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Merging applied gene conservation activities with advanced generation breeding initiatives: a case study of *Pinus radiata* D. Don

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Abstract Major challenges exist for applied gene conservation of forest genetic resources in native habitats of the Mexican and Central American Pines, *Pinus radiata* and the Southern US pines. They include population decline and population structure changes, due to forest removal, conversion of forest land to other uses, fires, climate change, diseases and pests. However, tree breeders continue to struggle with methods that would meaningfully integrate tree breeding and conservation populations. In this review, I will start by outlining the importance of gene conservation in tree breeding programs, then highlight some challenges and opportunities for applied gene conservation programs; and lastly, I share results of a large body of applied research and other activities aimed at genetically characterising the base population of *P. radiata* in Australia and New Zealand, for the purposes of effective ex situ gene conservation. Main threats for species grown in exotic environments also include introduced diseases and pests, and more recently, climate change. Consequently, movement of genetic material is often restricted and genetic resources of pine species are not readily expanded by further importations from overseas. Therefore, conservation of genetic material currently in these countries is likely to be important for the long-term viability of plantation forestry using pine species. In addition to understanding the largely unpredictable or speculative biological and economic worth of rare alleles, the greatest challenge that we have in ex situ gene conservation is to develop practical approaches for infusing genes from base populations of unimproved material into more advanced-generation breeding programs without greatly affecting productivity gains. Other notable challenges include perceived costs and benefits of gene conservation in the face of increasing privatisation of forest estate. While financial resources for domestication of alternative species are declining, a vast number of existing species and provenance/progeny trials of *P. radiata*, the Mexican and Central American pines and the Southern US pines provide an excellent gene resource for the future.

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Why we need gene conservation in tree breeding programs

Genetic diversity is widely recognised as the key component for long-term survival of most tree species. It is a foundation of sustainability because it provides raw material for adaptation, evolution, and survival of species and individuals, especially under changed environmental and disease conditions (e.g. Frankham et al. 2002; Reed and Frankham 2003). Genetic uniformity may leave a species vulnerable to new environmental and biotic challenges (FAO 2006). Long-term conservation of forest genetic resources (FGR) is a cornerstone of sustainable forest management. Through conservation and proper forest management, it is possible to maintain the evolutionary processes of species and the diversity of their gene pools for use now and in the future (Geburek and Konrad 2008). Traditionally, forest conservation has often been understood as a steady-state process, whose goal is to protect natural forests in their original state. Forests, however, are dynamic systems that are now being altered by human intervention as well as natural climatic changes. Human activities have modified forests and their biodiversity for millennia, even in seemingly pristine tropical forests (Kjaer et al. 2004).

In conserving forest genetic resources, we are concerned primarily with conserving genetic diversity within and among populations of a species. Our priorities are normally based on the economic and environmental importance of the species, its ecological functions, the level of risk, or other special features that contribute to the importance of a species. For example, quantitative traits (e.g. survival, resistance to biotic or abiotic stress and growth) are of economic significance and associated with population adaptation to different environments. Since different pictures of population genetic structure are often provided by molecular markers versus adaptive quantitative traits (e.g., Karhu et al. 1996; Merilä and Crnokrak 2001), integration of both kinds of information should be used to develop strategies for the genetic conservation of tree species (e.g., Frankham 2010). However, most studies aimed at formulating conservation strategies have used DNA markers to determine the level of genetic variation and population structure, although variation for such neutral markers may correlate poorly with traits under selection and does not necessarily reflect the evolutionary potential of the species (Reed and Frankham 2003; Leimu et al. 2006). Methods that assess important genetic variation are being developed (e.g., Avise 2010). These may include the application of single nucleotide polymorphisms (SNPs) (e.g., Neale and Savolainen 2004; Namroud et al. 2008). The end result of this is to ensure that functionally useful alleles will be identified and available in the future and can be captured in breeding programs within useful genotypic sets. For example, genes of intermediate frequency are relatively easy to conserve as they are commonly expressed. However, low-frequency genes (rare alleles) are more difficult to conserve even though they may well be needed for the future to meet new selection criteria such as resistance to new pests and diseases (e.g., Eldridge 1978; Burdon 1997; Yanchuk 2001; Gapare et al. 2005).

Gene conservation involves several sequential stages, ranging from the initial selection of target taxa and identification of conservation objectives, through field exploration and germplasm collection, to the actual storage and management of that germplasm over extended time periods. Existing forest resources and the genetic diversity they contain provide a basis for conservation measures. The selection of candidate species is one of the most important phases of the conservation process because future activities will be based on priorities set in the planning phase. As soon as priority setting has been completed, genetic diversity must be assessed and located for subsequent conservation activities. The selection of conservation measures depends on how the objectives of a conservation programme are defined and practical options available, especially in connection with in situ measures. These measures then provide a framework to implement practical conservation work.

Conservation of genetic resources can be accomplished through a variety of in situ and ex situ approaches (e.g., St. Clair and Howe 2011). In situ methods protect plants in their native habitats where they are subject to natural evolutionary processes. Ex situ methods involve storing genetic material in locations such as seed banks, genetic resource plantings (such as provenance and progeny trials and broadly-based gene-resource plantations), and seed- and breeding orchards. There is a general consensus among scientists and practitioners that no single conservation method is adequate, and that different methods should be applied in a complementary manner (e.g., Boffa et al. 2000). In situ gene conservation, however, has a number of benefits and so often forms the basis of conservation programs. It allows evolutionary processes to be maintained, including the adaptation of tree populations to changing environmental conditions. This is particularly important for breeding programs, since future human needs and environmental conditions are difficult to predict. As mentioned earlier, in situ and ex situ gene conservation should be used in a complementary fashion to conserve forest genetic resources. Both are an integral part of the conservation process, and both can be effective only after genetic diversity has been located and conservation priorities have been set. The main purpose of ex situ gene conservation is to capture and maintain a representative sample of the existing genetic diversity of a species. However, there will inevitably be selective pressure that does not match those conserved in situ. Moreover, the downside of any selection for commercial traits will tend to be offset by reducing the opportunity costs of maintaining a given area of gene-resource planting, which will hopefully enable greater genetic diversity to be maintained. And if one can maintain bigger areas of gene-resource plantings, then it is feasible to reduce the pressures of pollen contamination. For highly endangered tree species, ex situ conservation may be the only approach in the short to medium term. The main pitfalls of collecting germplasm samples for ex situ gene conservation are: (1) limited geographic coverage of genetic variation; (2) other biases in the collected plant material; and (3) samples that are too large to deal with (Brown and Hardner 2000). Because ex situ gene conservation plantings are typically (but not always) more costly than in situ gene conservation, it is particularly important that sampling of populations and germplasm within populations is given special attention to maximise the use of limited financial and human resources.

An important requirement in conserving quantitative variation is to maintain its dynamics (Yanchuk 2001). Maintenance of continuing evolution should be primarily emphasised in developing conservation strategy. Conservation ex situ in the forms of seed bank, and tissue bank, called static conservation, decouples from dynamic environments and implies a risk of maladaptation in the future and can easily result in large genetic differentiation between populations maintained ex situ and in situ, especially for loci with large or moderate effects (Hu and Li 2002). Adaptation of material in static conservation would be affected by the conditions in storage and the time elapsed. *Pinus radiata* seed had viability levels as low as 3 % after 25 years in cold storage (Gapare et al. 2012a). A robust gene conservation strategy combines elements of both approaches and is based on knowledge of the genetic structure of a species and the perceived threat to a species whether from natural disturbance processes, introduced insect and pathogens, or sensitivity to changing climate. Addressing these issues effectively depends on a well-integrated tree breeding strategy to serve the management of genetic resources.

As breeding programs have become more sophisticated, there have been moves towards expanding the genetic bases. For example, the original genetic base of the Australian breeding populations of *P. radiata* may have been of the order of 200–300 seed trees from a limited part of the natural range of *P. radiata* (Wu et al. 2007). The genetic base for the land race(s) and traditional breeding populations has been a very incomplete and unbalanced sample of the species' natural range and hence of its total genetic diversity. In most cases, the genetic base of populations derived from second- and third- generation selections are probably too narrow and there is a need to infuse new germplasm to expand the genetic base.

Because of anticipated adverse climatic change and resulting increases in risk of disease and insect attacks in forest plantations in the future, there is need to maintain broad genetic bases for adaptability and pest resistance. Ironically, the recent influx of tree diseases and insects in plantations around the world and the threat they pose to major commercial tree species has been a catalyst in renewing interest in applied tree conservation programs as sources of new, better-adapted, genetic material (Burdon 2010; Dvorak 2012). For example, in Chile, a new disease (Daño Foliar del Pino' (DFP)), caused by *Phytophthora pinifolia* (Pine needle and shoot blight) has severely affected more than 60,000 ha of prime *P. radiata* plantations in the country (Durán et al. 2008). *Phytophthora pluvialis* (Red Needle Cast) is an emerging disease threat of *P. radiata* in New Zealand (Reeser et al. 2013). In Australia and New Zealand, *Dothistroma septosporum* (Dothistroma needle blight) remains a challenge. The infection has a strong negative impact on growth. The economic impact of *Dothistroma septosporum* in New Zealand has been estimated at about $24 million per year, including chemical control costs of about $2.5 million per year in addition to direct growth loss costs (Bulman et al. 2004). *Essigella californica* (Monterey Pine Aphid) on *P. radiata* forests in New South Wales, Australia has been associated with severe upper crown yellowing and premature needle cast, resulting in some tree death. In South Africa, pitch canker fungus is now established on *P. patula* and *P. greggii* in nurseries and rarely (so far) is found on trees in the field (Coutinho et al. 2007; Roux 2007; Mitchell et al. 2011). It is also major problem on *P. radiata* in the nursery and sometimes on older trees in the field.

Climate change, and the associated shifts and fluctuations in temperature and precipitation patterns, are likely to affect substantial areas of forest plantation production in the tropics and subtropics (e.g., Leibing et al. 2013). Progressive climate change may make the choice of which species and provenance to plant increasingly difficult in native environments. However, in exotic conditions, use of results from provenances trials planted at different locations may guide decisions on which genotypes to plant. This highlights the importance of continued investment in provenance trials establishment. Increases in the frequency, duration, and/or severity of drought and heat stress associated with climate change could fundamentally alter the composition, structure, and biogeography of forests in many regions. There are increases in tree mortality associated with climate-induced physiological stress and interactions with other climate-mediated processes such as insect outbreaks and wildfire. Climate change will require trees to cope with new biotic and abiotic environments and stresses, including: habitat shifting and alteration, fragmentation, drought, temperature extremes, wildfire, and novel insect and disease pressures. The specific effects of climate change will vary greatly over time and space. According to climate change predictions by the intergovernmental panel on climate change, seed material that is well matched under the current climate will have to grow in sub-optimal conditions within the production cycles of the upcoming decades (McKenney et al. 2009). This suggests that forest plantations will need to take anticipated climate conditions into account in order to maintain productivity in future harvest cycles. Therefore, seed material, adapted to the novel climate conditions, needs to be immediately identified and selected (Spittlehouse and Stewart 2003).

Current in situ gene conservation efforts: challenges and opportunities

Geist and Lambin (2002) highlighted that tropical deforestation is still continuing and it is clear that many in situ conservation efforts in the tropics have not been effective. This lack of success can be attributed partly to inadequate participation by various stakeholders in natural resources management and conservation, and tree breeders (Koshy et al. 2002). For the last three decades, researchers and scientists have urged that the forest community be more pro-active in the development of sound gene conservation programs to promote sustainable forestry, which includes maintaining and protecting genetic base populations (e.g. Eldridge 1978, 1997; Dvorak 2012). However, there are differences on issues such as strategy and approaches (ex situ vs. in situ), focus on common versus low-frequency alleles, the cost/benefits of long-term programs to maintain gene pools, and the justification for protecting commercially important tree species represented by large areas of exotic plantations (Eldridge 1978; Dvorak 2012). Some have argued that rare alleles arise largely as unfavourable mutations, are merely evolutionary relics and contribute little to the overall fitness value (e.g., Brown 1989), whereas others (e.g., Gapare et al. 2005) suggested that rare alleles can be very important for long-term evolution. For example, recessive alleles for resistance to fungal pathogens are a very interesting case in point. Where they work, they tend to be much less prone to being ‘defeated’ by the pathogen mutation. If rare alleles become a target for future breeding objectives or for survival of populations, the possibility of relatedness among selected genotypes may not allow their effective use due to an excessive build-up of inbreeding. Burdon (1997) postulated that, with a mixed mating system for pines, the rare alleles can be expressed reasonably readily and may have played a role in some conifers flipping over into becoming selfing species. It is therefore desirable to raise the probability of maintaining rare alleles in sufficient unrelated genotypes for future use in breeding populations. Dvorak (2012) also argued that as forest diseases become more prominent in plantation forestry and our understanding improves about the gene action that controls resistance to tree diseases, we might need to rethink the value of capturing rare alleles for use in breeding programs. As an example, resistance to fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*), the most commercially damaging disease that affects *P. taeda* in the southern USA, costs the industry million of dollars in annual losses (Schmidt 1998) and is probably controlled by rare alleles (Dvorak 2012). Eight genes/alleles have been identified at the present time, but probably more exist. It is unclear at this time what kind of alleles control resistance mechanisms in trees to pitch canker (Dvorak 2012).

Some challenges

Threats to the genetic diversity of forest trees are manifold, and for the main part directly or indirectly anthropogenic (Geburek and Konrad 2008). Changing land use (e.g., conversion of forests for agriculture) and logging increase fragmentation and isolation of tree populations in the tropics. Inevitably, fragmentation of populations results in the loss of genetic diversity through genetic bottlenecks, and increased inbreeding eventually leads to negative long-term effects on the tree population (Ezard and Travis 2006). For example, in hardwood species, associated losses of the populations of bat species that are efficient pollinators between widely scattered individuals can be a big factor in loss of genetic diversity. New pests and pathogens, which may have been introduced or are newly evolving, inevitably seem to be on the increase as a result of the global movement of goods, further challenging the adaptive potential of an increasing number of tree species (Brasier 2001; Burley 2001; Scherm and Coakley 2003; Goss et al. 2011). For example, there are several threats to the Mexican and southern pine species in their native habitats that make in situ conservation a challenge. Suffering diseases, bark beetle attacks and excessive fires describe the situation for most pine species in Mesoamerica. For example, some *P. tecunumanii* and *P. maximinoi* stands in their native habitats are under threat primarily from agricultural expansion but are also threatened by fires and insects, notably *Dendroctonus* sp. As such, conservation status for *P. tecunumanii*, *P. maximinoi* is now critically endangered and endangered, respectively (Camcore 2008). Both these species have proved to be alternative species for commercial forestry in the tropics, in particular in Southern Africa. *P. tecunumanii* is being used as a hybrid parent with *P. patula* in South Africa, highlighting the need for ex situ conservation of the species (Camcore 2010).

Monterey and Cambria populations of *P. radiata* are severely being encroached upon by urban development and exotic invasive organisms in California. *P. radiata* stands on Guadalupe Island have been severely impacted by grazing from feral goats, with fewer than 220 mature trees left based on a 2001 census (Rogers 2004), although there may have been some recovery since then (A.C. Matheson, pers. comm.). However, there are efforts to purchase land to protect the remaining radiata pine forests from degradation or conversion to other uses.

Because of the diseases and pests now present in native habitats, importation of seed and other material from any pine species is now subject to stringent quarantine controls in some countries. For example, there is currently a moratorium on importing *P. radiata* germplasm from native stands into Australia and New Zealand. Consequently, the genetic material of pine species currently in Australasia cannot readily be augmented by further importations from overseas. Therefore, conservation of genetic material currently in Australasia is likely to be important to support the long-term viability of plantation forestry using pine species in Australasia. Cook and Matheson (2008) estimate that delaying the entry and spread of pitch canker in Australia by as little as two or three years is worth nearly $13 million to the Australian forest industries. As a consequence of the extreme risk posed by pitch canker to the Australian forest industries, importation of seed is prohibited. Resistance to fungal diseases has been an important breeding objective in some tree breeding programs (Burdon and Wilcox 2007). Because fungal diseases can cause biotic crises, they can impose new and crucial breeding objectives that can place extreme demands on breeding populations (Burdon 2010; Ivković et al. 2010).

Maintaining unimproved gene-resource stands is expensive, and likely to become more so as progressive genetic gain increases the opportunity costs of such material. For example, the real significance of the boost in genetic diversity from broadening the provenance base from unimproved gene-resource stands may lie in recruiting genetic resistance to various biotic factors and abiotic factors (e.g., Gapare et al. 2011). In some cases, the unimproved gene resources, while promising low costs and the benefits of natural selection, are, if ex situ, highly vulnerable to pollen contamination which may badly affect their value as sources of new unrelated germplasm. Some tree-improvement programs have started with too narrow a genetic base, thus decreasing the value of their conservation efforts. There is now a realisation that for ex situ conservation plantings to succeed, they must hold some economic or aesthetic importance to the receptor institution (Dvorak 2012). However, there appear to be little information on the valuation of forest genetic resources. Laarman and Dvorak (1988) investigated the financial feasibility of participation in an international seed cooperative for tropical pines. They reported that it is financially viable at annual planting levels of 100–500 ha if the opportunity cost of capital is 8 %. A literature search revealed that valuation of genetic resources up to now has only been done in one woody species, namely coffee (*Coffea arabica*) (Hein and Gatzweiler 2006; Shumeta et al. 2012). The monetary value of coffee genetic resources was determined by calculation of the productivity gain through hypothetical breeding programs for increased yield and pathogen resistance. Geburek and Konrad (2008) suggested that a similar approach could be tried for forest tree species, such as in the simplified form of modelling the additional monetary profit gained by the use of superior clones or offspring originating from phenotypically superior (plus) trees. In such an approach, the profit could be transferred to the whole forest area from which valuable forest genetic resources (FGR) have been selected and used to indicate the value of the genetic information located there. Such valuation would provide decision makers with valid arguments that would allow them to defend conservation programs against budget cuts.

Evidently, the questions of requisite population sizes and appropriate management systems have become increasingly pressing. Setting the sizes of breeding populations and gene resources may be based on the size of the breeding program and may depend on: (1) acceptable probabilities of retaining alleles present at certain frequencies; (2) threshold frequencies at which alleles are worth trying to conserve; (3) expected ongoing and long-term utilisation of breeding populations; (4) acceptable costs (Burdon and Wilcox 2007). While breeding populations may contain a few hundred individuals, and gene resources a few thousand (e.g. White 2004), such numbers may be interdependent, since the appropriate size of a breeding population, for instance, may depend on what is available or can be maintained as gene resources.

Resources allocated for domestication of new species and gene conservation continue to decline. For example, there are several species with commercial potential that have been assembled by Camcore (an International Tree Breeding and Conservation Program) at North Carolina State University, USA, but they have not been domesticated (Table 1 in Dvorak 2012). Commercial forest land is expensive and use of any piece of land is expected to generate an income. A key challenge for managing ex situ populations is meeting the opportunity cost of using land for conservation. Management of ex situ gene resource stands, while crucial to long-term genetic gain, does not directly earn revenue for commercial breeding programs. It is therefore often more resource-limited than activities that generate revenue directly (e.g. seed-orchard production, mass clonal propagation) (Burdon and Wilcox 2007). Meanwhile, tree breeders must often deal with shareholders who seek guaranteed returns from the direct costs and opportunity costs involved in gene conservation activities. Better knowledge will therefore be extremely welcome, especially as the opportunity costs are being increased by genetic gain already achieved (Burdon and Wilcox 2007). A further challenge is of a more organisational nature: forestry is a long-term business, at least for the pines, with rotation ages around 25–30 years for sawlogs. Other deeper structural challenges exist within the industry. For example, on the one hand, it is indeed long-term, yet it tends to be very cyclical, with alternating shortages and over-capacity of very capital-intensive processing plants that has long lead times to come on stream. Forestry companies are changing ownership increasingly frequently, there is lack of continuity in management, and thus conservation plantings often do not get protected.

Some opportunities

Even though provenance/progeny trials were not necessarily set up with conservation in mind, they can be used for the purpose, provided that future propagation from them is done with careful selection of unrelated individuals. More recently, international multi-site provenance trials, ones that measure growth performances of different seed sources in a range of different climates, are being used to address climate change issues (for example: re-analyse spatial patterns of genetic variation in relation to predicted future climates; validate species-suitability models; and monitor germination, growth, phenology, and resistance to insects and diseases) (e.g., Leibing et al. 2009; van Zonneveld et al. 2009; Wang et al. 2010). These trials provide a wealth of information on the adaptive capacity of species and provenances that may facilitate selection of seed material for changing climatic conditions (Leibing et al. 2013). It is imperative, therefore, for tree-breeding programs to take pre-emptive action to protect genetic diversity for current and future generations, for a wide range of commercial species.

The provenance/progeny trials also offer some opportunities to examine trends of population genetic structures in time and space through new DNA marker technology (single nucleotide polymorphisms (SNP). The use of SNPs has much promise for characterising base populations and undomesticated pine species, helping to interpret the results of evaluation trials, and monitoring the maintenance of the genetic bases in future breeding. It may also help in making policy decisions on the size of the genetic resources to be used for breeding and in the actual selection (e.g., Burdon 1995). For example, more than 2000 SNPs responsible for corewood formation was discovered using a 25-year-old *P. radiata* provenance trial established in Batlow, New South Wales, Australia in 1980 (Dillon et al. 2010). Other studies have also utilised provenance-trial material to identify significant associations between SNP markers in *P. taeda* and wood properties in relation to carbon-isotope discrimination, height growth, or resistance to a fungal pathogen, *Fusarium circinatum* (González-Martínez et al. 2007, 2008; Eckert et al. 2010; Cumbie et al. 2011). Some members of Camcore have received more than 20 pine species and established provenance/progeny trials. Such a resource offers a great opportunity to identify candidate genes for growth and disease traits.

Most Mexican and Central American pine provenance/progeny trial studies have revealed significant amounts of genetic variation. For example, provenance differences for DBH growth between the worst and best provenances of species like *P. tecunumanii* and *P. maximinoi* are as much as 30 % (Hodge and Dvorak 2012). Similarly, great differences are also found in adaptability. For example, sources of *P. leiophylla* and *P. herrerae* from northern Mexico are more cold-hardy than southern sources when planted in South Africa (Dvorak 2012). These materials offer opportunities to broaden the genetic bases of most tree breeding programs. Broadening the genetic bases of breeding populations favours the retention of new alleles and pre-existing but rare ones (Burdon 1997; Otto and Whitlock 1997). In some cases, historical introductions have often been haphazard, and may not represent the best-adapted provenances even though the existing material may perform well. For example, using isozymes and cortical oleoresin monoterpenes, the present Australian and New Zealand plantations of *P. radiata* have been shown to be from Año Nuevo and Monterey with none from Cambria (Moran and Bell 1987; Burdon 1992). Infusion of Cambria material is bound to increase the overall genetic base of the radiata pine breeding programs with potential long-term benefits (Gapare et al. 2011), even though the adaptive advantages of pure Cambria provenance are often outweighed by adaptive problems. Similarly, *P. patula* introduced in Zimbabwe and South Africa in the 1920s to 1950s was reported to have come from a narrow base (Barrett and Mullin 1968) and later collections made by Camcore in the mid-1990s could broaden the base of the species (Nyoka et al. 1996).

Through genetic infusion, genes are introduced from external sources into a breeding population at advanced-generation level. Such infusion makes possible not only the maintenance of genetic diversity but also potential increase of genetic gain (Gapare et al. 2011). However, the greatest challenges are to develop practical approaches and overcome institutional inertia for infusing genes from base populations of unimproved material into more advanced-generation breeding programs without greatly affecting productivity gains (Gapare et al. 2012a). While genetic diversity is desirable in itself, maximising diversity is liable to include material that is markedly suboptimal, in respect of adaptation and/or quality traits, so there is no simple formula for an overall optimal genetic base. The real significance of the boost in genetic diversity from broadening the genetic bases may lie in recruiting genetic resistance to various biotic and abiotic factors and/or in crucial provenance differences in wood properties coming to light (Gapare et al. 2012b). For example, hybrids between *P. patula* and *P. tecunumanii* are being used to reduce the susceptibility of young *P. patula* seedlings to *Fusarium circinatum* (Nel et al. 2006; Kanzler et al. 2012).

The germplasm assembled by Camcore provides a basket of options—various species/populations to choose from in order to meet the challenges and demands of the future. This is a key avenue for ensuring sustainability of the forestry industry in a changing world. Only rarely are ex situ and in situ conservation used in a complementary manner as is done by Camcore, as part of a holistic approach to conserving important species. Moreover, the few complementary efforts that do exist are seldom based on a well-documented knowledge of the genetic diversity of a given species within a country, much less an entire region. More studies are needed on the distribution of genetic diversity in material assembled by Camcore, and how effective current in situ conservation efforts are at safeguarding this diversity.

Lastly, forest geneticists have to find a common language to convey their ideas and to become more effective in the decision-making process. Successful conservation programs for forest genetic diversity require the development of clear objectives. As a first step, a strict distinction between the protection of genetic resources for utilitarian and ethical conservation purposes needs to be made; a point that often fails to emerge clearly in discussions and that has probably also had a major influence on the effectiveness of gene resource conservation activities (e.g., Geburek and Konrad 2008). Because forest genetics often has its roots in economically-oriented provenance research, its context tends to focus on tree breeding rather than conservation. Therefore, it needs to be clarified whether or to what extent (1) a genetic resource (forest area) to be conserved has been chosen purely for a commercial purpose (as is the traditional way of selecting superior-quality stands or trees and thus serving immediate breeding purposes rather than conservation per se) or (2) whether a resource has been protected based on its (assumed) high genetic variability or genetic uniqueness (Garnier-Géré and Ades 2001). In the future all parties (e.g., foresters, geneticists, conservationists) must try harder to promote forest genetic resource conservation through collaboration. Instead, concerted gene conservation efforts between forest geneticists and conservation agencies are desperately needed.

Overall, goals such as conserving adaptive variation and adaptability are appreciated by everyone, but it is nearly impossible to map actions to this goal. Forest geneticists tend to avoid giving clear precedence to specific action, perhaps because they believe that all activities are equally important and will somehow help to reach the overall goal. Nevertheless, the consequence of this failure to assign weights to actions is that the decisions are often deferred and probably made later through a different rationale. Decision makers need smaller steps that they can "sell" or "push," and to do so they rely on expert advice (e.g., McNeely and Vorhies 2000). Therefore assigning different weights to actions must be done wisely and responsibly, but it must be done. Forest geneticists should not be afraid to make mistakes. In fact, failures are almost inevitable if decisions are by default made later by those lacking expertise (e.g., Failing and Gregory 2003).

Radiata pine gene conservation and utilisation: a case study

The introduction, genetic base and state of *P. radiata* breeding populations in Australia and New Zealand

Pinus radiata was introduced into Australia and New Zealand, via England, in the mid 1800s (Wu et al. 2007; Johnson et al. 2008). Initially the species was used for ornamental purposes in botanic gardens. Further seed was imported directly from California to New Zealand in the 1870s with the largest consignment of 11 kg in 1876 probably originating from a large number of trees (Wu et al. 2007). From 1859 into the mid-1860s importations were made basically on a specimen-tree scale, from England (Wu et al. 2007; Burdon et al. 2008). The species thrived so well that by the late 1860s larger-scale importations had begun from California, and are known to have continued until 1882, by when New Zealand plantings could evidently meet the considerable demand for seed (Raymond and Henson 2009). However, records of the exact origin and breadth of the original genetic base have never been found. From the early 1900s seed from these early plantings was used to establish increasing areas of radiata plantation in southern Australia and New Zealand (Moran and Bell 1987; Johnson et al. 1997, 2008).

Small scale provenance research was embarked on in Australia and New Zealand from the late 1930s through into the 1950s, and there were small experimental plantings of island material in Australia. This, however, was done with no real commitment to provenance research, because of a prevailing belief that provenance would not be a real issue with radiata pine. A key change in thinking emerged after work published by Bannister (1959) that suggested that the entire geographic range of the species needed to be embraced, and should include both the Guadalupe and Cedros populations. During the 1960s two major collections were carried out—one by Forde was around 1962 and the second one by Dr Reid Moran on Guadalupe Island, supplemented by an expedition by him and Libby to Guadalupe and Cedros Islands in early 1964 (Forde 1964; Hood and Libby 1980). A Genetic Survey provenance/progeny experiment was subsequently established using seed arising from Forde's cone sampling, a seed collection made in Guadalupe by Dr Reid Moran, incorporated two New Zealand landrace population samples as controls, and Cedros Island from the 1964 Libby collection.

Results from the Genetic Survey showed that New Zealand land-race material was very predominantly, if not entirely from Año Nuevo and Monterey. However, the isozyme data gave a pretty weak signal, in respect of the Año Nuevo/Monterey ratio. Isozyme studies also suggested that Australian radiata pine originated from Monterey and Año Nuevo, the two best adapted of the five natural populations (Moran and Bell 1987; Burdon 1992). The isozyme work also showed that the first generation of existing breeding programs had captured a substantial proportion of the genetic diversity (in terms of allelic representation) in Año

Nuevo and Monterey provenances (Moran and Bell 1987). However, the three southern provenances (Cambria, Guadalupe and Cedros) did not appear to be represented in breeding programs. A combination of these early results from the Genetic Survey, monoterpene studies (Burdon et al. 1997a), some step-out provenance trials using spare stock and evidence that edaphic adaptation was an important issue, led to the joint New Zealand/Australia 'Eldridge' expedition. As breeding programs became more sophisticated in terms of pedigree, thought was also given to expanding the genetic base by re-collecting in the original stands in California, and this was also a contributing factor to the joint New Zealand/Australia expedition.

A comprehensive collection was carried out in 1978 (referred in this paper as the 1978 'Eldridge collection'). The collection was done as a collaboration between New Zealand and Australia with joint funding from United States of America/Australia Cooperative Science Program, CSIRO Division of Forest Research, New Zealand Forest Research Institute, and Forest Resources Division of Food and Agricultural Organisation. Seed was collected from a total of 621 mother trees, at least 22 trees from each native population and the trees were selected for having at least 40 collectable cones and being well grown and of good form (Eldridge 1978) (see Fig. 1; Table 1). Camcore and the Forest Genetic Center, Mexico made a further collection from 176 trees in all populations except Cedros in 1991 (Rogers 2002). A collection targeting the island populations (Guadalupe and Cedros) was carried out in 2001 by a multinational group of 14 scientists and conservationists, organised by Dr. Rodgers of the University of California, Davis Genetic Resources Conservation Program (Rogers 2002). The collection was in collaboration with scientists from the Colegio de Postgraduados in Montecillo, Mexico and CSIRO in Canberra, Australia.

The 1978 'Eldridge collection' comprised open-pollinated (OP) seed from individual trees from the Año Nuevo, Monterey, Cambria, Guadalupe and Cedros populations (Fig. 1). The 1978 'Eldridge collection' was used to establish provenance trials and large-block gene-resource plantings between 1979 and 1982 at many locations in Australia, New Zealand, South Africa and Chile. The Australian plantings included provenance progeny trials, whereas New Zealand only did provenance trials (by ecological subdivisions) of mainland material (except for a single-site planting of Guadalupe families). The shorter-term objective was to evaluate the adaptive and commercial characteristics of the provenance material. The longer-term objective was to provide material for infusion into breeding populations (while maintaining largely unimproved gene resources), meeting that objective being informed by the results of meeting the shorter-term one.

Findings from 23 different sites in New Zealand involving just the Californian mainland provenances showed different profiles of site adaptation among provenances (Burdon et al. 1997b, 1998). For example, Año Nuevo and Monterey are the best adapted overall to New Zealand conditions, but Año Nuevo is much less adapted to P-deficient clays, yet better adapted to cold, snow-hazard sites. Cambria is susceptible to needle-casts, shoot dieback, and frost and snow damage, but has tolerated poor soils. In Australia, Monterey was usually the best of the natural populations, but Año Nuevo grew better on the highest productivity sites and Cambria grew well on some low productivity sites in New South Wales (Johnson et al. 1997). In five South African trials (Falkenhagen 1991), Monterey was overall the best of the three mainland populations at age 8 years, being significantly superior to Año Nuevo at three sites and Cambria at one site out of five. At age 6 years in three trials in Chile, Monterey was superior for volume, although not significantly different from the other mainland populations (Jayawichrama and Balocchi 1993). Monterey also ranked highest for growth traits in one trial in Turkey at age 6 years (Toplu et al. 1987). In Turkey, Año Nuevo population was slightly inferior overall to Monterey in height, and

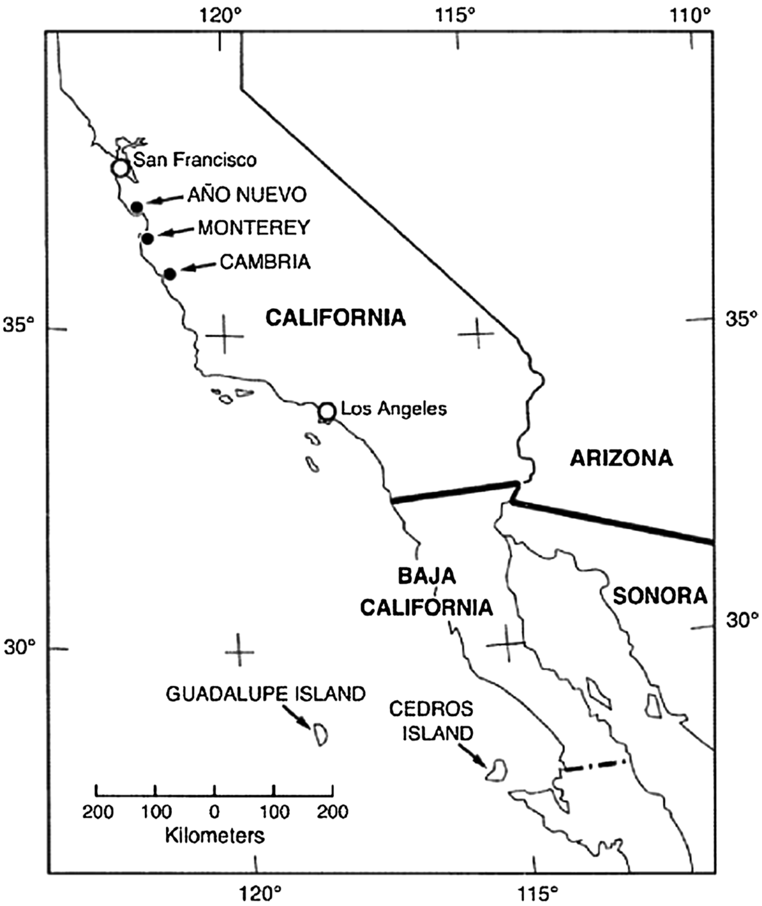

Fig. 1 Location of *Pinus radiata* populations: Año Nuevo, Monterey and Cambria native to California and Guadalupe and Cedros Islands in Mexico. Adapted from Ledig et al. (1998)

inferior to Monterey and Cambria in mean diameter and stand volume (Toplu et al. 1987). It was also slightly poorer than the other mainland populations for mean tree volume in Chile (Jayawichrama and Balocchi 1993). The fastest growing populations in Greece were Año Nuevo and Monterey while Cedros was completely unadapted to conditions in Greece (Matziris 1995).

Interpopulation hybrids including Cambria have grown well in comparison with pure Monterey population trees in a trial planted in 1973 on a fertile site in New South Wales (K.G.Eldridge unpubl. data). Such hybrids may combine better adaptation to certain environments with higher general growth rates, and could prove very useful in a generally adapted breed of *P. radiata.* Guadalupe population had promising performance at a low altitude site that represents low-rainfall area that is close to the hot and dry limit and soil that is sub-optimal for radiata pine (Boardman and McGuire 1997). A comparison study of native-population and New Zealand land-race samples of *P. radiata* using cortical oleoresin monoterpenes confirmed strong differences between Monterey and Cambria and also showed that local land race samples were evidently derived from Año Nuevo and Monterey (Burdon 1997).

Table 1 Seed-origin information for *Pinus radiata* populations sampled in California in 1978 (from Eldridge 1978)

Provenance	No. of mother trees	Latitude[a] (°N)	Longitude[a] (°W)	Altitude (m)	Rainfall (mm/annum)[b]
Año Nuevo	179	37°08′	122°18′	15–300	700
Monterey	244	36°37′	121°57′	5–580	500
Cambria	99	35°37′	121°09′	30–180	500
Guadalupe[c]	48	29°10′	118°15′	400–1,200	330–510
Cedros	51	28°22′	115°20′	380–640	150
Total	621				

[a] Latitude and longitude are derived directly from map locations and represent approximate centre points of the island and mainland populations

[b] Annual rainfall figures are approximate and average

[c] Substantial occurrence of fog during spring, summer and autumn with fog are especially important in complementing the normal precipitation in drier years. Rainfall figures from Oberbauer (2006)

The details of the base-population field trials and ex situ gene conservation trials where pedigree information is available are provided in Table 2 (Australia-based trials), Table 3 (New Zealand-based trials). The near-rotation ages of most provenance trials and conservation-block plantings, and a gradual loss of plantings at more than 20 sites highlighted the need to implement a strategy for re-conservation of radiata pine. The rest of the trials have reached rotation age and are due for clear-felling by 2015. The range-wide *P. radiata* 1978 ‘Eldridge collection’ also provided an opportunity for boosting the genetic base of the existing Australian and New Zealand breeding populations (Eldridge 1997). To ensure genetic sustainability and further increase genetic gain for *P. radiata*, infusion of new genetic material from the range-wide *P. radiata* 1978 ‘Eldridge collection’ was recommended (Burdon 1992; Eldridge 1997; Wu et al. 2007).

In order to explore what potential benefits infusions of native-population material into breeding programmes are likely to confer, initial characterisation of quantitative genetic variation of the native provenances would be critical in assessing the size and usefulness of genetic variation and for directing efficient selection of the genetic material. In addition, the ‘Eldridge collection’ germplasm had not yet been utilised in breeding programs. Infusion of conserved ‘wild’ genes from natural populations of radiata pine was seen as providing a new opportunity for improvement of Australian and New Zealand *P. radiata*. However, such expansion of genetic diversity will have a cost as germplasm in the breeding programs began at an estimated 2–5 generations are between three (Australia) and five (New Zealand) generations removed from the wild, and would be up to 2–3 additional generations thereafter and have been genetically improved for adaptation to their exotic environments and industrial objectives.

The case for allocating resources and effort for ex situ gene conservation of this important forest genetic resource is strong from both an international and national perspective, including documented threats to the native populations Año Nuevo, Monterey and Cambria, on the Californian mainland coast and Guadalupe and Cedros Islands, off the coast of Baja California. From a commercial forest industry perspective, this importance is due to the fact that: (1) the *P. radiata* resource underpins a significant industry; (2) the breeding programs in Australia and New Zealand appear to have a relatively restricted genetic base; and (3) opportunities to expand the genetic base through direct importation of native germplasm is now limited due to the risk of introducing pitch canker disease which

Table 2 Details of current base provenance trials and ex situ conservation trials (family identities records maintained) in Australia

Trial name	Location	State	Provenances represented	#Families	Survival %	Clearfell
Buccleuch	Bondo cpt 869	New South Wales	An, Ca, Gu, Ce	81	>90	2013
Green hills	Batlow, cpt 777	New South Wales	An, Mont, Cam, Gu, Ce, TSO	506	>92	2012
Green hills	Batlow, cpt 777	New South Wales	Gu	39	<45	2012
Green hills	Batlow, cpt 777	New South Wales	Ce	26	<40	2012
Billapallolla	Billapallolla, cpt 1106	New South Wales	Gu, Ce	78	<40	2012
Longford	Salicki, cpt 69	Victoria	An, Mont, Cam, Gu, Ce, GSO	506	<60	Indefinite
Longford	Salicki, cpt 70	Victoria	Gu	36	<30	Indefinite
Longford	Salicki, cpt 70	Victoria	Ce	25	<25	Indefinite
Paramount	Paramount, cpt 28	Victoria	An, Mont, Cam, Gu, Ce, 3 controls	450	>80	2015
Longford	Longs, cpt 9	South Australia	An, Mont, Cam, Gu, Ce, 3 controls	500	>75	2015
Tantanoola	Tantanoola reserve	South Australia	Gu	120	>90	2015
Second valley	Second Valley	South Australia	An, Mont, Cam, Gu, Ce, 2 controls	324	>90	2015
Wirrabara	Mt Ellen cpt	South Australia	An, Mont, Cam, Gu, Ce, 2 controls	250	<50	2015
West Takone	West Takone, cpt TR04	Tasmania	An, Mont, Cam, Gu, Ce, 5 controls	55	>80	2015
Paramount	Paramount, cpt 27	Victoria	An, Mont	Bulk	>75	2015
Busselton	Baudin, cpt 16	Western Australia	An, Mont, Cam, Gu, Ce, 2 controls	120	>85	2015

An Año Nuevo, *Mont* Monterey, *Cam* Cambria, *Gu* Guadalupe, *Ce* Cedros, *TSO* Tallaganda Seed Orchard, *GSO* Gippsland Seed Orchard

Table 3 Details of current base provenance trials (no family identity records) planted in New Zealand, mainland provenances only

Trial identity	Location	#Treatments	Status
AK793	Mangaokewa	16	Current
AK844	Aupouri	16	Terminated
AK845	Waitangi	16	Terminated
AK846	Riverhead	16	Current
AK865	Pouto	16	Terminated
CY533	Balmoral	16	Terminated
CY534	Waimate	16	Terminated
NN349	Golden Downs	16	Terminated
NN501	Tasman	16	Current
NN502	Wairau	16	Current
RO664/12	Kaingaroa	16	Terminated
RO1801	Waimihia	16	Terminated
RO1802	Rotoehu	16	Terminated
RO1803	Ruatoria	16	Terminated
SD425	Dean	16	Terminated
SD426	Longwood	16	Terminated
SD427	Naseby	16	Terminated
SD428/1	Berwick	16	Inactive
SD428/2	Berwick	16	Inactive
WD271	Kaniere	16	Terminated
WD400	Nemona	16	Terminated
WN271	Waitarere	16	Terminated
WN272	Ngaumu	16	Terminated
WN273	Mohaka	16	Terminated

is impacting native stands in California. The need for expanding the genetic base of the breeding populations is mainly argued on the grounds of needs to: (1) maintain genetic diversity for coping with climate change (including growth on drier sites) and conferring resistance pests or diseases; (2) make good any reduction in genetic variance in the current population; and (3) enhance opportunities of adaptation to changing market demands.

The project was carried out under a joint funding scheme by Forest and Wood Products Australia (FWPA), Southern Tree Breeding Association (STBA), Radiata Pine Breeding Company (RPBC), Scion (New Zealand Forest Research Institute Ltd) and Forests New South Wales (FNSW)). The objectives of the project were to:

1. Provide for *P. radiata* gene conservation for the future
2. Infuse new genotypes into breeding populations for increased genetic gain (especially increased growth and wood stiffness) and increase the effective population size.

Conservation

The project has made significant progress in the management, conservation and utilisation of native radiata pine germplasm. A catalogue of existing provenance and genetic conservation trials of *P. radiata* in Australia provides forest managers with a one-stop-shop that lists details of trial establishment, location, owners and collaborators of the trials, and proposed schedule of measures recommended for each trial, including possible prolonging of rotations and collecting seed at time of harvesting the trees. Large amounts of seed from all five provenances were collected from ex situ provenance large block plantings and are being kept in cold storage for long-term future use, while some genetic material is being used to establish second-generation gene-conservation plantings at different sites in Australia and New Zealand to ensure continued evolution and long-term genetic security. However, these populations are likely to diverge from the native stands. The conservation plantings at different locations in Australia and New Zealand offer the most secure gene conservation of all five populations. Pollen collected from multiple trees across all provenances will be used for controlled crosses in order to increase genetic diversity. The strategy should conserve not only existing genetic diversity, but enhance the genetic base needed to adapt to changing environments and market demands.

Utilisation

A comprehensive and large-scale genetic analysis of growth-, tree-form and wood-quality traits derived from the 1978 ‘Eldridge collection’ trials showed that was abundant genetic variation in these populations and provide an opportunity for breeding programs to select superior trees for solid-wood products that will combine superior growth with desirable wood traits (Gapare et al. 2011, 2012a, b). For example, progeny of 10 unrelated parents ranked above control seed lots from the older open-pollinated seed-orchard stock for DBH growth in New Zealand, and would be potential candidates for infusion. This result fitted very well with the RPBC breeding strategy which recommended infusion of 10 unrelated parents from the native population selections from the 1978 ‘Eldridge’ collection (Dungey et al. 2009). The selected parents are now being progeny-tested as part of 500 selections in the breeding-population trials. The 10 parents comprised six unrelated families from Monterey, one from Cambria and one from Año Nuevo, which all ranked above a control seedlot rated at GF14 (represents Growth and Form of older open-pollinated seed orchard stock) (see Fig 2 in Gapare et al. 2011). Two additional families from Monterey ranked just below GF14. The best individual trees from those 10 unrelated families would be potential candidates for infusion in line with the current breeding strategy.

The analysis of data on growth- and wood-quality traits for the Australia trials showed significant differences in wood properties among provenances, families and/or individual trees. This provided an opportunity for breeding programs to select superior trees for solid-wood products that will combine superior growth with desirable wood traits. The results from these analyses, including trial-specific estimates of additive genetic, and error variances, and between-trait correlations, were entered into DATAPLAN® (Powell et al. 2004) for TREEPLAN® runs by STBA to estimate individual-tree breeding values (McRae et al. 2003). The estimated breeding values were used to select elite trees for grafting into seed orchards. A total of 210 elite trees representing all five provenances of *P. radiata* were selected for possible infusion into existing breeding populations in Australia. The scions collected from the elite trees were grafted into the national genetic resource centre arboreta in South Australia for conservation and use in a controlled crossing program in order to increase genetic diversity. The infusion of the selected germplasm would extend the future responses to selection by contributing favourable genes not present in the existing breeding populations. For example, unique genes in the Guadalupe, Cedros and Cambria populations which are currently not in the breeding populations will now be included in the breeding populations and enable genetic adaptation to projected future environments (e.g. adaptation to climate change, pests and disease resistance).

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References

Avise JC (2010) Perspective: conservation genetics enters the genomics era. Conserv Genet 11:665–669

Bannister MH (1959) Artificial selection and *Pinus radiata.* NZ J For 8:69–90

Barrett RL, Mullin LJ (1968) A review of introductions of forest trees in Rhodesia. Research Bulletin No. 1. Rhodesia Forestry Commission

Boardman R, McGuire DO (1997) Responses of *Pinus radiata* provenances near the warmth-dry limit of their potential range in a Mediterranean-type climate. In: RD Burdon RD, Moore JM (eds) IUFRO'97 Genetics of Radiata Pine: proceedings of NZFRI—IUFRO Conference, December 1–4, and Workshop December 5 1997, Rotorua, NZ. New Zealand Forest Research Institute, FRI Bull. No. 203, pp 62–9

Boffa JM, Petri L, Amaral W (2000) In situ conservation, genetic management and sustainable use of tropical forests: IPGRI's research agenda. In: Krishnapillay B et al (eds) Forests and society: the role of research: XXI IUFRO World Congress, 7–12 August 2000 Kuala Lumpur Malaysia, vol 1. Sub-plenary sessions. International Union of Forest Research Organizations, Vienna

Brasier CM (2001) Rapid evolution of introduced plant pathogens via interspecific hybridization. Bioscience 51:123–133

Brown AHD (1989) Core collections: a practical approach to genetic resources management. Genome 31:818–824

Brown AHD, Hardner CM (2000) Sampling the gene pools of forest trees for ex situ conservation. In: Young A, Boshier D, Boyle T (eds) Forest conservation genetics: principles and practice. CSIRO Publishing, Collingwood

Bulman LS, Gadgil PD, Kershaw DJ, Ray JW (2004) Assessment and control of *Dothistroma* needle-blight. New Zealand Forest Research Insitute, Rotorua, New Zealand. For Res Bull 229

Burdon RD (1992) Genetic survey of *Pinus radiata*. 9: general discussion and implications for genetic management. New Zealand J For Sci 22:274–298

Burdon RD (1995) Strategies for exploitation of base populations. In: Potts MM, Borralho NMG, Reid JB, Cromer RN, Tibbits WN, Raymond CA (eds) Eucalypt plantations: improving fiber yield and quality. Proceedings of the CRC-IUFRO conference Hobart, 19–24 Feb. CRC for Temperate Hardwood Forestry, Hobart, pp 146–151

Burdon RD (1997) Genetic diversity for the future: conservation or creation and capture? In: Burdon RD, Moore JM (eds) Proceedings of the NZFRI—IUFRO conference: IUFRO'97 genetics of radiata pine, 1–4 December 1997, Rotorua, NZ. New Zealand Forest Research Institute, FRI Bull. No. 203, pp 237–246

Burdon RD (2010) Conservation and management of potentially resistant germplasm: a key but easily neglected part of a robust biosecurity strategy. NZ J For Sci 40:115–122

Burdon RD, Wilcox PL (2007) Population management: potential impacts of advances in genomics. New For 34:187–206

Burdon RD, Broekhuizen P, Zabkiewicz JA (1997a) Comparison of native population and New Zealand land-race samples of *Pinus radiata* using cortical oleoresin monoterpenes. In: Burdon RD, Moore JM (eds) IUFRO'97 Genetics of radiata pine: proceedings of NZFRI—IUFRO Conference, December 1–4, and Workshop December 5 1997, Rotorua, NZ. New Zealand Forest Research Institute, FRI Bull. No. 203, pp 50–56

Burdon RD, Firth A, Low CB, Miller MA (1997b) Native provenances of *Pinus radiata* in New Zealand: performance and potential. NZ J For Sci 41(4):32–36

Burdon RD, Firth A, Low CB, Miller MA (1998) Multi-site provenance trials of *Pinus radiata* in New Zealand. FAO, Rome, Forest Genetic Resources No. 26, pp 3–8

Burdon RD, Carson MJ, Shelbourne CJA (2008) Achievements in forest tree improvement in Australia and New Zealand 10. *Pinus radiata* in New Zealand. Aust For 71:263–279

Burley J (2001) Climate change can intensify biotic risks. Can J For Res 31:561–565

Camcore (2008) Progress in hybrid testing. Camcore Annual Report 2008. College of natural resources. North Carolina State University, Raleigh, NC, United States. pp 43–44

Camcore (2010) Progress in pine hybrid testing. In: Camcore annual report 2010. Department of Forestry and Environmental Resources, North Carolina State University, Raleigh

Cook DC, Matheson AC (2008) An estimate of the potential economic impact of pine pitch canker in Australia. Aust For 7:107–112

Coutinho TA, Steenkamp ET, Mongwaketsi K, Wilmot M, Wingfield MJ (2007) First outbreak of pitch canker in a South African pine plantation. Aust Plant Pathol 36:256–261

Cumbie WP, Eckert A, Wegrzyn J, Whetten R, Neale D, Goldfarb B (2011) Association genetics of carbon isotope discrimination, height and foliar nitrogen in a natural population of *Pinus taeda* L. Hered 107:106–114. doi:10.1038/hdy.2010.168

Dillon SK, Nolan M, Li W, Bell C, Wu HX, Southerton SG (2010) Allelic variation in cell wall candidate genes affecting solid wood properties in natural populations and land races of *Pinus radiata*. Genetics 185:1477–1487

Dungey HS, Brawner JT, Burger F, Carson M, Henson M, Jefferson P, Matheson AC (2009) A new breeding strategy for *Pinus radiata* in New Zealand and New South Wales. Silvae Genet 58:28–38

Durán A, Gryzenhout M, Slippers B, Ahumada R, Rotella A, Flores F, Wingfield BD, Wingfield MJ (2008) *Phytophthora pinifolia* sp. nov. associated with a serious needle disease of *Pinus radiata* in Chile. Plant Pathol 57:715–727

Dvorak WS (2012) The strategic importance of applied tree conservation programs to the forest industry in South Africa. South For 74(1):1–6

Eckert AJ, van Heerwaarden J, Wegrzyn JL, Nelson CD, Ross-Ibarra J, González-Martínez SC, Neale DB (2010) Patterns of population structure and environmental associations to aridity across the range of loblolly pine (*Pinus taeda* L., Pinaceae). Genetics 185:969–982

Eldridge KG (1978) Refreshing the genetic resources of radiata pine plantations. In: Division of Forest Research: Genetics Section Report Number 7 CSIRO, pp 1–120

Eldridge KG (1997) Genetic resources of radiata pine in New Zealand and Australia. In: Burdon RD, Moore JM (eds) IUFRO ’97 Genetics of Radiata Pine: proceedings of NZFRI – IUFRO Conference, December 1–4, and Workshop December 5 1997, Rotorua, NZ. New Zealand Forest Research Institute, FRI Bull. No. 203, pp 26–41

Ezard THG, Travis JMT (2006) The impact of habitat loss and fragmentation on genetic drift and fixation time. Oikos 114:367–375

Failing L, Gregory R (2003) Ten common mistakes in designing biodiversity indicators for forest policy. J Environ Manag 68:121–132

Falkenhagen E (1991) Provenance variation in *Pinus radiata* at six sites in South Africa. Silvae Genet 40:41–50

FAO (Food and Agriculture Organization) (2006) Global forest resources assessment 2005—progress towards sustainable forest management. FAO, Rome. Available from http://www.fao.org/forestry/index.jsp. Accessed Feb 2007

Forde MB (1964) Variation in natural populations of *Pinus radiata* in California. I. Sampling methods and branch characteristics. NZ J Bot 2:213–236

Frankham R (2010) Where are we in conservation genetics and where do we need to go? Conserv Genet 11:661–663

Frankham R, Briscoe DA, Ballou JD (2002) Introduction to conservation genetics. Cambridge University Press, Cambridge

Gapare WJ, Aitken SN, Ritland CE (2005) Genetic diversity of core and peripheral Sitka spruce (*Picea sitchensis* (Bong.) Carr) populations: implications for conservation of widespread species. Biol Conser 123:113–123

Gapare WJ, Baltunis BS, Ivkovich M, Low CB, Jefferson P, Wu HX (2011) Performance differences among ex situ native-provenance collections of *Pinus radiata* D. Don. 1: potential for infusion into breeding populations in Australia and New Zealand. Tree Genet Genomes 7:409–419

Gapare WJ, Ivkovich M, Dutkowski GW, Spencer DJ, Buxton P, Wu HX (2012a) Genetic parameters and provenance variation of *Pinus radiata* D. Don. 'Eldridge collection' in Australia 2: wood properties. Tree Genet Genomes 8:391–407. doi:10.1007/s11295-011-0449-4

Gapare WJ, Ivkovich M, Dillon SK, Chen F, Evans R, Wu HX (2012b) Genetic parameters and provenance variation of *Pinus radiata* D. Don. 'Eldridge collection' in Australia 1: growth and form traits. Tree Genet Genomes 8:895–910. doi:10.1007/s11295-012-0475-x

Garnier-Géré PH, Ades PK (2001) Environmental surrogates for predicting and conserving adaptive genetic variability in tree species. Conserv Biol 15:1632–1644

Geburek T, Konrad H (2008) Why the conservation of forest genetic resources has not worked. Conser Biol 22:267–274

Geist HJ, Lambin EF (2002) Proximate causes and underlying driving forces of tropical deforestation. Bioscience 53:143–150

González-Martínez SC, Wheeler NC, Ersoz E, Nelson CD, Neale DB (2007) Association genetics in *Pinus taeda* L. I. Wood Prop Traits Genet 175:399–499

González-Martínez SC, Huber D, Ersoz E, Davis JM, Neale DB (2008) Association genetics in *Pinus taeda* L. II. Carbon isotope discrimination. Hered 101:19–26

Goss EM, Cardenas ME, Myers K, Forbes GA, Fry WE, Restrepo S, Grunwald NJ (2011) The plant pathogen *Phytophthora andina* emerged via hybridization of an unknown *Phytophthora* species and the Irish potato famine pathogen *P. infestans*. PLoS ONE 6(9):e24543. doi:10.1371/journal.pone.0024543

Hein L, Gatzweiler F (2006) The economic value of coffee (*Coffea arabica*) genetic resources. Ecol Econom 60:176–185

Hodge GR, Dvorak WS (2012) Growth potential and genetic parameters of four Mesoamerican pines planted in the Southern Hemisphere. South For 74:27–49

Hood JV, Libby WJ (1980) A clonal study of intrapsecific variability in radiata pine. I. cold and animal damage. Aust For Res 10:9–20

Hu XS, Li BL (2002) Linking evolutionary quantitative genetics to the conservation of genetic resources in natural forest populations. Silvae Genet 51:177–183

Ivković M, Gapare WJ, Wharton T, Jovanovic T, Elms S, McRae TA, Wu HX (2010) Incorporating risk into economic breeding objective for radiata pine in Australia. Aust For 73:265–278

Jayawichrama KJS, Balocchi C (1993) Growth and form of provenances of *Pinus radiata* in Chile. Aust For 56:172–178

Johnson IG, Ades PK, Eldridge KG (1997) Growth of natural Californian provenances of *Pinus radiata* in New South Wales, Australia. NZ J For Sci 27:23–38

Johnson IG, Cotterill IM, Raymond CA, Henson M (2008) Half a century of radiata pine improvement in NSW. NZ J For Sci 52:7–13

Kanzler A, Payn K, Nel A (2012) Performance of two *Pinus patula* hybrids in southern Africa. South For 74:19–25

Karhu A, Hurme P, Karjalainen M, Karvonen P, Karkkainen K, Neale D, Savolainen O (1996) Do molecular markers reflect patterns of differentiation in adaptive traits in conifers? Theor Appl Genet 93:215–221

Kjaer ED, Amaral W, Yanchuk AD and Graudal L. (2004) Strategies for conservation of forest genetic resources. In: Forest genetic resources: conservation and management, vol 1. Overview, concepts and some systematic approaches. IPGRI, Rome, Italy, pp 4–24

Koshy MP, Namkoong G, Kageyama P, Stella A, Gandara F and Neves do Amaral WA (2002) Decision-making strategies for conservation and use of forest genetic resources. In Engels JMM, Ramantha Rao V, Brown AHD, Jackson MT (eds) *Managing plant genetic diversity*. International Plant Genetic Resources Institute, Rome, and CABI, Wallingford

Laarman JG, Dvorak WS (1988) Financial feasibility of participating in an international seed cooperative for tropical pines. New For 2:161–172

Ledig TF, Vargas-Hernández JJ, Johnsen KH (1998) The conservation of forest genetic resources. J For 96:32–42

Leibing C, van Zonneveld M, Jarvis A, Dvorak WS (2009) Adaptation of tropical and subtropical pine plantation forestry to climate change: realignment of *Pinus patula* and *Pinus tecunumanii* genotypes to 2020 planting site climates. Scan J For Res 24:483–493

Leibing C, Signer J, van Zonneveld M, Jarvis A, Dvorak WS (2013) Selection of provenances to adapt tropical pine forestry to climate change on the basis of climate analogs. Forests 4:155–178. doi:10.3390/f4010155

Leimu R, Mutikainen P, Koricheva J, Fischer M (2006) How general are positive relationships between plant population size, fitness, and genetic variation? J Ecol 94:942–952

Matziris DI (1995) Provenance variation of *Pinus radiata* in Greece. Silvae Genet 44:88–95

McKenney D, Pedlar J, O'Neill G (2009) Climate change and forest seed zones: past trends, future prospects and challenges to ponder. For Chron 85:258–266

McNeely JA, Vorhies F (2000) Economics and conserving forest genetic diversity. In: Young A, Boshier D, Boyle T (eds) Forest conservation genetics—principles and practice. CSIRO Publishing, Collinwood, Vic, Australia pp 253–262

McRae TA, Apiolaza LA, Dutkowski GW, Kerr RJ, Pilbeam DJ, Powell MB, Tier B (2003) TREEPLAN®—a genetic evaluation system for forest trees. In: proceedings 27th Biennial Southern Forest Tree Improvement Conference Stillwater, Oklahoma, USA 24–27 June 2003

Merilä J, Crnokrak P (2001) Comparison of genetic differentiation at marker loci and quantitative traits. J Evol Bio 14:892–903

Mitchell RG, Steenkamp ET, Coutinho TA, Wingfield MJ (2011) The pitch canker fungus: implications for South African forestry. South For 73:1–13

Moran G, Bell C (1987) The origin and genetic diversity of *Pinus radiata* in Australia. Theor Appl Genet 73:616–622

Namroud MC, Beaulieu J, Juge N, Laroche J, Bousquet J (2008) Scanning the genome for gene single nucleotide polymorphisms involved in adaptive population differentiation in white spruce. Mol Ecol 17:3599–3613

Neale DB, Savolainen O (2004) Association genetics of complex traits in conifers. Trends Plant Sci 9:325–330

Nel A, Kanzler A, Dvorak W (2006) Development of a commercial breeding program for *Pinus tecunumanii* in South Africa. In: Isik, F I (ed) proceedings of the IUFRO Division 2 joint conference: low input breeding and conservation of forest genetic resources: Antalya, 9–13 October 2006, pp 158–161

Nyoka IB, Gapare WJ, Mangezi T, Mhongwe J, Maruzane D, Barnes RD (1996) The Forest Genetics Programme in Zimbabwe Part1. plan of work for 1996/97 Zimbabwe Forest Research Centre, Harare, 198 pp

Oberbauer T (2006) La Vegetacion de isla Guadalupe.Entonces Y Ahora. Gaceta Ecologica 081. Instituto Nacional de Ecologia. Distrito Federal, Mexico pp 47–58

Otto S, Whitlock M (1997) The probability of fixation in populations of changing size. Genetics 146:723–733

Powell MB, McRae TA, Wu HX, Dutkowski GW, Pilbeam DJ (2004) Breeding strategy for *Pinus radiata* in Australia. 2004 IUFRO Joint Conference of Division 2: Forest Genetics and Tree Breeding in the Age of Genomics: progress and Future. Charleston, South Carolina, USA, 1–5 November, 2004, pp 308–18

Raymond CA, Henson M (2009) Genetic variation within the native provenances of *Pinus radiata* D. Don. 1. Growth and form to age 26 years. Silvae Genet 58:242–252

Reed DH, Frankham R (2003) Correlation between fitness and genetic diversity. Conserv Biol 17:230–237

Reeser PW, Sutton W, Hansen EM (2013) *Phytophthora pluvialis*, a new species from mixed tanoak-Douglas-fir forests of western Oregon, U.S.A. North American Fungi 8:1–8

Rogers DL (2002) In situ genetic conservation of Monterey pine (*Pinus radiata* D. Don): information and recommendations genetic resources conservation program, report no 26. University of California, Davis, CA

Rogers DL (2004) In situ genetic conservation of a naturally restricted and commercially widespread species, *Pinus radiata*. For Ecol Manag 197:311–322

Roux J (2007) Further outbreaks of pitch canker in South Africa. http://www.fabinet.up.ac.za/tpcp/pitch_canker_mature_trees

Scherm H, Coakley SM (2003) Plant pathogens in a changing world. Aust Plant Pathol 32:157–165

Schmidt RA (1998) Fusiform rust disease of southern pines: biology, ecology, and management. Bulletin (Tech.) no. 903. University of Florida, Agricultural Experiment Station, Institute of Food and Agricultural Sciences, Gainesville

Shumeta Z, Urgessa K, Kebebeew Z (2012) Analysis of market chains of forest coffee in Southwest Ethiopia. Acad J Plant Sci 5:28–39

Spittlehouse DL, Stewart RG (2003) Adaptation to climate change in forest management. BC J Ecosyst Manag 4:1–11

St. Clair JB, Howe GT (2011) Strategies for conserving forest genetic resources in the face of climate change. Turk J Bot 35:403–409

Toplu F, Tunctaner K, Tulukcu M (1987) Investigation on growth and resistance to European shoot moth *(Evetria buoliana* Schiff.) of radiata pine (*Pinus radiata* D. Don) origins in Kocaeli Peninsula. Poplar and Fast-growing Exotic Forest Trees Research Institute, Turkey, Annual Bulletin No 23:13–27

van Zonneveld MJ, Jarvis A, Dvorak W, Lema G, Leibing C (2009) Climate change impact predictions on *Pinus patula* and *Pinus tecunumanii* populations in Mexico and Central America. For Ecol Manag 257:1566–1576

Wang T, O'Neill GA, Aitken SN (2010) Integrating environmental and genetic effects to predict responses of tree populations to climate. Ecol Appl 20:153–163

White TL (2004) Breeding theory and genetic testing. In: Burley J, Evans J, Youngquist JA (eds) Encyclopedia of forest sciences. Elsevier, New York, pp 1551–1561

Wu HX, Eldridge KG, Matheson AC, Powell MB, McRae TA (2007) Achievements in forest tree improvement in Australia and New Zealand: successful introduction and breeding of radiata pine to Australia. Aust For 70:215–225

Yanchuk AD (2001) A quantitative framework for breeding and conservation of forest tree genetic resources in British Columbia. Can J For Res 31:566–576