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Breeding for value in a changing world: past achievements and future prospects

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Abstract Large-scale tree improvement programs began in the 1950s. Tree improvement is now part of operational silviculture programs in many companies and countries around the world and tree breeding programs have produced very impressive results: (1) realized gains in plantations being established today of some 40–50 % in volume yield above unimproved material for many programs; (2) increased efficiencies in all aspects of breeding, selection, testing and deployment; and (3) a shortening of the generation interval by a factor of two from approximately 30 years in the first generation to less than 15 years today for pine programs. What about the future? What should tree breeders be thinking, planning and doing to ensure that results 60 years from now are even more impressive than those from the previous 60 years? Tree breeders today live in a rapidly changing world faced with: increasing demands for food, energy and water; globalization leading to an interconnectedness of markets and rapid spread of exotic organisms; climate change and its implications for genetic deployment; burgeoning technology in robotics, communications and molecular tools; shifting ownership patterns of forest land; and the real possibility of completely new forest products and markets in the future. Three ideas for "Breeding for Value in a Changing World" are: (1) adopt a robust philosophy that aims to ensure maximum value produced per ha even in a future world that will be quite different; (2) embrace technology at every phase in the tree improvement process; and (3) encourage interdisciplinary teams of scientists to solve complex problems that require expertise ranging from molecular to landscape scales.

Keywords Tree improvement · Forest genetics · Realized gains · Global change · Globalization · Future tree breeding

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Introduction

Large-scale tree improvement programs began in the 1950s in 14 countries around the world (Zobel and Talbert 1984). A few pioneering scientists led the efforts, and spent the early years convincing corporate executives that tree improvement was important and worthy of sustained investment. Tree improvement has come a long way since its inception almost 60 years ago and is now an integral part of many company and agency silviculture programs for pines, eucalypts and other species around the world.

However, the world is changing rapidly and tree improvement, by its very nature, is a long-term undertaking. Therefore, we need to ask: what will tree improvement programs look like in another 60 years and how should tree breeders be planning and breeding for that future? This paper first looks back at the first 60 years of tree improvement to gain perspective for the future; programs in the southern US are used to exemplify similar accomplishments in other parts of the world. Second, we consider several of the drivers of global change that are at work now to make the world one of dynamic and rapid change. Finally, we look ahead and offer our perspectives on how tree improvement programs might best position themselves to have the best chance of "Adding Value in a Changing World".

Past achievements in tree improvement programs

Cooperative tree improvement programs of southern pines in the USA

For nearly 60 years, tree improvement programs for (*Pinus taeda* L.) and slash pine (*Pinus elliottii* var. *elliottii* Englem.) have been organized as cooperatives composed of university staff working with members consisting of private companies and government agencies. The three cooperatives in the southern USA are centered at North Carolina State University (http://treeimprovement.org/), Texas A&M University (http://texasforestservice.tamu.edu/main/article.aspx?id=1687), and the University of Florida (http://www.sfrc.ufl.edu/cfgrp/). They have very similar operating guidelines: (1) the universities provide financial and logistical support and housing for a few faculty and staff members who are responsible for the scientific leadership, research and development, technical support and data management and analysis; and (2) the members help set cooperative policy, provide financial support in the form of annual dues and conduct field activities on their lands (in-kind contributions).

This cooperative model, consisting of many organizations pooling their resources to decrease individual costs and increase gains, has been quite successful even in the face of major changes in the structure of the forest products industry and patterns of timberland ownership. In fact, all three cooperatives are now in their third cycle of breeding and testing. As a result, the plantations being established today with genetically-improved loblolly and slash pines in the southern USA are expected to yield between 35 and 50 % more volume per ha at harvest than plantations established with unimproved material. There are also gains in disease resistance and tree form that are more difficult to quantify, but nevertheless important.

When these genetic gains are coupled with silvicultural gains from enhanced site preparation, planting, competition control and fertilization, volume yields per ha (and hence mean annual increments) from current plantations are five to eight times those from harvests of natural stands of southern pines in the 1950s (Fox et al. 2007). Such impressive gains have resulted from a sustained commitment by many people and organizations through periods of strong and weak markets and through substantial structural changes in forestland ownership.

Similar successes and advances in tree improvement programs could be cited for other species of pines, eucalypts and other tree species in many countries around the world. Further, many economic analyses of programs in several countries have shown highly positive returns on investment (Chapter 11 in White et al. 2007). Thus, tree improvement programs that began as an unproven concept in the 1950s are now accepted as critical to optimizing value per ha and have become part of the operational fabric of most major plantation forest programs in the world.

Achievements in tree breeding theory and application

Concomitant with the impressive increase in realized genetic gains in plantation yields over the past 60 years have come equally important theoretical and practical advances in all phases of selection, breeding, genetic testing, deployment and breeding strategy development. Scores of forest geneticists around the world working with many different species have contributed to these advances and shared their findings at IUFRO conferences like this one. These theoretical and practical advances mean that, compared to first-generation tree improvement programs in the 1950s and 1960s, modern-day tree programs are less expensive, more efficient and require less time to deliver greater genetic gains (White et al. 2007). The following is not intended as a complete review of the achievements made in tree breeding theory and practice, but rather as a brief summary and statement of appreciation to all of the scientists and foresters whose careers have led to these advances.

First, in the process of making selections first-generation programs used phenotype-based mass selection methods, such as comparing a candidate tree to its neighbors. Modern-day programs employ selection indices developed through Best Linear Unbiased Prediction that combine data from different relatives, generations and test designs to improve gains and manage inbreeding (Chapters 13 and 15 in White et al. 2007). Also, selections are made much sooner today at 25 % or so of the rotation age compared to 50 % historically and this delivers more gain per unit of time. Second, in the area of breeding, there have been both theoretical advances, such as the use of structured breeding populations, flexible mating designs and non-random mate selection (Chapter 17 in White et al. 2007), as well as several new practical improvements to promote earlier flowering and improve methods of controlled pollination.

Third, in the area of genetic testing, there have been myriad improvements in all aspects of designing, establishing, maintaining, measuring, managing data and analyzing genetic tests (Chapter 14 in White et al. 2007). On the theoretical side, we now emphasize mating designs that ensure genetic connectedness, more efficient field designs (e.g. alpha lattices), single-tree plots instead of row plots, and mixed model analyses that treat genetic factors as random effects (Chapter 15 in White et al. 2007). On the practical side, tree breeders exercise extreme care in choosing homogeneous sites and strive to ensure that all phases of the nursery, establishment, competition control, fertilization, maintenance, measurement, and pedigree and data management are conducted with the utmost care to reduce environmental noise and ensure the integrity and quality of the data. Together these advances in genetic testing have increased heritabilities and genetic gains, shortened breeding cycles by facilitating early selection, and reduced costs by requiring smaller genetic tests in the field.

Finally, the theory and practice of deployment of genetically improved material has changed dramatically (Chapter 16 in White et al. 2007). Most first-generation tree improvement programs deployed seed collected in bulk from one of three sources: selections growing in the stands in which they were selected; seed production areas created from selective thinning of natural stands; or first-generation seed orchards composed of untested selections. Today, there are a range of more advanced options that hinge in part on species biology including: (1) intensively-managed seed orchards in which seed collections are made from only the best, well-tested selections in the orchard; (2) operational-scale production of polymix or full-sib families through efficient means of mass pollination and/or rooted cutting production; and (3) deployment of genetically tested clones through clonal forestry. In all of these cases, the advances in genetic gain have depended on development of efficient means of manipulating aspects of species biology (e.g. seed orchard management, mass pollination, and clonal propagation).

Taken together these advances in selection, breeding, testing and deployment have had a compounding effect on the efficiency, costs, and gains achieved per unit time. As just one example, using the slash pine improvement program at the University of Florida cooperative cited above, the first-generation program: (1) encompassed 34 years (1953–1986); (2) established more than 1,000,000 trees in genetic tests that had an average individual tree heritability of less than 0.10; and (3) generated genetic gains in volume yield of 10 %. The third-generation program generated the same incremental gain in volume yield (10 % above the second generation), but will be completed in 14 years (2003–2016) with approximately 32,000 trees in genetic tests that have an average heritability of 0.30. Similar examples could be cited from the other programs in the southern USA and around the world and such advances are why tree improvement programs are an integral component of the operational silviculture programs of major forest land owners around the world.

Present-day drivers of global changes

Clearly tree improvement programs have had a very successful first 60 years, but what will the next 60 years bring? How should tree breeders be designing and implementing tree improvement programs to maximize value in the future? We believe that the world is changing more rapidly than ever before and that to answer these questions, tree breeders should consider the myriad changes and their implications for forests, silviculture and tree improvement. The following is a brief discussion of some of the drivers of global change and our perspectives on the implications of these changes on forestry and tree improvement. We have somewhat arbitrarily divided these drivers into exogenous drivers that are more independent of forestry and endogenous drivers that are more related to the forest sector.

Exogenous drivers of global change

A major driver of change is the need to double the world's food production by 2050 as a result of both the increasing world population and higher per capita incomes (Tilman et al. 2011). Achieving this 100 % increase in global food production would most likely come from a combination of agricultural intensification (increasing yields per ha) and extensification which could mean the clearing of nearly 1 billion ha of land globally by 2050 (Tilman et al. 2011). The latter suggests that some forest land will be converted to crop production and implies the need to maximize yield per ha of forest plantations to offset this loss and also meet the similarly growing global demand for forest products.

Globalization is another major driver of change in today's world (Friedman 2007; Stiglitz 2007) and is loosely defined as the growing interconnectedness of the world as evidenced by increasing flows of information, goods, services, people and technology. One implication of globalization is that markets for forest products will likely continue to change rapidly for the next several decades. A second implication is that forest health will become increasingly more challenged as exotic plants, diseases and pests are transported around the world and local pests and diseases become problematic on increasing areas of exotic plantations. Therefore, we believe that breeding for disease and pest resistance will be increasingly more important.

Climate change is yet another major driver shaping the future with trends including warming global temperatures, more frequent periods of hot days and nights, milder winters with less frequent cold snaps and increasing atmospheric carbon dioxide concentrations (National Research Council 2010). All of these trends are impacting forested ecosystems and tree improvement programs are faced with the dilemma of breeding for climatic conditions that could be much different in the future both locally (e.g. regional impacts of climate change that could require increased tolerance to drought, warm temperatures, etc.) and globally (e.g. carbon dioxide enrichment which could differentially impact different species and genotypes).

Differential growth of developed versus emerging markets will also likely have major influence on both the locations of future markets and types of products being demanded. As one example, consider the so-called PIIGS (Portugal, Italy, Ireland, Greece and Spain) that have mature economies, ageing populations and high levels of national debt compared to the BRIC countries (Brazil, Russia, India and China) with faster growing economies (The Economist 2012). As a second example, North America and the European Union have had less than 3 % annual growth in Gross Domestic Product (GDP) in every year since 2000 (with at least three of those years negative growth), while Sub-Saharan Africa (excluding South Africa) has averaged 6 % annual GDP growth and was largely unaffected by the global recession (The Economist 2013). These trends imply that tree breeders should design robust tree improvement programs that will deliver value even when markets and products change.

Burgeoning technology of all kinds is another major global driver that is and will continue to impact global markets, create new products, and change the way business is conducted. Examples include: the explosion of communications technologies; the use of robotics and other new industrial technologies in many industries; nanotechnology creating new products; rapidly increasing computing power; and new molecular tools being developed every day at lower costs. It is truly amazing that the human genome cost more than $100 million to sequence in 2001 and that by 2012 that had dropped to less than $10,000 per genome (National Human Genome Research Institute 2013). There are at least two implications of this explosion of technologies of all kinds: (1) it is very difficult to predict the new forest products that will be developed over the next few decades making it difficult to breed for specific products; and (2) tree improvement programs need to embrace all appropriate technologies to deliver maximum value.

Finally, the growing global desire for triple-bottom-line sustainability indicates the need to seek a balanced combination of economic, social and environmental sustainability. The increasing demand for global food, water and energy mentioned earlier coupled with this demand for sustainability means that plantation forests and tree improvement programs need to maximize yield per ha. This will minimize the number of hectares established in plantations globally so that more land can be available for production agriculture and to preserve natural forests.

Endogenous drivers of global change

Changes in forest land ownership

In 1990, the majority of industrial forest plantations in the United States belonged to vertically-integrated forest products companies (VIFPCs) that owned both timberlands and mills. During the past 20 years there has been a complete transformation in ownership such that today no major VIFPCs exist, having been replaced by a group of forest products companies that only owns mills (e.g. Georgia-Pacific and International Paper Company) and other types of business structures that own the timberlands (e.g. real estate investment trusts, REITs, and timber investment management organizations, TIMOs) (Lutz 2006; Zhang et al. 2012). The mill owners are mainly interested in holding down wood costs to maximize mill profits; whereas; the landowners are mainly interested in maximizing returns from their lands. The TIMOs and REITs tend to have relatively shorter-term investment horizons for their timberlands and less interest in longer-term investments and research than the former VIFPCs. This means that tree improvement programs should be cost efficient and return value quickly, and also implies that wood quality improvements may not be highly valued since the mill owners tend to purchase by weight and desire low costs.

Another major change occurring in the forestry sector is the rapidly increasing demand for biomass for electrical power plants and wood pellets, and potentially for biofuels. Spurred by the desires both for energy independence from foreign oil and for more use of renewable energy, the number of biomass-fueled power plants in the world grew from 800 in 2005 to 2,000 in 2010 and with another 5,000 commissioned to go online by 2015 (Price 2011). Similarly, the global market for wood pellets used in home and community heating was extremely small in the year 2000 but reached 15 million tons in 2010 and is growing at nearly 20 % per year (Peksa-Blanchard et al. 2007). In the southern United States alone, there are 30 new existing or proposed biomass power plants and an additional 40 pellet plants that did not exist 15 years ago (TimberMart South 2012). Does this mean that breeders should be targeting biomass, rather than just stem volume, yield per ha as a trait for breeding or will these policy-driven markets collapse for political or economic reasons (e.g. the shale oil extraction method of hydraulic fracturing, “fracking”, that has lowered price of natural gas)? These policy-driven markets point to the dynamic uncertainty of future wood markets.

A final driver of change in the forestry sector is the continual and rapid development of new products and markets. Who would have thought 30 years ago that the world would have saws that can cut on a curve or that most of the LCD screens would contain cellulose acetate as a key component? What future products will be made of nanocrystalline cellulose and what other new products will dominate markets 30 years from now? On the forest side of the markets, will the demand for ecosystem services materialize in such a way that people are willing to pay forest growers for carbon sequestration, watershed services, preserving biodiversity or ecotourism? All of these factors contribute to the long-term uncertainty regarding future products and markets.

Breeding for value in the future

Tree improvement programs in southern pines and many other species have added tremendous value over the past 60 years and have become ensconced in many organizations’ operational silviculture programs. However, pine breeding is a long-term effort requiring 15 or so years of breeding and testing and another 15–30 years of plantation growth with the newly bred material prior to harvest when value is realized. So what will the future world be like in 30–50 years and how does that impact breeders today?

As described above, the world is changing rapidly. The production forestry sector of the future will likely reflect: (1) new circumstances such as new markets, new products and new patterns of forest ownership; (2) new challenges such as climate change, invasives and competition for land with agriculture striving to feed a growing population; and (3) new technologies including mill technologies, molecular tools, computing power, robotics and nanotechnologies.

We advocate a tree breeding philosophy that will be robust to these changes occurring in the world and deliver near-optimal value regardless of the exact complexion of markets, products, technologies, etc. This "robust for value" tree breeding philosophy could have three components: (1) focus on increasing the volume of wood produced per ha planted—this has always been a good strategy and seems even better in a period of high uncertainty; (2) embrace technology of all kinds and at all scales to ensure that tree improvement programs benefit from new advances; and (3) encourage the formation of multi- and transdisciplinary teams of scientists composed of molecular biologists, physiologists, geneticists, silviculturists, pathologists, entomologists, biometricians, computational scientists and landscape-level ecologists to solve the complex problems of unraveling how genomes impact phenotypic expression at the tree, stand and landscape levels.

The first part of this breeding philosophy, increasing wood volume yield per ha, implies focusing on traits that are directly related to stand-level volume yield such as growth rate and disease and pest resistance. As we learn about the genetics of tree-to-tree competition, breeding for "good neighbor" ideotypes (e.g. Martin et al. 2001) might also increase stand-level volume yield and resource use efficiency. Breeding for adaptation to climate change might also fall into this category. Target traits that might be less robust to the changing markets, products, technologies and ownerships are those associated with today's current products and markets (e.g. specific wood properties or internode characteristics); we believe these traits involve more risk of being less valuable in the future world. Finally, exploring the notion of physiological plasticity as a trait (Peperkorn et al. 2005; Vitasse et al. 2010) may be worthwhile, given the need to produce trees that can acclimate to a wide range of uncertain future environments.

The second idea, embracing technology, means being early adopters of appropriate new advances in all types of technologies. Looking into the future a few possibilities of technological advancements could mean: (1) large-scale application of operational clonal forestry in southern pines as has been so successful in eucalypts and poplars; (2) widespread use of pine hybrids including the use of assisted introgression and hybrids involving more than two species; (3) appropriate operational use of pines with genomes modified perhaps to increase pest resistance or enhance adaptation and resilience to climate change; (4) incorporation of genome-wide selection in southern pine breeding to increase gains, reduce the generation interval from 15 to 5 years, and require field testing only every third generation (Resende et al. 2012); and (5) utilization of mate-pair allocation in breeding based on molecular markers to increase gains by choosing mates that maximize the complementarity of allelic combinations (Harfouche et al. 2012). These possibilities are just a few that could be realized in the foreseeable future, and there are certain to be many more not already on the horizon for tree breeders to take advantage of.

The third aspect of the proposed breeding philosophy, multidisciplinary teams for complex problems, recognizes that even with the ongoing rapid advances in genomic sciences, it will still be a complex task to understand the causal molecular basis of phenotypic traits, such as stand-level volume production. That said, we believe that teams of scientists working together across scales (from molecular to landscape) should be able to accomplish this in the not-too-distant future. Imagine if breeding, testing and deployment were all transformed into “smart, precision” genetics to complement precision silviculture? It would then be conceivable to rapidly breed for changing climates, changing products and changing threats from pathogens and pests.

Summary and conclusions

Many tree improvement programs that began in the 1950s are now in their third or fourth generation of breeding. These, and other programs started more recently, are planting genetically improved trees that contribute to enhanced growth, improved health, superior product quality and economic vitality of plantation forests around the world. Along the way, forest geneticists have developed better breeding strategies, testing designs, statistical methodology and much more that collectively have made tree improvement programs much more efficient: achieving more gains per generation at lower cost. Tree improvement programs have a rich history of adding value and we believe that this will continue, as it has for crop species, long into the future. We also believe that traditional aspects to tree breeding programs such as recurrent selection, field testing and proper data analyses will always play a pivotal role in future programs even as new technologies and approaches accelerate the breeding cycle.

At the same time, we are living in a dynamic world in which climates, markets, products, technologies, forest ownership patterns and global interconnectedness are all evolving and changing at an ever increasing rate. We encourage tree breeders to think creatively about positioning their programs to be robust to the vagaries of an uncertain future by: (1) focusing on key traits to improve that will transcend change and continue to be important under many future scenarios; (2) developing breeding strategies that are nimble and can be adapted to changing conditions; (3) embracing new technologies to increase the efficiency and effectiveness of selection, breeding, testing and deployment; and (4) creating multidisciplinary teams of scientists to solve complex problems and integrate across scales from the molecular to landscape levels to ensure that genetic gains in tree performance translate into enhanced plantation performance in a variety of conditions.

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