

# Breeding southern US and Mexican pines for increased value in a changing world

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## Introduction

Pine tree improvement and breeding programs have been ongoing in the southern US and elsewhere in the tropics and subtropics since the 1950s and 1960s. Efforts have focused primarily on improving the performance of *Pinus taeda* and *P. elliottii* in the southern US and Latin America, *P. radiata* in the Pacific Rim, Mediterranean regions of Western Europe, and the western and southern Cape of South Africa and *P. patula* in southern Africa and the highlands of western South America (Mullin et al. 2011). In the last three decades, great efforts also have been made by forest industry to systematically test the myriad of pine species (and populations) native to Central America and Mexico (e.g., *P. chiapensis*, *P. greggii*, *P. herrerae*, *P. tecunumanii* and *P. maximinoi*) throughout the tropics and subtropics (Hodge and Dvorak 2012). The hope is that these lesser-known species will someday serve as alternatives to commercially accepted plantation species if current plantings are attacked by insects or diseases, or prove to be maladapted to global climatic fluctuations. Applied and practical conservation programs to protect base populations of genetic material are, therefore, critical for long term success of breeding programs (Dvorak 2012).

Since the 1950s, a number of large-scale tree improvement programs have gone through 3–5 cycles of breeding. There have been tremendous advances in breeding strategy, mating designs, field testing designs, data analysis techniques, seed orchard management, and vegetative propagation (White et al. 2014). These advances have resulted in more efficient breeding, more precise selection of outstanding genotypes, and faster delivery of genetic gain into operational plantations. However, technology continues to change, and tree breeding approaches in the future might be vastly different than the traditional methods of selection and progeny testing that characterized programs of the last six decades. Improvement in DNA-based technologies and lower costs for molecular markers have

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spawned interest in using “genomic selection” (Grattapaglia and Resende 2011) and “breeding without breeding” techniques (El-Kassaby and Lstiburek 2009) as tools to improve genetic gains per unit time. The question remains whether these tools will work cost-effectively, and if they do, to what extent might they displace traditional approaches to breeding. Some organizations around the world have had success using rooted cuttings as the plantation deployment option for pure species such as *P. taeda* and *P. radiata* (e.g., de Alcantara et al. 2007; Menzies et al. 2001). This has contributed to a growing interest in the potential of pine hybrids, as vegetative propagation would almost certainly be needed to multiply scarce hybrid seed. The commercial development of the *P. patula* × *P. tecumanii* hybrid in South Africa to improve *Fusarium circinatum* (Pitch canker) resistance of susceptible *P. patula* has been a major success story in plantation forestry (Mitchell 2012; Mitchell et al. 2013). Hybrids of US southern pines with Mexican pines (e.g., Camcore 2012, 2013) may offer opportunities to improve wood properties and create “varieties” that are better adapted to specific exotic environment, or more broadly adapted to variable climatic conditions.

What traits we breed for might also be changing. Traditionally, most breeding programs prioritize improving productivity (i.e., volume growth), with lesser emphasis on stem form and wood density. These traits will continue to be of importance, but in the future, breeding or selecting for traits like pulp yield, specific fiber properties, drought and cold tolerance, or resistance to disease problems might be more common.

Finally, the fiber composition of products at the mill is changing. Most existing pine programs in the tropics and subtropics are gradually switching to growing short-rotation eucalypts for better economic returns. Most new plantation programs in the southern hemisphere are exclusively planting eucalypts rather than pines in areas where the climate and soils are suitable for both genera. Mills that operated on 70 % pine fiber a decade ago are now using predominantly eucalypt fiber. All tree breeders must continue to find ways to reduce the length of breeding cycles, improve efficiencies of breeding and testing, and concentrate on improving (new) traits that will become important to the mill over the next several decades; perhaps the challenge for pine breeders is even greater.

## Background and the objectives of conference

The international conference, “Breeding for Value in a Changing World” was organized by Camcore (International Tree Breeding and Conservation Program), NC State University and was sponsored by IUFRO Working Group 2.02.20 on Breeding and Genetic Resources of the southern US and Mexican pines (including *Pinus radiata*). The conference focused primarily on the fast-growing pine species used in plantation forestry around the world. The current working group represents a joint assembly of past working groups on Breeding Tropical Trees S2.08.01, Breeding Theory S2.04.02, Progeny Testing S2.04.03 and Seed Orchards S2.03.03. The conference was held in Jacksonville, Florida February 4–7, 2013.

The main objective of the conference was to define the “state of the art” in pine breeding practices being used by the forestry private sector either independently or through industry sponsored forestry cooperatives. A second objective of the conference was to bring together the leaders in the tree breeding profession from countries like Australia, Brazil, Chile, New Zealand, the US, and South Africa to promote discussion on the direction of future collaborative research and development. A total of 90 participants from 14 countries attended the conference, and there were 10 invited papers and 35 voluntary papers presented covering nine broad thematic areas, including breeding strategies,

genomic selection, wood properties, hybrid breeding, somatic embryogenesis, clonal forestry, reproductive biology, gene conservation, climate change, and disease resistance.

### Brief overview of special issue content

This Special Issue contains a total of eight original review articles covering a diverse but interconnected range of topics that will have impact on pine breeding over the next decade. Below is a brief overview of these papers, highlighting some of the important points in each.

Tim White began the conference with a review of the notable accomplishments of tree breeding programs worldwide since the 1950s, and then discussed a number of drivers of global change that present both challenges and opportunities to tree breeders for the future (White et al. 2014). Some factors include a growing world population and a potential conversion of forest land to crop production, globalization of markets, rapid movement of forest diseases and other pests, climate change and technology development. Within the forest industry, land ownership patterns are changing, investment horizons are contracting, and the range of wood products in the marketplace is expanding. All of these uncertainties may impact breeding objectives when considering the time scales required for tree breeding and plantation growth. White et al. suggest a strategy primarily focused on becoming more efficient at improving volume growth per hectare, which incorporates growth rate, disease and pest resistance, environmental plasticity, and stand-level genotype behavior (e.g., the competition vs. crop ideotype, Dickman et al. 1994). The idea is that this approach is “robust for value”, i.e., it will almost certainly produce net benefit for landholders even over a long investment horizon and with very uncertain future biological, climatic and economic conditions.

Washington Gapare spoke about the continuing importance of gene conservation efforts to advanced generation breeding (Gapare 2014). Access to forest genetic resources in native environments is becoming more and more restricted, and importation of pollen and seed is likewise becoming more difficult. Yet maintenance of genetic diversity in a breeding population, or at least in a conservation population so that, in the future, valuable genes might be infused into a breeding population, is likely to be critical in the face of changing climates, increased disease risk, and changing economic markets. Even for commercially important species, gene conservation is not an area of endeavor which attracts large amounts of financial support. For many years, tree breeding has been accomplished in collaborative or cooperative programs involving government, universities and forest industry (White et al. 2014); Gapare (2014) suggests that forest gene conservation must also be collaborative, and deliberately undertaken with the involvement of the whole forestry community.

Danilo Fernando reviewed what we know about pine reproductive biology (Fernando 2014), an important topic for efficient operational seed production, and perhaps even more important for optimizing breeding of pure species and hybrids. The reproductive cycle of the pines is complex, and extends over multiple years. It has been relatively well studied in some temperate species (e.g., *Pinus taeda*, *P. contorta*, and *P. monticola*), and the effects of climate, temperature and humidity on cone maturation, pollen release, and fertilization are reasonably well understood. In contrast, the reproductive biology of sub-tropical pines has not been thoroughly examined. The warmer, more uniform climates experienced by many sub-tropical pines may lead to less uniform seed cone and pollen cone maturation.

What is the impact of this variability on genetic architecture in native populations, and on seed production when these species are planted as exotics?

Gerald Pullman reviewed the current state of the art regarding pine somatic embryogenesis (Pullman and Bucalo 2014). Somatic embryogenesis (SE) is the critical first step necessary if clonal forestry of pine is ever to become a reality. SE with pines has been an area of research for some 30 years, and much of the research has focused on the two most important commercial species, *P. taeda* and *P. radiata*. For these two species, genetically-tested clonal varieties are available in the marketplace. For other species, developing SE protocols will be both time-consuming and costly, developed primarily by painstaking trial and error. Pullman and Bucalo (2014) suggest some approaches that may make this process more efficient, utilizing careful examination of the nutritional and hormonal status of tissues in both natural embryogenesis and somatic embryogenesis, and the use of gene expression studies to modify SE protocols and confirm that natural and SE embryos are following the same path of development.

Fikret Isik provided a review of genomic selection and pedigree reconstruction, and discussed the potential use of these technologies in forest tree breeding (Isik 2014). Genomic selection is being used operationally in animal breeding, and for tree breeders, the major advantage of this approach is the potential to reduce the time required to complete the testing phase of the breeding cycle, which is perhaps the major obstacle facing tree breeders today. Genomic selection takes advantage of advances in molecular marker and statistical computing to move us closer to being able to evaluate genotypes directly, rather than inferring genetic quality from observations of phenotypes. This might allow breeders to complete two or three cycles of breeding for each round of traditional progeny testing. Many questions and technical challenges remain, but this is an exciting area of research.

Steve McNulty discussed climate change and the challenge it offers to tree breeders (McNulty et al. 2014). The authors warn us to expect increasing climatic variability, that is, more frequent extreme events of precipitation, drought, heat, and cold. They observe that chronically stressed trees (i.e., those growing on sub-optimal, challenging sites) appear to survive extreme events better than non-chronically stressed trees (those growing on optimal sites that promote fast growth). This may be true both at the tree and stand level, and at the species level. This raises some interesting questions for the tree breeder. How much of this phenomenon reflects the individual tree's ability to acclimate to changing environmental conditions, and how much is due to selection and genetic variation? Is it necessary to change our testing and breeding strategies to identify genotypes that are more resilient to extreme events? If so, how would we do it? How do we value genetic diversity, among and within-species, knowing that increased climatic variability is coming?

Arnulf Kanzler discussed the development of the *P. patula* × *P. tecunumanii* hybrid as a commercial plantation variety in South Africa (Kanzler et al. 2014). This was a 20-year process, beginning with the conservation and provenance/progeny testing of *P. tecunumanii* in the mid 1980s. Some hybrid crosses were initiated in the early 1990s, which was around the time that *Fusarium circinatum* began to cause disease problems in *P. patula* nurseries, and later in young plantations. This accelerated a shift to using the hybrid, due to the increased tolerance to the disease brought in by *P. tecunumanii*, although advantages in growth and wood quality are also expected. There was some serendipity, but also some planning involved in the fact that the industry had the genetic resources necessary to respond and make a “species” shift so quickly.

Luis Apiolaza closed the conference with a discussion of some general ideas about breeding objectives and selection methods, built around the breeder's equation and using

an example of *P. radiata* breeding in New Zealand (Apiolaza 2014). A focus of this paper is breeding for sawtimber wood quality at rotation age, and incorporating wood quality with growth and other traits of interest. Aggregate-trait breeding objectives rely on assigning proper economic weights to different traits, but this is difficult for wood property traits, given long breeding cycles and uncertainty about future market conditions. Rather than ignore wood properties in the breeding objective, this paper suggests that breeders must focus on what can be done, which in this case means simplifying the breeding objective to improving the quality of the corewood (i.e., juvenile core), which may be both easier to achieve and more economically valuable. This echoes the idea expressed by White et al. (2014) at the opening of the conference—breeders must have a strategy that is robust to deliver value.

## Conclusions

This array of topics may initially seem quite disconnected, but for the tree breeder they are all important and they all interact. As one example, consider how an understanding of pine reproductive biology is crucial for the development of pine hybrids. Within the Camcore program, it has been very difficult to make successful hybrid crosses of Mexican pines with the commercially important species *P. taeda* and *P. radiata*. It is known that pines utilize some kind of signaling mechanism during reproduction, where developing pollen tubes somehow stimulate the development of megaspores into female gametophytes, and subsequently the female gametophyte signals the dormant pollen tubes to resume their development. However, the exact nature of the signaling mechanism is unknown (Fernando 2014). Could it be that the chemistry or the timing of the signal differs among different species? If this was better understood, perhaps some barriers to hybridization could be overcome.

For the tree breeder, there are many other examples of interconnectedness of these themes. Anticipated climate change and climatic variability increases the need for genetic diversity so that breeding and plantation programs can quickly respond to changing conditions. Hybrids may offer the combination of adaptability, disease tolerance, and resilience to extreme weather events needed for successful plantation forestry in new environments and climates. Somatic embryogenesis would be of particular utility in a hybrid plantation program; hybrid seed would need to be vegetatively multiplied for plantation establishment, and SE offers the potential of nearly unlimited multiplication rates. Genomic selection would be of great utility in any pine breeding program, but its advantages would be multiplied if SE was also a reality. Genomic selection could be used to screen thousands of SE clones, searching for genotypes with the best combination of traits, and then the more long-term field testing could be limited to a relatively small number of candidates.

In summary, foresters and tree breeders have a great challenge. There is much to learn and much to do if we hope to maximize our probability of returning value to forest landowners and to society.

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