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The Evolution of a Seedling Market for Genetically Improved Loblolly Pine in the Southern United States

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Abstract

Landowners in the southern United States have witnessed unprecedented changes in the availability of genetically improved loblolly pine (*Pinus taeda* L.) seedlings. Landowners can now purchase the most advanced seedlings bred by tree improvement programs to have increased productivity, improved stem and wood quality, and enhanced disease resistance. Until the mid-2000s, the best genetics were typically planted by forest product companies on their own lands to capture the maximum benefit from their investment in tree breeding. Other forest landowners typically did not have access to the very best genetics. Since the large, vertically integrated forest products companies no longer own or manage much of the land, virtually all seedling families are now available to all landowners. With the evolution of a more open market for seedlings, differential prices developed rapidly. The highest performing full-sibling families now sell for more than four times more than open-pollinated families of lower performance. Landowners who choose to invest in improved genetics are reaping the benefits of many years of selective breeding, which increases their own profitability as well as contributes to the long-term sustainability of cooperative tree improvement programs.

Keywords: economics, genetic gain, nurseries, *Pinus taeda* L., tree improvement

Plantation Forestry, Tree Improvement, and Genetic Gains

Plantation forestry began in earnest in the southern United States in the 1940s and 1950s (Carter et al. 2015). Large, vertically integrated forest products companies practiced aggressive forest management and invested heavily in plantation silviculture and tree improvement. At their peak, the vertically integrated forest products companies owned and managed 38 million acres in the South (Conner and Hartsell 2002). Tree improvement programs were initiated at land grant universities and at the USDA Forest Service in the 1950s to meet the needs of plantation programs (Zobel and Talbert 1984; Zobel and Sprague 1993). Since loblolly pine (*Pinus taeda* L.) and slash pine (*P. elliottii* Engelm.) were the most commonly planted species in the South, intensive selection and breeding programs were initiated with them in the cooperative tree improvement programs at the University of Florida, the Texas Forest Service at Texas A&M University, and at NC State University. These cooperative programs were financially supported by companies and state forestry agencies.

Breeding for all forest tree species is in its infancy compared with many crop and animal improvement programs. Beginning in the 1950s, foresters and tree breeders selected superior-looking trees in natural

Management and Policy Implications

Landowners and foresters in the southern United States have more options today of which loblolly pine genetics to plant than ever before. A landowner can opt to plant the highest-yielding families with superb stem form and disease resistance that will cost over $200 per thousand bareroot seedlings, or they can opt to plant lower performing families that may suit their management objectives for a quarter of the price. Third-party verification of the genetic quality of seedlings is now available from tree improvement cooperatives in the South, and landowners can make informed decisions about what to plant and where to plant it.

stands (Figure 1A) in the hope that selected parents would produce elite progeny. Cuttings or scions were collected from superior trees (phenotypes) and grafted on to seedling rootstocks in seed orchards to bring these selections together to inter-mate and produce progeny (Figure 1). A typical first-generation seed orchard of loblolly pine would have 25 to 35 selected parent trees with multiple grafts of each selection managed to produce seed.

Just as with most plant and animal species, the concept that selection of superior phenotypes would result in the production of superior progeny worked well in the southern pines. Genetic gains for stem volume, stem form, and resistance to fusiform rust (caused by the fungus *Cronartium quercuum* f. sp. *fusiforme*) resulted in increased value to landowners who established millions of acres of plantations (Talbert et al. 1985; Li et al. 1999; Vergara et al. 2004; McKeand et al. 2006).

Over the past decades, tree improvement programs have progressed to the second, third, and fourth cycles of improved material (McKeand and Bridgwater 1998). Recurrent or repeated rounds of selection over generations have resulted in continued genetic gains for all traits. For example, in the NC State University Cooperative Tree Improvement Program, progeny

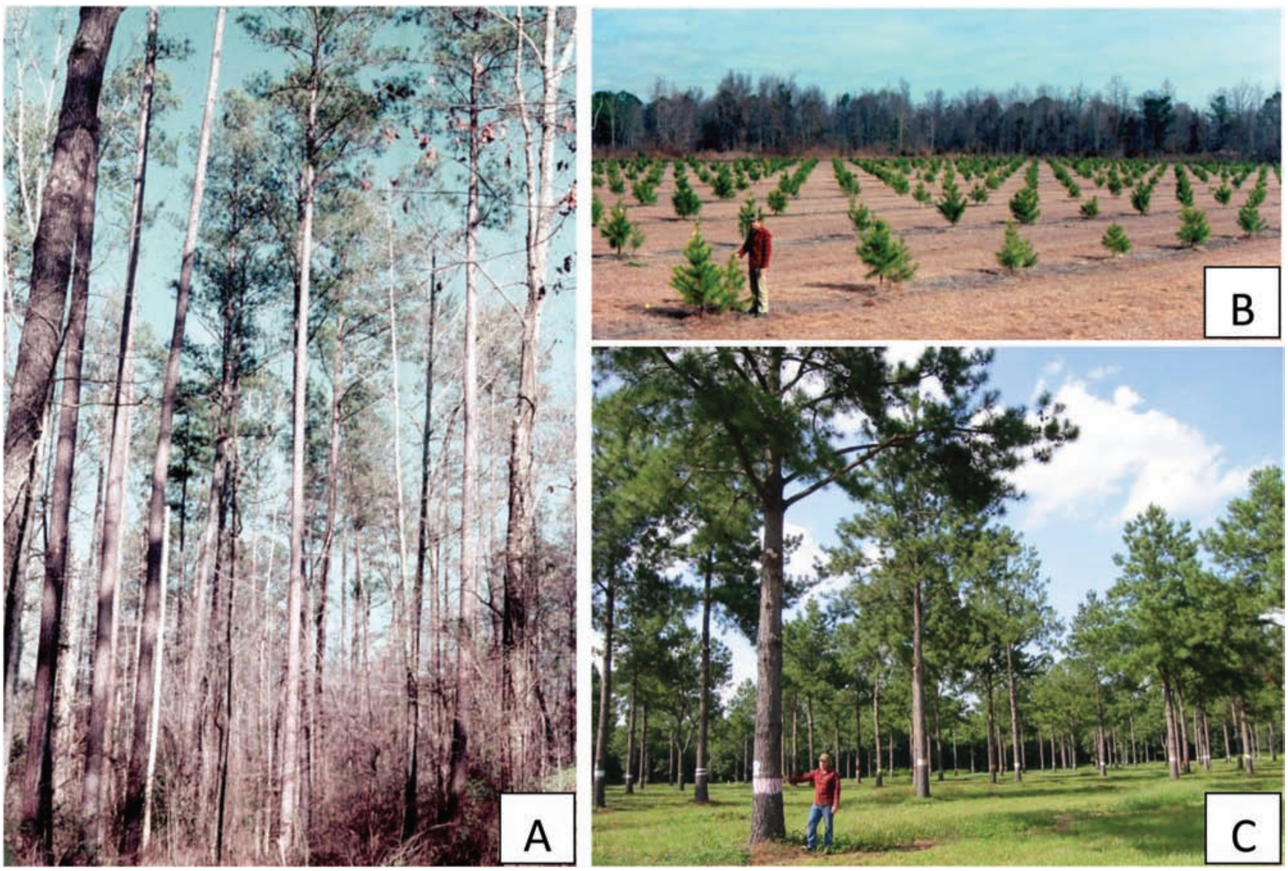

Figure 1. Tree improvement programs for loblolly pine started by selecting superior trees (A) in natural stands throughout the southeastern United States. Trees were grafted onto seedling rootstocks in seed orchards (B), and grafts were managed to produce seed (C) for nursery programs. Panels B and C are the same seed orchard at age 1 year and age 16 years.

from third-cycle selections (e.g., from the third round of breeding) are the most advanced families currently available for operational deployment. In the Coastal Plain breeding population, the largest and most advanced in the NC State Cooperative, there are 243 third-cycle selections out of a total of 2260 selections in the database. The estimated gain in volume at age 6 years for open-pollinated families that are progeny from these 243 selections is 48% compared with nonimproved seedling checklots. Of the top 100 families for volume gain, 43 are third-cycle selections that average 63% gain in volume over the nonimproved checklot in the regions where they were tested. Similar substantial gains are also seen for fusiform rust resistance and stem form traits in these third-cycle families. Similar gains are also available from seedlings produced from germplasm developed by the other cooperatives.

In addition to the gains from recurrent selection and deployment of open-pollinated families, tree improvement foresters have produced specific crosses or full-sibling (full-sib) seedlings in large quantities over the past 15 to 20 years (Figures 2 and 3). When the best parents are crossed, the gains in growth and quality traits are dramatic. For example, in the NC State Cooperative, when both the open-pollinated and full-sib families are compared together in the Coastal population database, 95 of the top 100 families for volume are full-sibs. This is to be expected because tree improvement foresters and seed orchard managers make production crosses only among the very best parent trees, and the mixed inferior pollen found in open-pollinated families is eliminated (Bridgwater et al. 1998). In addition to excellent volume production, the best full-sib families have much straighter stems and better fusiform rust resistance than the best open-pollinated families. For stem straightness, there are 503 full-sib families that rank higher than the top open-pollinated family. For rust resistance, there are 293 full-sib families that are superior to the best open-pollinated family, and for stem forking, there are 194 full-sib families that rank better than the top open-pollinated family.

Deployment of Genetic Gains

In the early years of tree improvement with loblolly pine, open-pollinated seeds were collected from all the trees in a seed orchard and were bulked together as an orchard mix and planted in nurseries (Figure 4). Genetic gains were essentially the same on every acre planted with improved seedlings. As tree improvement programs matured, there was a realization that deployment practices could be significantly enhanced. Rather than evenly distributing average genetic gain to every plantation, foresters began to establish plantations with individual open-pollinated or half-sib families in the 1970s (Gladstone 1975). The practice of the "family block system" evolved over the years (Duzan and Williams 1988), and for loblolly pine, the majority of plantations are now established with individual open-pollinated families (McKeand et al. 2003, McKeand et al. 2015).

Knowledgeable foresters recognized that financial returns could be significantly increased by judiciously planting specific families on specific sites. For instance, where fusiform rust resistance was critical, deployment of the most rust-resistant families (McKeand et al. 1999) resulted in significant improvement in stand value (Schmidt 2003). For volume production, the concept of planting the best families on the best sites (Duzan and Williams 1988) significantly enhanced southern pine plantation forestry. Foresters realized that financial gains could be maximized by planting the most productive families on the best sites or on sites where intensive silviculture was being practiced (McKeand et al. 1997). For example, if a landowner has the option to plant a very productive family that grows 20% faster than an average family on a site that produces 4 tons/acre/year versus a site that produces 8 tons/acre/year, the value from genetics will be much greater on the more productive site.

For years, the large forest products companies owned most of the seed orchards and seedling nurseries in the southern United States. Company foresters recognized the value of tree improvement, and the best families were planted on company lands. These organizations had long-term investments in developing genetic resources and recognized the value of genetically improved seedlings for increasing productivity and value of their plantations. They wanted to benefit from growing and harvesting the highest value trees on their own land. As a consequence, the best genetics were not typically available to other landowners except from the state agencies, and until the last decade or so, state agencies always sold mixtures of open-pollinated families (data used in McKeand et al. 2003). Although seedling vendors did not sell poor genetic material, the very best families were not widely available to all customers.

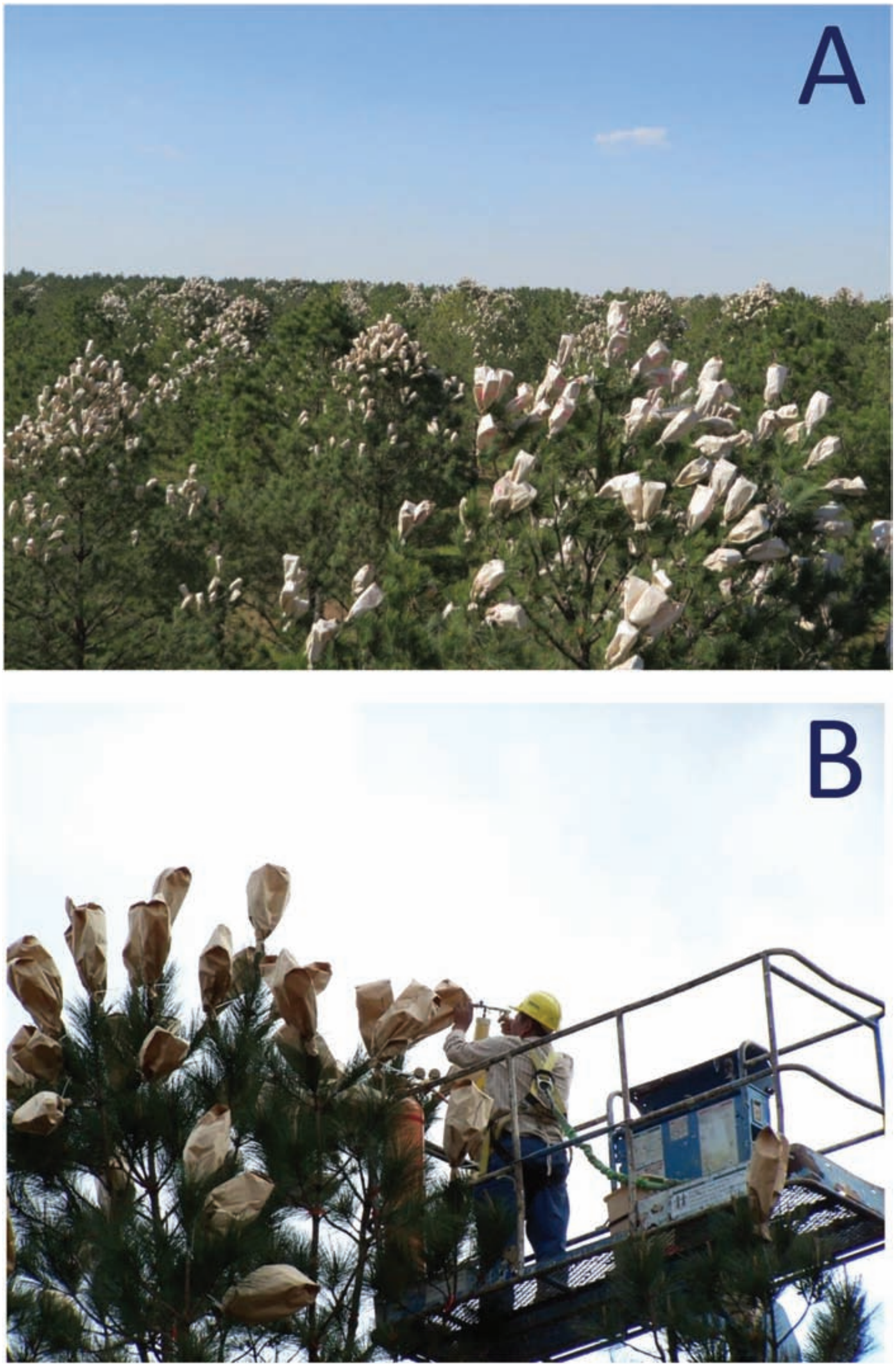

Figure 2. Mass production of control-pollinated seed. Female strobili ("flowers") are isolated from outside pollen with pollination bags (A) and pollinated with specific pollen collected from another parent tree (B) to produce a full-sibling family. Panel B, courtesy of Don Chastain, formerly with Timberland Investment Resources, LLC, Charlotte, NC.

A Major Change in the Genetics/Seedling Market

Over the last 20 years, forestland ownership has undergone a revolutionary change. The large vertically integrated forest products companies have merged, sold their lands to Timber Investment Management Organizations, or converted to Real Estate Investment Trusts (Butler and Wear 2013). At their peak ownership in 1989, forest products companies owned about 18% of the forestland (38 million acres) in the South (Conner and Hartsell 2002). Over a 10-year period from 1998 to 2008, forestland held by the vertically integrated forest products companies dropped from 23.4 million acres to 7.5 million acres; Timber Investment

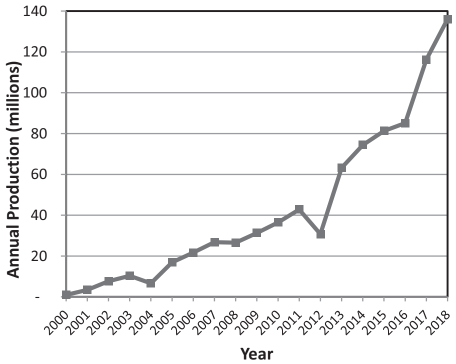

Figure 3. Annual number of seedlings produced of specific crosses (full-sibling families) of loblolly pine in the southern United States. In the 2017–2018 planting season, over 136 million seedlings of specific crosses of loblolly pine were planted on about 17% of all loblolly pine plantations in the South. Over 810 million seedlings of specific crosses have been planted since 2000.

Management Organization ownership increased from 2.2 to 13.4 million acres; Real Estate Investment Trust ownership went from 5.4 to 6.5 million acres (see Table 6.1 in Butler and Wear 2013). Over a very short period of time, this change in ownership has had a profound effect on the deployment of loblolly pine genetics and how tree improvement programs have been managed.

Genetically improved southern pines became available to a wider range of landowners primarily due to the change in land ownership and the structure of the forest products industry. The most important change has been with the ownership of nurseries and tree improvement programs, and the chronology of those changes is described here.

The first major effect occurred in 2007 when International Paper Company's (IPCo) and MeadWestvaco's (MWV) tree improvement and nursery operations were converted to ArborGen, Inc. When IPCo and MWV combined owned over 7 million acres of forestland, the vast majority of the best genetics from their tree improvement programs went to their own lands. When ArborGen started commercial production of seedlings in 2008, virtually every loblolly pine seedling family from the IPCo and MWV tree improvement programs became available to any landowner.

Around 2008, state nursery programs began selling individual families of loblolly pine. This was a significant change from the more conservative practice of selling only mixtures of families collected from seed orchards. Since there was little evidence of risk of deploying individual families (McKeand et al. 2003), state nurseries adopted the practice.

Starting in 2013, International Forest Company (IFCO), a nursery company, joined the cooperative tree improvement programs in the South, and they also started selling loblolly pine seedlings with a wide level of genetic improvement. In 2017, IFCO's ability

Figure 4. In the early days of tree improvement with loblolly pine in the southern United States, cones were harvested from all the trees in first-generation orchards (A) and were bulked together (B). In the 1960s and into the 1980s, almost all plantation acres were established with the same, average bulked seedlings from a given nursery or seed orchard program. In the last few decades, orchard managers have collected and processed cones by parent so that forest managers can purchase individual families and tailor genetic improvement to best meet landowner objectives.

to provide a wide variety of seedlings to landowners increased dramatically when Weyerhaeuser Company sold four of its southern nurseries to IFCO. When Weyerhaeuser owned these nurseries, the majority of the best loblolly pine families were planted on company lands[1] for all the reasons cited above.

All nursery providers grow loblolly pine seedlings of a wide variety of genetic quality, but the big changes in the availability of elite seedlings to all landowners are the results of changes cited above. Some of these nurseries grow primarily for their own land, and some grow seedlings exclusively for market sales. The best way for a landowner to know the genetic quality of seedlings being purchased is to discuss details with the nursery vendor (see PRS™ discussion below).

Forestland ownership changes also affected the cooperative tree improvement programs that had been the mainstream of genetic improvement for decades. Direct participation by industry tree improvement foresters in the breeding, testing, and selection activities of cooperative tree improvement programs plummeted with the loss of the vertically integrated forest products companies. Many of the new landowners were not willing or interested in directly supporting tree improvement (Byram et al. 2005), and membership in cooperatives declined (Wheeler et al. 2015). Full membership in the NC State Cooperative dropped from a high of 29 members in the mid-1980s to only 10 in 2018 (Figure 5).

In response to the reduced membership and the reduction in the capacity to continue an aggressive breeding program, the NC State Cooperative initiated a contributing membership category in 2008, designed for the nonvertically integrated forest landowners, smaller vertically integrated solid-wood products companies, forestry consulting firms, and nurseries. These members understand the benefits of tree improvement to their organizations and management practices, but they do not have the capacity or desire to carry out the breeding, testing, and selection activities like full members.

Each contributing member has joined the cooperative primarily to gain access to the performance data of all the families in the program. Their investment in tree improvement and research provides the information needed for their business services and management plans. Organizations in this membership class have increased substantially over the past 10 years (Figure 5), and contributions support the cooperative's breeding, testing, and selection program and the continued development of germplasm that is available to a wide range of landowners in the South.

The Effect of the Newly Evolved Seedling Market on Seedling Prices

With nurseries in the South now producing over 550 million improved loblolly pine seedlings for market

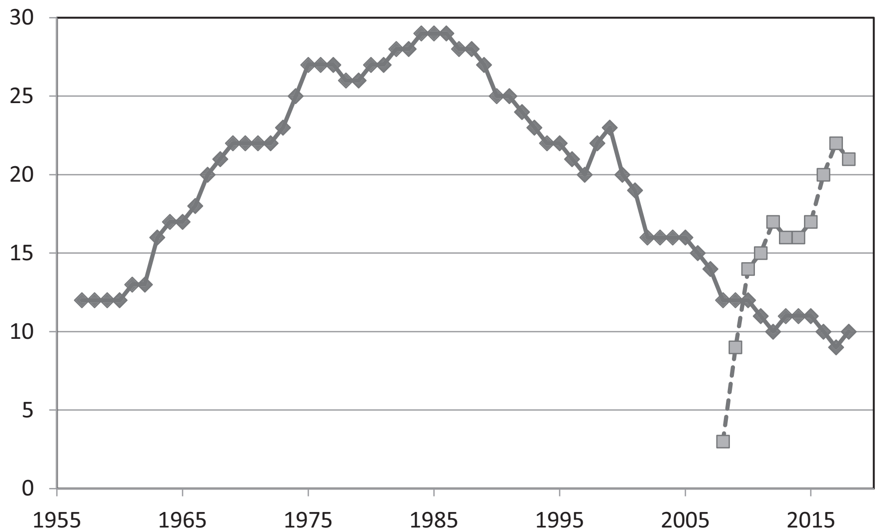

Figure 5. Full membership (solid line, diamonds) and contributing membership (dashed line, boxes) in the NC State University Cooperative Tree Improvement Program from 1956 to 2018. Similar trends in full membership have been seen in all the southern tree improvement cooperatives (see Figure 2 in Wheeler et al. 2015). In all the cooperatives, full members have access to all the germplasm and can establish seed orchards with the highest-value germplasm and deploy and sell seedlings from their nurseries. Contributing members have joined the cooperative primarily to gain access to the performance data of all families in the cooperative.

sales to all landowners (data from McKeand et al. 2015), a fundamental change has occurred in the seedling market. When the vertically integrated forest products companies existed, and the best seedlings were not regularly available on the open market, little price differentiation developed. Over the last 10 years, there has been a dramatic change in the price structure of loblolly pine seedlings. For bareroot seedlings, today's prices range from as low as about $50 per thousand seedlings for average open-pollinated families to over $230 per thousand for the very best full-sib families. Clonal varieties are sold at even higher prices ($350 per thousand) but are currently a minor component of the seedling market (McKeand et al. 2015). Forest seedling nurseries are also aggressively marketing the best genetics. When seedling customers visit nursery vendor web sites, a major emphasis is placed on the genetic quality of the seedlings being sold.

The development of the seedling market for loblolly pine genetics is a classic example of how markets evolve, and supply and demand change when both customers and vendors have open information about their products. According to George A. Akerlof who won the 2001 Nobel Prize in economics for "… analyses of markets with asymmetric information"[2], when vendors and customers have the same estimates about the quality of individual products, prices will represent the expected price of one quality unit (Akerlof 1970). As exemplified in the loblolly pine seedling market, when landowners were provided data about the differential performance of families, and a wide range of seedlings with different genetic qualities were available, differential prices evolved. Some landowners are eager to invest in the best genetics, and when a product is in high demand, prices of the best genetics increase.

Many southern landowners obtain information about the value of different seedling families directly from seedling vendors as well as from the three tree improvement cooperatives. The cooperatives provide "third-party" assessment and verification of the productivity, disease resistance, and stem quality of the hundreds of loblolly pine families that are available from nurseries. One such example is the loblolly pine Performance Rating System[3] (PRS) developed by the NC State University Cooperative Tree Improvement Program. The PRS is a tool that allows landowners and foresters to compare the genetic quality of thousands of different open-pollinated and full-sib families of loblolly pine. Of even greater value, the PRS information gives adaptability guidelines showing where families can be planted with acceptable risk due to cold damage. This information helps seedling consumers understand the genetic potential of a family and its relative value compared with other families. Again, when customers and vendors both understand the value of a product, markets develop and differential prices evolve.

One thing that should be emphasized in the loblolly pine nursery business is that the price of some categories of seedlings has not changed significantly for many years. If a landowner does not opt to invest in high-priced, high-value genetics, there are millions of genetically improved seedlings of lower genetic worth available for lower prices. What has changed dramatically is the price of the best genetics. The most readily available source of information about seedling prices is from ArborGen's seedling catalog (http://www.arborgen.com/wp-content/uploads/2018/05/arborgen-2018-product-catalog-electronic.pdf; last accessed December 17, 2018). Since they first started publishing their Seedling Product Catalog in 2008–09, the highest price of their Mass Control Pollinated or full-sib seedlings has increased by 67%, a clear indication that the demand for high-value loblolly pine seedlings has increased (e.g., Figure 3), and the market has responded to that demand with higher prices.

Concluding Remarks

Tree breeding has long-lasting effects on forest productivity, forest values, and ecosystem services such as carbon sequestration (Aspinwall et al. 2012) and has permanently changed the practice of forestry in the southern United States by helping to maintain a sustainable source of wood for future generations. More than ever before, forest landowners today recognize the value of planting the appropriate genetics to meet their management objectives. For example, a landowner managing for high-value sawtimber and poles, should plant families that grow well and also have excellent stem form and necessary levels of fusiform rust resistance. A landowner managing for pulpwood will likely put less emphasis on stem quality but will have fewer options if markets change.

As the number of acres of pine plantations continues to increase in the southern United States (Huggett et al. 2013), landowners are expected to increase their focus on the genetics of the seedlings they are planting. The breeding programs managed by members of the tree improvement cooperatives will continue to provide a wide range of options for landowners to meet their land management objectives.

Glossary of Technical Terminology and Additional Information

Tree breeding **cycle** refers to the timing of breeding activities and breeding strategies used. For example, in the second cycle of breeding in the NC State Cooperative, about 600 true second-generation selections were bred, but the vast majority of selections (3000+) were actually first-generation phenotypic selections from plantations (see McKeand and Bridgwater 1998 for details). In the fourth-cycle breeding program, parents from first, second, third, and fourth generations have been bred.

Seedling **family** refers to seedlings that are closely related to each other having one or two parents in common.

A **half-sibling (half-sib) family** is a group of seedlings that have the same mother tree but different father trees, since the female strobili or "flowers" are wind pollinated with pollen from multiple male trees. They are often referred to as open-pollinated or OP families.

A **full-sibling (full-sib) family** is a group of seedlings that have the same mother tree and the same father tree as parents. Control crosses are produced by applying pollen from a specific male tree to female strobili that are isolated from outside pollen using a pollination bag (Figure 3).

Germplasm equates to select trees or selections developed in the breeding, testing, and selection program. Progeny from these selections are seedling families.

There are three **tree improvement cooperatives** in the southern United States: The NC State University Cooperative Tree Improvement Program (http://TreeImprovement.org/), The Cooperative Forest Genetics Research Program at the University of Florida (http://www.sfrc.ufl.edu/CFGRP/), and the Western Gulf Forest Tree Improvement Program at the Texas A&M Forest Service (http://texasforestservice.tamu.edu/WesternGulfForest/). All web pages last accessed December 17, 2018.

In the NC State University Cooperative Tree Improvement Program, there are three types of members. Full members are the traditional company and state agency members who actively participate in the breeding, testing, and selection programs to develop new germplasm. Full members have access to all germplasm in the cooperative to commercialize for internal use and to produce seedlings for sale to all landowners. Contributing membership started in 2008 and was designed for companies, organizations, or individuals who own/manage forestland or for nurseries operating in the southern United States that desire information about the genetic value of loblolly pine. Contributing members have access to genetic performance data but not to germplasm. Research associate members participate in and contribute to the cooperative's research efforts and are partners in research with cooperative faculty, staff, and students. Similar memberships are available in the CFGRP and Western Gulf Cooperatives.

Vertically integrated forest product company. The following is from Lönnstedt and Sedjo (2012): "Generally defined, a "vertical integration" strategy keeps all aspects of management, production, sales, and distribution within a business, making the company less vulnerable to outside forces. For the forest industry the term usually refers to firms that provide large portions of their wood needs from their own forests."

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Endnotes

1 Weyerhaeuser owns approximately 7 million acres of timberlands located across 11 southern states (https://www.weyerhaeuser.com/timberlands/forestry/us-south/; last accessed December 17, 2018).

2 George A. Akerlof - Facts. *Nobelprize.org*. Nobel Media AB 2014. Web. 31 Oct 2017. https://www.nobelprize.org/prizes/economics/2001/akerlof/facts/; last accessed December 17, 2018.

3 Details about the *PRS* are available at http://treeimprovement.org/prs; last accessed December 17, 2018.

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