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The strategic importance of applied tree conservation programs to the forest industry in South Africa

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Because of anticipated adverse climatic change and resulting increases in disease and insect attacks in forest plantations in the future, forest industries must maintain broad genetic bases for adaptability and pest resistance. Since the early 1980s, the South African forest industry has obtained genetic material of 25 pine and eucalypt species that represent more than 4 200 trees from 260 natural populations around the world through its participation in Camcore (International Tree Breeding and Conservation Program) at North Carolina State University, USA. This combined genetic testing and conservation program has identified new productive pine species, such as *P. tecunumanii* and *P. maximinoi*, that grow well and are resistant in the seedling stage to the pitch canker fungus (*Fusarium circinatum*). Because of the industry's foresight to assemble genetic material and test alternate species over the last three decades, it was well prepared to immediately develop more-resistant pine hybrids such as *P. patula* × *P. tecunumanii* when the pitch canker situation became problematic. The South African forest industry has collectively worked together to established special 20–40 ha conservation parks across the country to hold and protect the original genetic material collected in Central America, Mexico and South-east Asia. Species are conserved in the parks at the population level and are represented by a minimum of 10 open-pollinated families, five trees per family across two sites. The design is based on maintaining an effective population size of approximately 30 with the goal to capture alleles at high frequencies as well as to include a number of rare alleles in the *ex situ* plantings. The overlying goal is to maintain well-adapted genetic material for future deployment.

Keywords: adaptability, *ex situ* conservation, climate change

Introduction

For forest companies to remain competitive and make profits, they must have a consistent supply of high-quality wood. Commercial plantation species must exhibit good productivity over a number of different environments, must be relatively easy to breed for improvement and to manage silviculturally, must have good disease resistance, and must produce a type of wood that is demanded by the market. Forestry research organisations go to great effort to collect seeds from many geographic regions characterised by different climatic and edaphic factors in order to establish broad genetic bases to ensure that commercial plantations possess sufficient adaptability.

For the last three decades, researchers and scientists have urged that the forest community be more proactive in the development of sound gene conservation programs to promote sustainable forestry, which includes maintaining and protecting genetic base populations. Almost everyone agrees that 'conservation is good', but the dialogue often stagnates on issues such as strategy and approaches (*ex situ* vs *in situ*), 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. Despite the importance of conservation to maintain wood supplies in changing environments and markets, talks on forest conservation at international tree breeding and biotechnology conferences have almost become perfunctory exercises, as though tradition dictates the topic be mentioned at least once before getting on with what some consider more scientifically interesting topics.

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 a source of new, better-adapted, genetic material. In Chile, a new disease, *Phytophthora pinifolia* (see Durán et al. 2008), has claimed more than 60 000 ha of prime *Pinus radiata* plantations in the country. *Phytophthora* spores are disseminated by air and, presumably, the severity of the disease will be cyclic in nature dependent on spore load and local weather conditions. In South Africa, pitch canker (*Fusarium circinatum*), a chronic problem for the last 18 years in *P. patula* and *P. radiata* nurseries in the country, has now escaped to plantation trees in the Cape region (Coutinho et al. 2007). The potential seriousness of the disease to plantations is still being assessed but the problem has reduced grafting success in seed orchards and has limited rooted cutting programs of *P. patula* in the KwaZulu-Natal and Mpumalanga provinces.

This paper provides a case study of how the *ex situ* conservation and testing program of Mexican pines has developed over the last three decades in South Africa and discusses its importance to the local forest industry. A brief section is provided on the genetic basis of tree conservation. A summary of the pine and eucalypt introductions made by Camcore (International Tree Breeding and Conservation Program), North Carolina State University, USA, into South Africa is presented and the challenges facing future germplasm acquisitions are enumerated. The author suggests that sound conservation approaches for maintenance of base populations are closely linked to the level of economic returns in tree improvement programs because the more natural variation available, the greater the genetic gains through breeding, selection and testing. This translates to higher profits at the mill. Evidence is provided that demonstrates that well-planned tree conservation programs give industry the flexibility to change wood supply and quality rapidly if economic markets shift or climate and environment alters species choice.

Genetic basis for tree conservation

Even though we often speak of 'gene conservation', the science deals more with capturing alleles or allele conservation. Alleles are different forms of the same gene on the chromosome. Examples include brown and blue eye color in humans and black, chocolate, or yellow fur colour of Labrador retrievers. Alleles come in different frequencies. Major alleles are found at high frequency in almost all tree populations. Rare alleles are found at frequencies of 1% or less in tree populations, and private or unique alleles are, as their name implies, are found in only one population. Alleles at high frequency are difficult to lose in a well-structured breeding program; for alleles held at low frequency, only the size of the breeding population is the crucial factor, not the specific mating design (Namkoong 1997).

The crux of forest gene conservation lies in the importance of rare alleles (Lindgren and Gregorius 1976). The most cogent argument is that rare alleles contribute little to the overall fitness value, arise largely as unfavourable mutations and may be evolutionary relics (Brown 1989). However, 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 devastating 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 (H Amerson, North Carolina State University, USA, pers. comm., 2009). 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.

We tend to forget sometimes that there are two measures of genetic diversity; molecular diversity quantified in assessment of DNA, and metric diversity quantified by the response of trees to site factors influencing their survival (adaptability) and growth differences in field trials and plantations. Reduced molecular genetic diversity suggested by DNA assessments does not necessarily translate into reduced adaptability (Lambeth and McCullough 1997). In all of the molecular studies conducted by Camcore on tropical pines over the last 20 years, only one species, *P. maximinoi,* exhibited significant correlation between field performance and molecular marker results (Dvorak et al. 2002). If adaptability is the key concern, Lambeth and McCullough (1997) suggest that the ability of a tree to survive and produce useful wood should be emphasised, not the results from a molecular genetic diversity analysis. In line with this thinking, Camcore sampled 60 populations of *Tsuga canadiensis* (eastern hemlock) in the southern and eastern USA to capture adaptability differences among regions even though molecular analysis suggested low levels of population diversity exist across most of the species range (Potter et al. 2008). Generally, in the most successful tree conservation programs, molecular data are used to fine-tune provenance/population selection based on the results of metric data (productivity and adaptability), not the reverse (Dvorak et al. 2008).

Camcore introductions

The South African forest industry has been working with Camcore for the past 28 years. Seven organisations in South Africa now belong to Camcore: Komatiland Forests, Mondi, Sappi, Merensky, MTO, PG Bison and York Timbers. Since 1983, Camcore has provided the South African membership with research amounts of seeds from 25 pine and eucalypt species representing 261 provenances and 4 262 family seedlots (Table 1). The collections sample the entire natural geographic range of most of the species. The seeds are planted in genetic (provenance/progeny) trials and field conservation banks by the membership throughout the eastern and southern part of South Africa. The Camcore introductions of the pines do not represent the first or only effort to bring tree genetic material into South Africa but certainly represents the most long-standing and comprehensive attempt (also see Loock 1950, Poynton 1977).

In most cases, an individual Camcore organisation is given eight to 16 families per provenance for testing. The family pedigree is kept separate in both testing and conservation plantings. We estimate that the sampling schemes used by Camcore when making collections in natural stands in places such as Central America capture most alleles at frequencies of 5% or greater in that provenance (Dvorak et al. 1999). What is not planted by one organisation in the field is planted by others. The goal is not only to bring new, relatively untested species such as *P. cooperi*, *P. greggii*, and *P. jaliscana* into the country, but also to expand the genetic base of well-known existing commercial species such as *P. patula*. Some of the base populations established by Camcore across its membership include hundreds of thousands of trees.

Genetic diversity as measured by adaptability

Provenance differences for growth between the worst and best provenances are as much as 30% in the pines and 40% in eucalypts (see Hodge and Dvorak 2012). 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

Table 1: Eucalypt and pine species, provenances and families provided to South African Camcore members over the past 27 years

Species	No. of provenances	No. of families
Eucalyptus dorrigoensis	5	38
Eucalyptus pellita	6	99
Eucalyptus urophylla	34	594
Pinus arizonica	3	48
Pinus ayacahuite	12	115
Pinus caribaea	12	106
Pinus chiapensis	9	150
Pinus cooperi	3	86
Pinus durangensis	3	58
Pinus englemanii	3	47
Pinus greggii	16	285
Pinus hartwegii	1	37
Pinus herrerae	10	138
Pinus jaliscana	9	65
Pinus leiophylla	11	188
Pinus maximartinezii	1	59
Pinus maximinoi	22	335
Pinus muricata	2	58
Pinus oocarpa	13	156
Pinus patula	22	471
Pinus pringlei	6	95
Pinus pseudostrobus	12	135
Pinus radiata	3	84
Pinus tecunumanii	40	734
Pinus teocote	3	81
25 Species	261	4 262

South Africa (Dvorak et al. 2007a, 2007b). The highland sources of *P. tecunumanii* from Chiapas, Mexico, are about 3–4 °C more cold hardy than other high-elevation sources from Guatemala (Hodge et al. 2012). Significant provenance variation in pitch canker resistance exists in seedling studies for *P. patula*, high-elevation populations of *P. tecunumanii* and *P. leiophylla*. The approach to collecting seed samples from a number of different geographic locations seems well justified to improve the overall adaptability of any species.

Genetic diversity as measured by molecular markers

Molecular analyses indicate that the Camcore species introduced into South Africa have highly variable levels of genetic diversity (Table 2). Some species such as *P. caribaea* var. *hondurensis* have very high levels of molecular diversity, whereas other species such as *P. greggii* var. *greggii* have very low levels. Knowledge about levels of genetic diversity is important because it affects the sampling strategy in natural stands. The lower the diversity, the greater the number of trees that need to be sampled to capture alleles at a certain frequency (Dvorak et al. 1999). Eventually, functional genomic studies will start to decipher the roles of genes/alleles that currently provide us with our genetic diversity estimates (Burdon and Wilcox 2007), and as we learn more about their expression, correlations between molecular and metric assessments of diversity will improve.

Changes that have affected research seed introductions in the last 10 years

Building up genetic bases of a useful size common in international testing and *ex situ* conservation programs requires much work and consistent funding and is best done using a cooperative approach. There have been many changes over the last 10 years that influence the success of forest tree conservation. Some of these changes are positive, whereas others are negative. These include:

- A growing hesitancy by individual countries to allow their tree genetic material to be used by others.
- More strict phytosanitary rules and regulations (which in principle are good) that are often poorly defined and increase paper work and cost of collections to the point of discouraging anyone to attempt to legally exchange research amounts of seeds. Wait times can be two to four years to receive seeds sent across international borders for some countries after collections are made.
- A realisation that for *ex situ* conservation plantings to succeed, they must hold some economic or aesthetic importance to the receptor institution.
- For some species, *ex situ* conservation approaches have changed from being 'complimentary' to *in situ* efforts but often serve as the only viable alternative for species and population protection.
- Disease and insect attacks are on the increase and threaten entire commercial forestry operations in exotic environments (this highlights the importance of alternative species and populations).

Regarding the last point, to counteract the effects of the *Fusarium circinatum* disease problem, researchers in South Africa are working to develop pine hybrid programs that combine the good growth of *P. patula* with the *Fusarium* resistance of pine species from Central America such as *Pinus tecunumanii* and *P. oocarpa* (see Camcore 2010, Kanzler et al. 2012). One of the main reasons that South Africa is in a position to have alternate pine species available for hybrid crosses is that both the government and private sector have participated in the Camcore program, and have tested and protected a number of alternate species and populations for nearly three decades. Because of this, the *P. patula* × *P. tecunumanii* hybrid is being planted commercially in some areas of South Africa only after a few years since the *Fusarium* problem became evident. Another commercially important pine species in South Africa, *P. radiata*, is also very susceptible to the pitch canker fungus. The crossability of *P. radiata* with other pine partners is more problematic because of natural reproductive barriers and possible solutions are being studied at Stellenbosch University, South Africa.

Generally, it will become increasingly difficult for countries to obtain tree genetic material of different tree species from international donors in the future for reasons stated above. Forestry organisations will be forced to use the genetic material that they can access presently within the country, and the 'winners' will be those who have a large array of populations to choose from to make advances in productivity through tree breeding and silviculture.

The South African conservation parks

Driven to better protect the Camcore genetic material collected over the last 28 years, especially after important plantings were lost in the large fires of 2003 and 2007,

Table 2: Levels of molecular genetic diversity found in several species introduced into South Africa

Species	Maximum level of tree improvement	Genetic diversity assessment: marker type/results
Pinus caribaea	Third generation	Electrophoresis/high diversity (Dvorak et al. 2005)
Pinus greggii	First generation	Electrophoresis/moderate to very low diversity (Ramírez-Herrera et al. 1997)
Pinus maximinoi	Beginning second generation	Electrophoresis and RAPD/average to below average diversity (Dvorak et al. 2002)
Pinus oocarpa	First generation	Microsatellites/average to above average (Dvorak et al. 2009)
Pinus patula	Third generation	Electrophoresis and microsatellites/average diversity (Butterfield 1990, Dvorak et al. 2009)
Pinus tecunumanii	Beginning second generation	Electrophoresis,RAPD and microsatellite/average to above average (Dvorak et al. 1999, 2009, Furman and Dvorak 2005)
Eucalyptus urophylla	Second generation	Microsatellite, chloroplast DNA/average to low genetic diversity (Payn et al. 2007, 2008)

the South African Camcore members agreed to develop 'conservation parks' throughout forested regions in the country (Mitchell 2010). The conservation parks are tracts of land 20–40 ha in size that will be protected and will conserve the species and populations of trees originally collected in Central America, Mexico and Indonesia *(Eucalyptus urophylla*). The decision to conserve the Camcore material at the provenance level rather than just the species level demonstrates that the industry recognises the importance of 'maintaining' natural variation characterised by individual seed sources.

Initially, six conservation parks were established and included 18 pine and one eucalypt species (Table 3). Each population is represented by at least 10 open-pollinated families and five trees per family across two sites. The numbers of families and trees per family were based on the need to have an effective population size of approximately 30, which was thought to be large enough to conserve most alleles at a frequency of 5% or greater in that provenance. The conservation parks are being established by grafting material from the original Camcore introductions still in field tests in South Africa or planting seeds from the original introduction that are still in cold storage at Camcore, North Carolina State University.

In addition to holding the original base populations for future use, the conservation parks can serve as clonal archives for controlled breeding, and arboreta for those interested in learning more about the exotic species that form the basis of the South African forestry industry.

Future opportunities and challenges

As mentioned previously, the recent renewed interest in conservation has been brought about by the increase of diseases and pests in forest plantations and the need to have alternate species available in case of problems. The South Africa forest industry is in a strong position with respect to alternate species at the present time, but as the fires of 2003 and 2007 demonstrated, three decades of dedicated testing and conservation work can be lost in one weekend. There must be program continuity to ensure that these base populations are protected for the long term and the support needs to come from both industry and the public. The conservation parks must remain 'protected' even when forest companies are bought and sold.

In the future, more eucalypt species will be added to the conservation parks as Camcore collections of these increase in wild stands. For example, Camcore recently completed a seed collection of *E. pellita* in eastern Indonesia. It is also working with local governmental organisations and private seed collectors in Australia to sample populations of eucalypt species with very restricted geographic ranges.

It is not clear if the increase of forest disease and pest problems are related to global climatic changes. However, it is anticipated that temperature changes will gradually alter what forest species are planted by the South African industry in the future. As an example, Leibing et al. (2009) predicted that most of the areas currently being planted to *P. patula* in South Africa would need to be replaced by *P. tecunumanii* as climates warm.

Interestingly, van Zonnefeld et al. (2009) using the same data set found that pine species such as *P. patula* and *P.tecunumanii* exhibited a broader range of climatic adaptability as an exotic than one would conclude by simply looking at where the species occur in their natural ranges in Mexico and Central America. The 'take home' message is that both pines and eucalypts exhibit much natural variation for adaptability but that alternate species must always be available in the case problems arise that adversely affect the plantation establishment of commercial species.

For the economic value of these conservation efforts to be realised, many of the original plantings of these exotic species need to go through at least one generation of genetic improvement to see their true worth. This is why the physical effort of establishing conservation parks must be linked to tree improvement, development by the industry and profits at the mill. What would be the lost revenue to the South African forestry industry if researchers did not have a *P. patula* × *P. tecunumanii* hybrid to rely upon?

The greatest challenge that we have in *ex situ* conservation (in addition to understanding the biological and economic worth of rare alleles), 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. Sometime in the future, alleles captured in the conservation parks are going to need to be inserted into mainline breeding programs, or why conserve them in the first place? Currently, this is one of the major challenges in *ex situ* conservation programs of *P. radiata* in New Zealand and Australia. Old unimproved conservation plantings of original collections made in California and Mexico in the late 1970s are near harvest age, whereas local breeding

Table 3: Composition of Camcore conservation parks established in South Africa

Company[1]	KLF	Sappi	Mondi	Merensky	PG Bison	MTO
Area	Eastern Mpumalanga	Zululand	KwaZulu-Natal Midlands	Southern KwaZulu-Natal	Northern Eastern Cape	Western Cape
Location	Brooklands nursery	Teza nursery	Mountain Home	Weza	Glen Cullen	Jonkershoek
Climate	Warm temperate	Tropical	Subtemperate to temperate	Subtemperate	Temperate	Mediterranean
Elevation (m)	1 100	20	1 100	900	1 350	100
No. of species and varieties conserved	7	6	7	6	6	7

[1] York Timbers, Camcore's most recent member in South Africa, is in the process of establishing its conservation park

programs are in their third cycle of improvement (W Gapare, CSIRO, Australia, pers. comm., 2010).

How we conduct conservation in the future will also change as we learn more about the function of specific genes. The *Populus* genome has already been sequenced (Tuskan et al. 2006) and great progress is being made on eucalypts (Myburg et al. 2008) and pines (Kovach et al. 2010). Our understanding of what a gene or allele actually represents might be different in the future as we learn more about trait expression.

Finally, one simple but important recent activity of the Camcore membership is the reintroduction of genetic material back into the areas where it was originally collected (López Restrepo and López Upton 2007). These 'reintroduction' plantings are especially important because many of the Central American and Mexican pine populations have been destroyed or genetically high-graded since the original collections occurred in the early 1980s. As an example, *Pinus maximinoi* seeds collected in Camcore field trials in South Africa and Colombia have been given to the Guatemalan government and grown in field trials. More work is needed to determine how 'reintroduced' material differs from native material in molecular genetic diversity, adaptability, productivity, pest resistance, and cold and drought hardiness.

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