- Hewitt, N., Klenk, N., Smith, A.L., Bazely, D.R., Yan, N., Wood, S., MacLellan, J.J., Lipsig-Mummé, C., Henriques, I., 2011. Taking stock of the assisted migration debate. *Biol. Conserv.* 144, 2560–2572.
- Hitt, R.G., 1952. Forest tree breeding in Sweden and other European countries. *J. Forest.* 50, 924–928.
- Huang, D., Haack, R.A., Zhang, R., 2011. Does global warming increase establishment rates of invasive alien species? A centennial time series analysis. *PLoS ONE* 6, e24733.
- Jamnadas, R., Lowe, A., Dawson, I.K., 2009. Molecular markers and the management of tropical trees: the case of indigenous fruits. *Trop. Plant Biol.* 2, 1–12.
- Kadu, C.A.C., Schueler, S., Konrad, H., Muluvi, G.M.M., Eyog-Matig, O., Muchugi, A., Williams, V.L., Ramamonjisoa, L., Kapinga, C., Foahom, B., Katsvanga, C., Hafashimana, D., Obama, C., Geburek, T., 2011. Phylogeography of the Afromontane *Prunus africana* reveals a former migration corridor between East and West African highlands. *Mol. Ecol.* 20, 165–178.
- Kaosa-ard, A., Apavatjrit, P., Paratasilpin, T., 1987. Teak tissue culture. In: *Proceedings of His Majesty's Fifth Cycle Commemorative Conference of USAID Science Research*. USAID and Silpakorn University, Bangkok, Thailand, pp. 201–206.
- Kaosa-ard, A., Suangtho, V., Kjaer, E.D., 1998. Experience from tree improvement of teak (*Tectona grandis*) in Thailand. In: *Technical Note No. 50*. Danida Forest Seed Centre, Humlebæk, Denmark.
- Kaplan, J.O., Krumhardt, K.M., Zimmermann, N., 2009. The prehistoric and preindustrial deforestation in Europe. *Q. Sci. Rev.* 28, 3016–3034.
- Karan, M., Evans, D.S., Reilly, D., Schulte, K., Wright, C., Innes, D., Holton, T.A., Nikls, D.G., Dickinson, G.R., 2012. Rapid microsatellite marker development for African mahogany (*Khaya senegalensis*, Meliaceae) using next-generation sequencing and assessment of its intra-specific diversity. *Mol. Ecol. Resour.* 12, 344–353.
- Keiding, H., Wellendorf, H., Lauridsen, E.B., 1986. Evaluation of An International Series of Teak Provenance Trials. Danida Forest Seed Centre, Humlebæk, Denmark.
- Keogh, R.M., 1980. Teak volume growth and thinning practices in the Caribbean, Central America, Venezuela and Colombia. In: *Proc. IUFRO Working Group S1 07 09 Symposium on Wood Production in Neotropics*, Inst. Trop. Forest Rio Piedras, Puerto Rico.
- Kertadikara, A.W.S., Prat, D., 1995. Isozyme variation among teak (*Tectona grandis* L.f.) provenances. *Theor. App. Gen.* 90, 803–810.
- Kim, I.-K., Mendel, Z., Protasov, A., Blumberg, D., La Salle, J., 2008. Taxonomy, biology, and efficacy of two Australian parasitoids of the eucalyptus gall wasp, *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae: Tetrastichinae). *Zootaxa* 1910, 1–20.
- Kjaer, E.D., Suangtho, V., 1997. A review of the tree improvement plan for teak in Thailand. Royal Forest Department, Bangkok, Thailand and Danida Forest Seed Centre, Humlebæk, Denmark (unpublished report).
- Kjaer, E.D., Siegismund, H., 1996. Allozyme diversity of two Tanzanian and two Nicaraguan landraces of Teak (*Tectona grandis* L.). *Forest Gen.* 3, 45–52.
- Kjaer, E.D., Lauridsen, E.B., Wellendorf, H., 1995. Second Evaluation of An International Series of Teak Provenance Trials. Danida Forest Seed Centre, Humlebæk, Denmark.
- Kjaer, E.D., Lobo, A., Myking, T., 2014. The role of exotic tree species in Nordic forestry. *Scand. J. Forest Res.* 29, 323–332. <http://dx.doi.org/10.1080/02827581.2014.926098>.
- König, A.O., 2005. Provenance research: evaluating the spatial pattern of genetic variation. In: Geburek, T., Turok, J. (Eds.), *Conservation and Management of Forest Genetic Resources in Europe*. Arbora Publishers, Zvolen, Slovakia, pp. 275–333.
- Koskela, J., Vinceti, B., Dvorak, W., Bush, D., Dawson, I., Loo, J., et al., 2010. The use and movement of forest genetic resources for food and agriculture. In: *Background Study Paper No. 44*. The Commission on Genetic Resources for Food and Agriculture, Food and Agriculture Organization of the United Nations, Rome, Italy.
- Kull, C.A., Rangan, H., 2008. Acacia exchanges: wattles, thorn trees and the study of plant movements. *Geoforum* 39, 1258–1272.
- Lamarque, L., Delzon, S., Lortie, C., 2011. Tree invasions: a comparative test of the dominant hypotheses and functional traits. *Biol. Invas.* 13, 1969–1989.
- Langlet, O., 1971. Two hundred years geneecology. *Taxon* 20, 653–722.
- Ledig, F.T., 1992. Human impacts on genetic diversity on forest ecosystems. *Oikos* 63, 87–108.
- Lee, S.L., Ng, K.K.S., Saw, L.G., Lee, C.T., Muhammad, N., Tani, N., Tsumura, Y., Koskela, J., 2006. Linking the gaps between conservation research and conservation management of rare dipterocarps: a case study of *Shorea lumutensis*. *Biol. Conserv.* 131, 72–92.
- Lefèvre, F., Barsoum, B., Heinze, B., Kajba, D., Rotach, P., de Vries, S.M.G., Turok, J., 2001. EUFORGEN Technical Bulletin: *In situ* Conservation of *Populus nigra*. International Plant Genetic Resources Institute, Rome, Italy.

- Lengkeek, A.G., Kindt, R., van der Maesen, L.J.G., Simons, A.J., van Oijen, D.C.C., 2005. Tree density and germplasm source in agroforestry ecosystems in Meru, Mount Kenya. *Gen. Res. Crop Evol.* 52, 709–721.
- Lentz, D.L., 2000. Anthropocentric food webs in the Precolumbian Americas. In: Lentz, D.L. (Ed.), *Imperfect Balance: Landscape Transformations in the Pre-Columbian Americas*. Historical Ecology Series. Columbia University Press, New York, USA, pp. 89–119.
- Liebold, A.M., Brockerhoff, E.G., Garrett, L.J., Parke, J.L., Britton, K.O., 2012. Live plant imports: the major pathway for forest insect and pathogen invasions of the US. *Front Ecol. Environ.* 10, 135–143.
- Lillesø, J.-P.B., Graudal, L., Moestrup, S., Kjaer, E.D., Kindt, R., Mbor, A., Dawson, I.K., Muriuki, J., Røsbild, A., Jamnadass, R., 2011. Innovation in input supply systems in smallholder agroforestry: seed sources, supply chains and support systems. *Agroforest Syst.* 83, 347–359.
- Louafi, S., Schloen, M., 2013. Practices of exchanging and utilizing genetic resources for food and agriculture and the access and benefit sharing regime. In: Kaman, E.C., Winter, G. (Eds.), *Common Pools of Genetic Resources: Equity and Innovation in International Biodiversity Law*. Routledge, Abingdon, UK, pp. 193–223.
- Madsen, S.F., 1995. International beech provenance experiment 1983–1985: analysis of the Danish member of the 1983 series. In: Madsen, S.F. (Ed.), *Genetics and Silviculture of Beech: Proceedings from the 5th Beech Symposium of the IUFRO Project Group P1.10-00*. Forskningsserien 11, pp. 35–44.
- Magri, D., Vendramin, G.G., Comps, B., Dupanloup, I., Geburek, T., Gömöry, D., Latalowa, M., Litt, T., Paule, L., Roure, J.M., Tantau, I., van der Knaap, W.O., Petit, R.J., de Beaulieu, J.-L., 2006. A new scenario for the quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytol.* 171, 199–221.
- Mathauda, G.S., 1954. The all-India teak seed origin sample plots. *Indian Forester* 80, 10–23.
- Mather, A., 2001. The transition from deforestation to reforestation in Europe. In: Angelsen, A., Kaimowitz, D. (Eds.), *Agricultural Technologies and Tropical Deforestation*. CAB International, Wallingford, UK, pp. 35–52.
- Mátyás, C., 1994. Modelling climate change effects with provenance test data. *Tree Physiol.* 14, 797–804.
- Mátyás, C., 1996. Climatic adaptation of trees: rediscovering provenance tests. *Euphytica* 92, 45–54.
- Midgley, S., Blyth, M., Howcroft, N., Midgley, D., Brown, A., 2010. *Balsa: Biology, Production and Economics in Papua New Guinea*. Australian Centre for International Agricultural Research, Canberra, Australia, p. 98.
- Mitchell, R.G., Wingfield, M.J., Hodge, G.R., Steenkamp, E.T., Coutinho, T.A., 2013. The tolerance of *Pinus patula* × *Pinus tecunumanii*, and other pine hybrids, to *Fusarium circinatum* in greenhouse trials. *New Forest* 44, 443–456.
- Mohan Jain, S., Priyadarshan, P.M. (Eds.), 2009. *Breeding Plantation Tree Crops. Tropical Species*. Springer Science + Business Media, New York, USA.
- Muriuki, J.K., 2005. Informal agroforestry tree seed quality and supply systems: a case of peri-urban Nairobi, Meru and western Kenya. M.Sc. Thesis, Kenyatta University, Nairobi, Kenya.
- Nagarajan, B., Varghese, M., Nicodemus, A., Sashidharan, K.R., Bennet, S.S.R., Kannan, C.S., 1996. Reproductive biology of teak and its implications in tree improvement. In: Dieters, M.J., Matheson, A.C., Nikles, D.G., Harwood, C.E., Walker, S.M. (Eds.), *Tree Improvement for Sustainable Tropical Forestry*. Queensland Forestry Research Institute, Indooroopilly, Australia, pp. 244–248.
- Natural Resources Canada, 2012. Report on the State of Canada's Forest Genetic Resources. Natural Resources Canada, Canadian Forest Service, New Brunswick, Canada.
- Neale, D.B., Kremer, A., 2011. Forest tree genomics: growing resources and applications. *Nat. Rev. Gen.* 12, 111–122.
- Nel, J.L., Richardson, D.M., Rouget, M., Mgid, T., Mdzeke, N.P., Le Maitre, D.C., van Wilgen, B.W., Schonegevel, L., Henderson, L., Naser, S., 2004. A proposed classification of invasive alien plant species in South Africa: towards prioritizing species and areas for management action. *S. Afr. J. Sci.* 100, 53–63.
- Nichols, J.D., Vanclay, J.K., 2012. Domestication of native tree species for timber plantations: key insights for tropical island nations. *Int. Forest Rev.* 14, 402–413.
- Nikles, D.G., 2006. The domestication of African mahogany (*Khaya senegalensis*) in northern Australia. *Aust. Forest* 69, 68–69.
- Nikles, D.G., Bevege, D.L., Dickinson, G.R., Griffiths, M.W., Reilly, D.F., Lee, D.J., 2008. Developing African mahogany (*Khaya senegalensis*) germplasm and its management for a sustainable forest plantation industry in northern Australia: progress and needs. *Aust. Forest* 71, 33–47.
- Orr-Ewing, A.L., 1962. An Analysis of the Breeding Programme for Coastal Douglas-Fir. British Columbia Forest Service, British Columbia, Canada.
- Palupi, E., Owens, J.N., 1996. Reproductive biology of teak (*Tectona grandis* L.f.) in East Java, Indonesia. In: Dieters, M.J., Matheson, A.C., Nikles, D.G., Harwood, C.E., Walker, S.M. (Eds.), *Tree Improvement for Sustainable Tropical Forestry*. Queensland Forestry Research Institute, Indooroopilly, Australia, pp. 255–260.
- Pâques, L. (Ed.), 2013. *Forest Tree Breeding In Europe: Current State-of-the-Art and Perspectives*. Managing Forest Ecosystems, vol. 25. Springer, Dordrecht, The Netherlands.
- Pegg, G., Perry, S., Carnegie, A., Ireland, K., Giblin, F., 2012. Understanding Myrtle Rust Epidemiology and Host Specificity to Determine Disease Impact in Australia. Cooperative Research Centre for National Plant Biosecurity, Bruce, Australia.
- Petit, R.J., Csaikl, U.M., Bordacs, S., Burg, K., Coart, E., Cottrell, J., et al., 2002. Chloroplast DNA variation in European white oaks: phylogeography and patterns of diversity based on data from over 2600 populations. *Forest Ecol. Manage.* 156, 5–26.
- Potts, B.M., Barbour, R.C., Hingston, A.B., 2001. The Risk of Genetic Pollution from Farm Forestry Using Eucalypt Species and Hybrids. Rural Industries Research and Development Corporation, Kingston, Australia.
- Potts, B.M., Vaillancourt, R.E., et al., 2004. Exploration of the *Eucalyptus globulus* gene pool. In: Borralho, N.M.G., Pereira, J.S., Marques, C., Coutinho, J., Madeira, M., Tomé, M. (Eds.), *Eucalyptus in a Changing World*. RAIZ, Instituto Investigação de Floresta e Papel, Aveiro, Portugal, pp. 46–61.
- Powis, T.G., Cyphers, A., Gaikwad, N.W., Grivetti, L., Cheong, K., 2011. Cacao use and the San Lorenzo Olmec. *Proc. Natl. Acad. Sci.* 108, 8595–8600.
- Poynton, R.J., 1977. *Tree Planting in Southern Africa*. The Pines, vol. 1. Department of Forestry, Pretoria, South Africa.
- Pritchard, H.W., Moat, J., Ferraz, J.B.S., Marks, T.R., Camargo, J.L.C., Nadarajan, J., Ferraz, I.D.K., 2014. Innovative approaches to the preservation of forest trees. *For. Ecol. Manage.* 333, 88–98.
- Procheş, Ş., Wilson, J.R.U., Richardson, D.M., Rejmánek, M., 2012. Native and naturalized range size in *Pinus*: relative importance of biogeography, introduction effort and species traits. *Glob. Ecol. Biogeogr.* 21, 513–523.
- Rehfeldt, G.E., Tchekakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A., Milyutin, L.L., 2002. Intraspecific responses to climate in *Pinus sylvestris*. *Glob. Change Biol.* 8, 912–929.
- Rhymer, J.M., Simberloff, D., 1996. Extinction by hybridization and introgression. *Annu. Rev. Ecol. Syst.* 27, 83–109.
- Richardson, D.M., 2006. *Pinus*: a model group for unlocking the secrets of alien plant invasions? *Preslia* 78, 375–388.
- Richardson, D.M., Rejmánek, M., 2011. Trees and shrubs as invasive alien species - a global review. *Divers. Distrib.* 17, 788–809.
- Richardson, D.M., Carruthers, J., Hui, C., Impson, F.A.C., Miller, J.T., Robertson, M.P., Rouget, M., Le Roux, J.J., Wilson, J.R.U., 2011. Human-mediated introductions of Australian acacias - a global experiment in biogeography. *Divers. Distrib.* 17, 771–787.
- Rogers, D.L., 2004. *In situ* genetic conservation of a naturally restricted and commercially widespread species, *Pinus radiata*. *Forest Ecol. Manage.* 197, 311–322.
- Rogers, D.L., Ledig, F.T. (Eds.), 1996. *The Status of Temperate North American Forest Genetic Resources*. In: Report No. 16, Genetic Resources Program, Division of Agriculture and Natural Resources, University of California, Davis, USA.
- Russell, J.R., Hedley, P.E., Cardle, L., Dancy, S., Morris, J., Booth, A., Odee, D., Mwaura, L., Omondi, W., Angaine, P., et al., 2014. TropiTree: an NGS-based EST-SSR resource for 24 tropical tree species. *Publ. Lib. Sci. One (PLoS ONE)* 9, e102502. <http://dx.doi.org/10.1371/journal.pone.0102502>.
- Rymer, P.D., Sandiford, M., Harris, S.A., Billingham, M.R., Boshier, D.H., 2013. Remnant *Pachira quinata* pasture trees have greater opportunities to self and suffer reduced reproductive success due to inbreeding depression. *Heredity*. <http://dx.doi.org/10.1038/hdy.2013.73>.
- Sabadi, R., 2003. The position of Pedunculate Oak in Spačva, Europe, and the world. In: *A Retrospective of Managing Forests of Pedunculate Oak in Croatia*, Vinkovci, Zagreb, Croatia.
- Sacandé, M., Joker, D., Dulloo, M.E., Thomsen, K.A., 2004. *Comparative Storage Biology of Tropical Tree Seeds*. International Plant Genetic Resources Institute, Rome, Italy, p. 363.
- Samuel, C.J.A., 2007. The introduction, evaluation and use of non-native conifer species in Britain. In: Koskela, J., Samuel, C.J.A., Mátyás, C.S., Fady, B. (Compilers), *Conifers Network*, Report of the fourth meeting (18–20 October 2003, Pitlochry, UK). Biodiversity International, Rome, Italy, pp. 31–34.
- Santini, A., Ghelardini, L., De Pace, C., Desprez-Loustau, M.L., Capretti, P., Chandelier, A., et al., 2013. Biogeographical patterns and determinants of invasion by forest pathogens in Europe. *New Phytol.* 197, 238–250.
- Shiferaw, H., Teketay, D., Nemomissa, S., Assefa, F., 2004. Some biological characteristics that foster the invasion of *Prosopis juliflora* (Sw.) DC at Middle Awash Rift Valley Area, Northeastern Ethiopia. *J. Arid Environ.* 58, 135–154.
- Shrestha, M.K., Volkaert, H., Van Der Straeten, D., 2005. Assessment of genetic diversity in *Tectona grandis* using amplified fragment length polymorphism markers. *Can. J. Forest Res.* 35, 1017–1022.
- Singh, S., Cunningham, D., Davidson, J., Bush, D., Read, S., 2013. Status of Australia's forest genetic resources. In: *ABARES Research Report 13.3*. Australian Bureau of Agricultural and Resource Economics and Sciences, Canberra, Australia.
- Smulders, M.J.M., Cottrell, J.E., Lefèvre, F., van der Schoot, J., Arens, P., Vosman, B., et al., 2008. Structure of the genetic diversity in black poplar (*Populus nigra* L.) populations across European river systems: consequences for conservation and restoration. *Forest Ecol. Manage.* 255, 1388–1399.
- Sreekanth, P.M., Balasundaram, M., Nazeem, P.A., Suma, T.B., 2012. Genetic diversity of nine natural *Tectona grandis* L.f. populations of the Western Ghats in Southern India. *Conserv. Gen.* 13, 1409–1419.
- Steenkamp, E.T., Makhari, O.M., Coutinho, T.A., Wingfield, B.D., Wingfield, M.J., 2014. Evidence for a new introduction of the pitch canker fungus *Fusarium circinatum* in South Africa. *Plant Pathol.* 63, 530–538.
- Tarigan, M., Roux, J., Wyk, M.V., Tjahjono, B., Wingfield, M.J., 2011. A new wilt and die-back disease of *Acacia mangium* associated with *Ceratocystis manginecans* and *C. acaciivora* sp. nov. in Indonesia. *S. Afr. J. Bot.* 77, 292–304.
- Tchoundjeu, Z., Asaah, E.K., Anebebe, P., Degrande, A., Mbile, P., Facheux, C., Tsoheng, A., Atangana, A.R., Ngo-Mpeck, M.L., Simons, A.J., 2006. Putting participatory domestication into practice in West and Central Africa. *Forests, Trees Livelihoods* 16, 53–69.

- Thomas, E., Jalonen, R., Loo, J., Boshier, D., Gallo, L., Cavers, S., Bordács, S., Smith, P., Bozzano, M., 2014. Genetic considerations in ecosystem restoration using native tree species. *For. Ecol. Manage.* 333, 66–75.
- Thomson, L., 2006. Low input breeding and genetic conservation of Pacific Islands forest tree species. In: Isik, F. (Ed.), *Proceedings of IUFRO Division 2 Conference: Low input breeding and genetic conservation of forest tree species*. North Carolina State University, Raleigh, USA, pp. 208–215.
- Tulstrup, N.P., 1959. International trade in forest tree seed. *Unasylva* 13 (4), 196–201.
- van der Merwe, M., McPherson, H., Siow, J., Rossetto, M., 2014. Next-gen phylogeography of rainforest trees: exploring landscape-level cpDNA variation from whole-genome sequencing. *Mol. Ecol. Res.* 14, 199–208.
- Van Klinken, R.D., Campbell, S.D., 2001. The biology of Australian weeds 37. *Prosopis* L. species. *Plant Prot. Q.* 16, 2–20.
- Varghese, M., Harwood, C.E., Hegde, R., Ravi, N., 2008. Evaluation of provenances of *Eucalyptus camaldulensis* and clones of *E. camaldulensis* and *E. tereticornis* at contrasting sites in southern India. *Silvae Gen.* 57, 170–179.
- Verhaegen, D., Fofana, I.J., Logossa, Z.A., Ofori, D., 2010. What is the genetic origin of teak (*Tectona grandis* L.) introduced in Africa and in Indonesia? *Tree Genet. Genomes* 6, 717–733.
- Wang, T., O'Neill, G.A., Aitken, S.N., 2010. Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecol. Appl.* 20, 153–163.
- Wellendorf, H., Kaosa-Ard, A., 1988. Teak improvement strategy in Thailand. *Forest Tree Imp.* 21, 1–43.
- Wickneswari, R., Rajora, O.P., Finkeldey, R., Aravanopoulo, F., Bouvet, J.-M., Vaillancourt, R.E., Kanashiro, M., Fady, B., Tomita, M., Vinson, C., 2014. Genetic effects of forest management practices: Global synthesis and perspectives. *For. Ecol. Manage.* 333, 52–65.
- Wilhelm, E., 2005. Micro- and macropropagation of forest trees. In: Geburek, T., Turok, J. (Eds.), *Conservation and Management of Forest Genetic Resources in Europe*. Arbora Publishers, Zvolen, Slovakia, pp. 623–650.
- Winter, G., 2013. Common pools of genetic resources and related traditional and modern knowledge: an overview. In: Kaman, E.C., Winter, G. (Eds.), *Common Pools of Genetic Resources: Equity and Innovation in International Biodiversity Law*. Routledge, Abingdon, UK, pp. 3–25.
- Wood, P., 1967. Teak plantings in Tanzania. *Proceedings from FAO world symposium on man-made forests*. Document 3, Canberra, Australia, pp. 1631–1644.
- Wu, H.X., Eldridge, K.G., Matheson, C.A., Powell, M.B., McRae, T.A., Butcher, T.B., Johnson, I.G., 2007. Achievements in forest improvement in Australia and New Zealand 8. Successful introduction and breeding of *Pinus radiata* in Australia. *Aust. Forest* 70, 215–225.