Proceedings

34th Southern Forest Tree Improvement Conference

Applying genetics and genomics to accelerate breeding
enhance genetic gain and improve adaptation

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School of Forest Resources and Conservation
Institute of Food and Agricultural Sciences
University of Florida

Melbourne, Florida, USA June 19-21, 2017

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Proceedings of the 34th Southern Forest Tree Improvement Conference

Melbourne, Florida, USA
June 19-21, 2017

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Forward

The 34th Southern Forest Tree Improvement Conference (SFTIC), marking 66 years of biennial technical conferences, was held June 19-21, 2017 in sunny Melbourne Beach, FL at the Crowne Plaza Oceanfront hotel. The conference theme was “Applying genetics and genomics to accelerate breeding, enhance genetic gain and improve adaptation”. There were 83 colleagues (13 students) attending the conference from 4 countries, 16 US states and 29 different organizations (14 universities, 8 companies and 7 government agencies).

The UF/IFAS School of Forest Resources and Conservation and the Cooperative Forest Genetics Research Program, in cooperation with the Southern Forest Tree Improvement Committee, was proud to host the 34th SFTIC and thank all presenters and attendees for their excellent presentations and discussions (see list of participant), the financial sponsors who without their generous support this conference would not be possible (see list of sponsors) and the University of Florida/IFAS Office of Conferences and Institutes for their detailed planning and organization of this conference!

The following awards were presented to individuals for their outstanding contribution to the 2017 SFTIC conference. All winners received a cash award and certificate signed by the 2017 SFTIC chairman, Josh Adams.

In honor of **Dr. Bruce Zobel** a $300 cash prize and signed certificate was awarded for best oral student presentation based on content, style and use of visuals. This year’s winner was **Austin Heine** for his presentation on “Pollination Bag Type Impacts Cone Survival and Seed Yield for Mass Production of Control Cross Seed in Loblolly Pine”.

In honor of **Dr. Tony Squillace** a $300 cash prize and signed certificate was awarded for best oral student or non-student presentation (excluding invited presentation) based on content, style and use of visuals. This year’s winner was **Donghwan Shim** for his presentation on “De Novo Assembly of Transcriptome and Identification of Transcriptional Network that Leads to Enhanced Strobilus Production by Branch Girdling in *Larix Kaempferi”.*

There were three awards for best student poster presentation based on content, clarity, organization and visual appeal. The **first place, Belle Baruch Institute Poster Award,** $200 cash prize was awarded *to* **Andrew Sims** for his presentation on “A Proposed Study on the Genetic Control of Fertilizer Response and Post-Senescence Nutrient Content Assessed via Foliar Sampling in Loblolly Pine”. The **second place, Hans van Buijtenen Poster Award,** $150 cash prize was awarded to **Rachel Landham** for her presentation on “Effects of Thinning Regimes on Genetic Variation of White Oak (*Quercus alba* L.) in Eastern Hardwood Forests”. The **third place, Hans van Buijtenen Poster Award,** $100 cash prize was awarded to **Ki-Won Kim** for his presentation on “Genetic Diversity and Clone Structure of the Endangered Species of *Thuja koraiensis*: Conservation Strategy in Response to Climate Change”.

2017 SFTIC Committee

Joshua Adams – Louisiana Tech University, Ruston, LA

Onesphore Bitoki – Virginia Department of Forestry, Henrico, VA

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Table of Contents

Plenary session: Tree Genome Structure and Evolution
Moderator: ***Dr. Gary Peter*****, UF/IFAS School of Forest Resources and Conservation, Gainesville, FL**

Computational Approaches to Decode Megagenomes and Develop Database Resources for the Forest Tree Community
Dr. Jill Wegrzyn...2

Analysis of Pinaceae Gene Family Evolution Suggests Accelerated Gene Turnover in Pine Trees
Dr. Claudio Casola 3

Plenary session: Accelerating Tree Improvement
Moderator: Dr. John Davis, **Associate Dean for Research, UF/IFAS, Gainesville, FL**

What is next in the Application of Genome-Wide Information to Tree Breeding?
Dr. Matias Kirst 5

Genome Editing in Forest Trees: Progress and Future Prospects
Dr. CJ Tsai 6

Session 1: Breeding Strategies
Moderator: ***Mr. Gregory Powell,*** **UF/IFAS School of Forest Resources and Conservation, Gainesville, FL**

Analysis and Selections of the CFGRP 4th Cycle Slash Pine Tree Improvement
Dr. Salvador Gezan 8

The Evolution of Breeding and Testing Strategies in the NC State University Cooperative Tree Improvement Program
Prof. Steve McKeand 9

A New Era for the Hardwood Tree Improvement and Regeneration Center
Dr. Carolyn Pike 10

Session 2: Disease Resistance Genes
Moderator: *Dr. Dana Nelson,* USDA Forest Service, Lexington, KY

Genetic Diversity in Candidate Disease- Resistance Genes in *Pinus taeda* L.
Dr. Daniel Ence 12

Whole-Genome Sequencing of Chestnuts (*Castanea*) Reveals Within- and Among-Species Genetic Variation in Regions Associated with Resistance to Chestnut Blight and Predicted Disease Resistance Genes
Mr. Nicholas LaBonte 13

Session 3: Biotechnology
Moderator: *Dr. Carol Loopstra,* Texas A&M University, College Station, TX

Tubulins, Rhythms and Cell Walls in Poplar Leaves; Timing Might Be Everything
Dr. Scott Harding 15

Capturing Loblolly Pine Chromosomes for Genome Sequencing Using Laser Capture Microdissection Microscopy
Dr. Nurul Faridi 16

A Novel Approach to Phenotypic Analysis of Forest Trees for Accelerating Breeding
Dr. Donghwan Shim 17

Session 4: Wood Yield
Moderator: *Dr. Salvador Gezan,* UF/IFAS School of Forest Resources and Conservation, Gainesville, FL

Benefits of Loblolly Pine Genetic Improvement for the Upper Coastal Plain of Mississippi
Ms. Valerie West 19

Loblolly Pine Biomass Cropping Study
Ms. Jessie Maynor 20

Benchmarking Gains from Planting Genetically Improved Loblolly Pine
Ms. Melissa Shockey 21

Session 5: Markers for Gene identification and Tree Improvement
Moderator: Dr. Gary Peter, UF/IFAS School of Forest Resources and Conservation, Gainesville, FL

Metabolomics Approaches for Tracking Biotic and Abiotic Stress Performance in Tree Improvement Programs
Dr. Anna Conrad 23

Progress on Pine SNP Discovery and SNP Array Design
Dr. Fikret Isik 24

Improving the Association Mapping Pipeline in a Loblolly Pine Population with a Complex Pedigree through Increased Marker Coverage Validation Using Disease Resistance Data
Dr. Tania Quesada 25

Whole Exome Genotyping in Loblolly Pine Identified 2.8 Million Single Nucleotide Polymorphisms Used for Association Analyses
Dr. Carol Loopstra 26

Session 6: Seed Orchards
Moderator: ***Prof. Steve McKeand,*** **North Carolina State University, Cooperative Tree Improvement Program, Raleigh, NC**

Role of Summer Fertilization in the Nutrition and Carbon Relations of Loblolly Pine Reproduction
Dr. Mary Anne Sayer and *Dr. She-Jean Susana Sung* 28

Use of Trunk Micro-Infusion Treatments for the Management of Specific Insect Pests of Seed Orchard and Plantation Trees
Dr. Donald Grosman 29

Pollination Bag Type Impacts Cone Survival and Seed Yield for Mass Production of Control Cross Seed in Loblolly Pine
Mr. Austin Heine 30

Cone and Seed Characteristics in the Second Generation Seed Orchard of *Pinus thunbergii:* Seeds are Significant Carbon Sink
Mr. Ki Won Kim 31

Session 7: Quantitative Genetics
Moderator: *Dr. Joshua Adams,* Louisiana Tech University, Ruston, LA

Acoustic Velocity and Drill Resistance Breeding Values and Genetic Parameter Estimates for Juvenile Loblolly Pine of the US Atlantic Coastal Plain
Mr. Trevor Walker 33

US Forest Service Longleaf Pine Progeny Test Review and Analysis
Dr. Dana Nelson 34

Genetic Parameter Estimates from a Large Cloned Population of Loblolly Pine
Mr. Mohammad Nasir Shalizi 35

Session 8: Disease Resistance
Moderator: *Dr. Scott Merkle,* University of Georgia, Athens, GA

Persea Species Restoration in Laurel Wilt Epidemic Areas
Ms. Katherine Smith 37

Population Genetics of the Laurel Wilt Pathogen, *Raffaelea lauricola*
Dr. Tyler Dreaden 38

Fusiform Rust Resistance in an Atlantic Coastal Elite Loblolly Pine Population
Mrs. April Meeks 39

Session 9: Genomic Selection
Moderator: *Dr. Matias Kirst,* UF/IFAS School of Forest Resources and Conservation, Gainesville, FL

Optimization of Genomic Selection Models for Slash Pine Advanced Breeding Population
Mr. Rodrigo Furtado dos Santos 41

Variability of Genetic Response to Selection under GBLUP Evaluation
Dr. Jan Stejskal 42

Analyzing Growth and Oleoresin Productivity of Loblolly and Slash Pine Pseudo-Backcross Hybrids
Ms. Jennifer Lauture 43

Session 10: Broadening Genetic Diversity
Moderator: ***Dr. Fred Raley,*** **Texas A&M University, College Station, TX**

Forest Service Southern Region National Forest System - It's All about GRITS
Ms. Barbara Crane 45

Performance of Sweetgum Varieties on Upland Sites in North Louisiana
Dr. Joshua Adams 46

Diversity of Non-Native Tree Populations in the Different Districts of Rwanda
Dr. Kabera Telesphore 47

Plenary session: Advances in Tree Improvement
Moderator: ***Dr. Timothy White,*** **Former Director and Professor, UF/IFAS School of Forest Resources and Conservation, Gainesville, FL**

Genetic Parameter Estimates of Height-Diameter Relationships in Loblolly Pine
Dr. W. Patrick Cumbie 49

Breeding without Breeding: Confirmation of Theoretical Concept Using Real-World Tree Improvement Program
Dr. Jiri Korecky 50

Conifer Terpenes: Manipulating an Ancient Plant Defense Pathway for Production of Renewable Chemicals and Biofuels
Dr. Gary Peter 51

Posters
Listed in alphabetical order by last name

Using Simple Sequence Repeat Markers to Identify Chestnut Species and Hybrids
Mr. Charles Burdine 54

Project CAPTURE: A U.S. National Prioritization Framework for Tree Species Threatened by Climate Change and Other Threats
Ms. Barbara Crane 55

Recent News - Longleaf Pine Genetics and Silviculture Activities on the Southern National Forests
Ms. Barbara Crane 56

DNA Markers to Identify Southern Pines and their Hybrids
Dr. Craig Echt 57

TIPRoot Database: A Tool for Managing Breeding, Testing, and Selection Data in the NC State University Cooperative Tree Improvement Program
Mr. Daniel Genung 58

Reproductive Biology of *Paulownia elongata*, a Multipurpose Tree
Dr. Nirmal Joshee 59

Genetic Diversity and Clone Structure of the Endangered Species of *Thuja koraiensis:* Conservation Strategy in Response to Climate Change
Mr. Ki Won Kim 60

Effects of Thinning Regimes on Genetic Variation of White Oak (*Quercus alba* L.) in Eastern Hardwood Forests
Ms. Rachel Landham 61

Optimum Neighborhood Seed Orchard Design - Software Package
Prof. Milan Lstiburek 62

Use of Recirculating Irrigation System to Contain Soilborne Pathogen *Phytophthora cinnamomi* in Operational Disease Resistance Trials
Ms. Sunny Lucas 63

New Advanced Generation Seedling Seed Orchards Use Methodology Developed for *Eucalyptus grandis* in Florida
Mr. Peter McClure 64

Development of an In Vitro Assay for Resistance to *Phytophthora cinnamomi* in Chestnut
Dr. Scott Merkle 65

Somatic Embryogenesis in Ozark Chinquapin
Dr. Scott Merkle 66

Soil Compaction in Loblolly Pine Seed Orchards and the Impacts on Tree Health and Cone Yields
Mrs. Serenia O'Berry 67

Pitch Canker Disease as a Model to Discover Biological Drivers of Pitch Canker Disease in a Changing Climate
Dr. Tania Quesada 68

A Novel Approach to Phenotypic Analysis of Forest Trees for Accelerating Breeding
Dr. Donghwan Shim 69

A Proposed Study on the Genetic Control of Fertilizer Response and Post-Senescence Nutrient Content Assessed Via Foliar Sampling in Loblolly Pine
Mr. Andrew Sims 70

List of Participants 71

Plenary Session

Tree Genome Structure and Evolution

Computational Approaches to Decode Megagenomes and Develop Database Resources for the Forest Tree Community
Dr. Jill Wegrzyn..2

Analysis of Pinaceae Gene Family Evolution Suggests Accelerated Gene Turnover in Pine Trees
Dr. Claudio Casola 3

COMPUTATIONAL APPROACHES TO DECODE MEGAGENOMES AND DEVELOP DATABASE RESOURCES FOR THE FOREST TREE COMMUNITY

Jill L. Wegrzyn*, Uzay Sezen, Nic Herndon, Emily Grau, Sean Beuhler, Sumaira Zaman, Alex Hart, Alex Trouern-Trend, and Madison Caballero*

University of Connecticut, Storrs, CT, USA

Forest trees are represented by over 60,000 species and exist in a wide variety of climates. These perennial, long-lived and sessile species create an ideal system to study adaptation to biotic and abiotic stress. Among the numerous forest tree species, only a handful of reference genome sequences exist. Similar to many plants, the genomes of forest trees are both large and complex. The gymnosperms, primarily represented by conifers, are some of the largest genomes sequenced to date.

Research in our plant computational genomics lab seeks to develop tools and techniques to assemble and annotate these exceptional genomes. Recent efforts have focused on annotation of the latest release of the loblolly pine genome (v2.01). In addition to improving contiguity of the reference and accuracy of gene models, we develop software to aid in transcriptome assembly and annotation.

Generating these reference genomes is paired with developing resources to integrate, analyze, and visualize related genomic and genetic information. Recent development in the TreeGenes database (http://treegenesdb.org) focused on cross-database data access and advanced analytical pipelines through the Tripal framework (http://tripal.info). Development of web-based tools that integrate a variety of genomic, phenotypic, and environmental resources to facilitate association mapping analysis is the primary objective of the CartograTree application.

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ANALYSIS OF PINACEAE GENE FAMILY EVOLUTION SUGGESTS ACCELERATED GENE TURNOVER IN PINE TREES

***Claudio Casola**, Weixi Zhu, and Tomasz E. Koralewski*
Department of Ecosystem Science and Management, Texas A&M University, College Station, TX, USA

Gene duplications and losses are major determinants of evolutionary change. We investigated patterns of gene duplications and gene losses in four Pinaceae species: loblolly pine, sugar pine, Norway spruce and Douglas-fir. After clustering orthologous groups in gene families using OrthoFinder, we applied the likelihood framework implemented in the CAFE software to estimate gene turnover rates and patterns in 16,118 gene families (~24,000-28,000 genes per species). We found that gene turnover is at least twice as high in the two pines (~110 gene gains and/or losses per million years) compared to Norway spruce and Douglas-fir, a result that was robust to changes in the model of gene family evolution implemented in CAFE. Additionally, we identified 1,192 gene families with significant expansion or contraction, and a high proportion of gene duplications vs. gene losses in Douglas-fir. Overall, our results indicate that no less than 1/5 of all gene families experienced gains or losses during the evolution of these Pinaceae. However, we observed that 31-48% of genes have a length <75% of the longest gene in the same gene family, supporting previous findings of extensive occurrence of pseudogenes in conifers. Following removal of putative pseudogenes from the 1,192 gene families with high gene turnover rates, we identified several genetic pathways in the four Pinaceae with significant expansions or contractions in multiple gene families, suggesting selection across gene families involved in these biological processes.

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Plenary Session

Accelerating Tree Improvement

What is next in the Application of Genome-Wide Information to Tree Breeding?
Dr. Matias Kirst 5

Genome Editing in Forest Trees: Progress and Future Prospects
Dr. CJ Tsai 6

WHAT IS NEXT IN THE APPLICATION OF GENOME-WIDE INFORMATION TO TREE BREEDING?

Matias Kirst
University of Florida, School of Forest Resources and Conservation, Genetics Institute, Gainesville, FL, USA

Almost three decades have passed since the first quantitative trait loci were identified in tree mapping populations. Despite the early excitement, the wide application of genomic information to forest breeding programs has hardly ever materialized. The difficulties in implementing genomic data in breeding programs have been many, but the most significant impediments have been the inability to uncover the majority of loci that control complex traits and high costs of genotyping technology. Recently, new developments in genome-wide prediction methods and the dramatic reduction in genome services have created a renewed interest in these approaches. Still, it remains unclear if current advances will be sufficient to unleash the wide use of genomics in tree breeding, or if they will once again remain the domain of academics.

I will briefly review the current application of genome-wide information to tree breeding and the outcomes of numerous pilot studies already completed or under way. While the preliminary results from these studies are exciting, they may not be sufficient to entice most tree breeders to incorporate genomic technology, unless decreasing costs and added value and efficiencies can be created. Thus, I will focus largely on what are likely to be the next major leaps in the use of genome-wide information in tree breeding, including the application of prediction models to guide the establishment of the most productive crosses based on specific combining ability, the use of methods that pool progeny to generate accurate predictive models at a fraction of current costs, and the application of low-density, ultra-low cost and high throughput methods of genotyping based on sequencing.

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GENOME EDITING IN FOREST TREES: PROGRESS AND FUTURE PROSPECTS

Chung-Jui Tsai
University of Georgia, Athens, GA, USA

The latest genome editing technology, called CRISPR, is revolutionizing all facets of biology including agriculture and forestry. It enables generation of transgenic null mutants with unprecedented precision and efficiency—a welcoming breakthrough for outcrossing tree species with long generation cycles. In this talk, I will present case studies of CRISPR genome editing in *Populus* for targeted manipulation of multigene family members, and for mutation of tandemly arrayed genes. Sequence polymorphisms in outcrossing species pose an underappreciated obstacle to efficient genome editing. However, sequence polymorphism data are usually inaccessible via current genome portals, and are not considered in popular gRNA design programs. I will discuss genomic resources and variant-sensitive bioinformatics pipelines that we have developed to address the genome editing challenges of outcrossing, hybrid or polyploid species. I will also discuss emerging applications of CRISPR beyond gene editing, and critical gaps in our ability to harness this powerful technology to advance forest biology. In conjunction with early flowering strategies, it will be possible to cross CRISPR null mutants to generate transgene-free progenies in one breeding generation. Elite clones carrying targeted gene mutation(s) without foreign DNA may ultimately help increase public acceptance of bioengineered agricultural products.

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Session 1

Breeding Strategies

Analysis and Selections of the CFGRP 4th Cycle Slash Pine Tree Improvement
Dr. Salvador Gezan 8

The Evolution of Breeding and Testing Strategies in the NC State University Cooperative Tree Improvement Program
Prof. Steve McKeand 9

A New Era for the Hardwood Tree Improvement and Regeneration Center
Dr. Carolyn Pike 10

ANALYSIS AND SELECTIONS OF THE CFGRP 4TH CYCLE SLASH PINE TREE IMPROVEMENT

Salvador A. Gezan, *Gregory L. Powell, Andrew D. Sims, Matias Kirst and Gary F. Peter*
University of Florida, Gainesville, FL, USA

During 2016-2017 the Cooperative Forest Genetics Research Program (CFGRP) of the University of Florida performed a large and detailed statistical analysis to make its 4th-cycle selections. This analysis combined a total of 24 field trials located in the southeastern United States. The variables considered for this analysis included individual tree volume increment and rust score. The trials considered were a mixture of polimix tests (PMX I and PMX II) and full-sib trials (FS) measured at ages ranging from 4 to 8 years since planting.

After data validation and checking, a multi-trial environment analysis was performed that considered for each of the sites its corresponding design effects (replicates, row, column or incomplete blocks within replicate), together with an additive-by-trial effect that was flexible enough to consider a different additive variance per sites and a single type-B genetic correlation between sites. In addition, a family term and its interaction with trial was incorporated, together with a different error variance for each trial. This model allowed to combine different levels of 'genetic signal' from each of the trials into a single analysis.

Breeding values were obtained across all trials, which were later used to select parents (backward selection) and offspring (forward selections). The latter were only performed in the full-sib trials established in 2012. Selections were restricted to have individuals from each of the breeding groups, with limitations on the numbers of individuals per family. A selection index based on 50/50 for volume and rust was used to select the best genotypes.

Preliminary results indicate of this large analysis resulted in a narrow-sense heritability of 0.20 and 0.25 with type-B correlations of 0.73 and 0.88 for volume and rust, respectively. These statistics are similar to those previously reported in other genetic studies of slash and loblolly pine, and they allow for selections of genotypes that produce interesting gains across all planting area. A total of 399 selections were identified with 34 backward and 365 forward selections distributed across the eight breeding groups and all trials. These selections will be evaluated and later used for planning future crosses to establish the new generation for the 5th cycle.

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THE EVOLUTION OF BREEDING AND TESTING STRATEGIES IN THE NC STATE UNIVERSITY COOPERATIVE TREE IMPROVEMENT PROGRAM

Steve McKeand *and Fikret Isik*
NC State University, Raleigh, NC, USA

Tree breeding and selections strategies have changed dramatically in the NCSU Cooperative Tree Improvement Program since its beginning in 1956. For the first and second cycles, random mating was used to generate full-sib crosses for testing. In the third and fourth cycles, parents with high breeding values were crossed more often than lower ranking parents, a form of positive assertive mating. For the fourth cycle, we have also implemented the MateSelect algorithm to balance diversity and genetic gain. For the testing program, early tests were established as randomized complete block experiments with families established in row plots. In the first generation, most full-sib crosses were evaluated in six trials with three or six replications of 10-tree row plots; on average, 270 seedlings were evaluated. In the second cycle of testing, 144 seedlings were tested per cross. For the fourth cycle, the program is implementing alpha cyclic incomplete block row-column designs with the goal of testing 60 seedlings per full-sib family.

Over the years, we have sought to increase the efficiencies of our breeding and testing strategies with the objective of reducing the generation intervals. We will discuss the lessons learned from the breeding and testing strategies implemented over the past 60 years of the program.

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A NEW ERA FOR THE HARDWOOD TREE IMPROVEMENT AND REGENERATION CENTER

Mark Coggeshall[1], ***Carolyn (Carrie) Pike***[2], *Liz Jackson*[3], *Lenny Farlee*[3], *and Robert Wagner*[3]
[1]US Forest Service, HTIRC, Purdue University, West Lafayette, IN, USA
[2]US Forest Service, Northeast Area S&P Forestry, Purdue University, West Lafayette, IN, USA
[3]Purdue University, West Lafayette, IN, USA

The Hardwood Tree Improvement and Regeneration Center (HTIRC) was initiated in 1999 as a national center for research, development and technology transfer for hardwood stewardship. Black walnut (*Juglans nigra*) was selected as the central hardwood flagship species due to its high timber value and veneer markets that continue to drive demand for quality planting stock in the region. Seed orchards at Indiana Division of Forestry's Vallonia State Nursery, developed in cooperation with the HTIRC, produce select black walnut seedlings with improvements for straightness and volume. We have also conducted research and made selections in other species including northern red oak (*Quercus rubra*), black cherry (*Prunus serotina*), and white oak (*Q. alba*). The HTIRC has established an extensive clone bank of butternut (*J. cinerea*) to aid in development of resistance to butternut canker, a devastating pathogen, to facilitate its restoration. We have cooperated with other USDA Forest Service Northern Research Station units to establish seed orchards with improved resistance to beech bark disease. Additionally, field trials of American chestnut (*Castanea dentata*) have been established in collaboration with the The American Chestnut Foundation (TACF), and refined nursery propagation and grafting techniques have been developed for *Juglans* spp.

Tree improvement efforts in the central hardwood region face many obstacles. For one, silvicultural systems are dominated by uneven-aged management which has led to dual emphases on increasing genetic diversity and improving highly heritable traits, such as stem form, in lieu of volume. In recent years, the region has experienced numerous invasions of exotic insects, diseases and plants along with a burgeoning white tailed deer population requiring exclosure of small trees. Further, demand for hardwood seedlings vacillates with availability of government cost-sharing programs, and wanes with surging crop prices that drive landowner decisions to farm rather than reforest newly planted acres.

In January 2017, Dr. Mark Coggeshall replaced Dr. Charles Michler, founding HTIRC project leader. In addition, Dr. Robert Wagner was hired in 2016 as the new Head of Purdue University's Forestry and Natural Resources (FNR) Department, where the HTIRC is located. A new strategic plan, developed by scientists from the US Forest Service and Purdue, identifies three programmatic themes for hardwood systems: tree improvement, management and threats. We are looking for new partners and collaborators as we aim to expand the program's scope to other parts of the region. We invite your interest and collaboration. Please visit our website at https://htirc.org/.

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Session 2

Disease Resistance Genes

Genetic Diversity in Candidate Disease- Resistance Genes in *Pinus taeda* L.
Dr. Daniel Ence 12

Whole-Genome Sequencing of Chestnuts (*Castanea*) Reveals Within- and Among-Species Genetic Variation in Regions Associated with Resistance to Chestnut Blight and Predicted Disease Resistance Genes
Mr. Nicholas LaBonte 13

GENETIC DIVERSITY IN CANDIDATE DISEASE-RESISTANCE GENES IN *PINUS TAEDA* L.

*Matias Kirst[1], **Daniel Ence**[1], Katherine E. Smith[1,2], Robin Paul[4], John M. Davis[1], Jill Wegrzyn[3]*
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[2] Southern Institute of Forest Genetics, Saucier, MS, USA
[3]University of Connecticut, Storrs, CT, USA
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Fusiform rust is a disease incited by the fungus *Cronartium quercuum* f.sp. fusiforme (*Cqf*) on southern pines (where it causes galls on stems and branches) and on oaks (where it causes minimal leaf damage). Fusiform rust is a major disease threat to the timber industry in the US. Rust galls cause annual yield losses that exceed US$100M. The genome annotation of loblolly pine (*Pinus taeda*) has become an essential resource for understanding the genetic basis of resistance to fusiform rust disease (Neale et al. 2014 and Wegrzyn et al. 2014). During the genome annotation process, an expressed sequence tag (EST) was identified that contains a single nucleotide polymorphism (SNP) mapping to the locus (*Fr1*) that interacts with the fungal avirulence gene, *Avr1*. This EST aligns to a full-length transcript from RNA-sequencing data and a TIR-NB-LRR protein, thus identifying it as a candidate *Fr1* gene. In order to understand the population genetic context of this and other pine resistance genes, we sequenced and assembled RNA sequencing data from 92 elite rust-resistant loblolly pine genotypes from five pine-growing regions, identifying candidate resistance genes in the process. Next we aligned the assembled transcripts to the loblolly pine genome and calculated population genetic measures. These results allow us to understand the diversity and conservation of resistance genes that interact with *Cqf* and in elite genotypes that are important to pine breeding for their fusiform rust resistance and growth traits.

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WHOLE-GENOME SEQUENCING OF CHESTNUTS (*CASTANEA*) REVEALS INTER- AND INTRASPECIFIC GENETIC VARIATION IN REGIONS ASSOCIATED WITH RESISTANCE TO CHESTNUT BLIGHT AND PREDICTED DISEASE RESISTANCE GENES

Keith E. Woeste[1], and ***Nicholas R. LaBonte**[2]*
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Uncovering the genetic basis of chestnut blight resistance is critical to transferring blight resistance into susceptible American chestnut (*Castanea dentata*). Three major blight resistance QTL have been discovered, but the genes underlying the QTL are not known. Furthermore, it is likely that genes entirely outside these three QTL regions play a role in blight resistance. Using the draft Chinese chestnut (*Castanea mollissima*) genome assembly and whole-genome sequences from 24 individual chestnuts, including highly resistant *C. mollissima*, moderately susceptible *C. mollissima*, highly susceptible *C. dentata*, hybrids, and “Clapper,” one of the resistance donors from the TACF breeding program, we carried out association tests to identify SNPs associated with blight resistance. The vast majority of associated SNPs were localized to 15 distinct regions on 9 of 12 linkage groups. Three of these regions appear to correspond to previously identified blight resistance QTL. Of the predicted genes that contain associated SNPs, many are similar to known resistance genes in other plants. Patterns of heterozygosity and nucleotide divergence in the predicted gene sequences indicate that while many are essentially “fixed” with one highly homozygous genotype in *C. mollissima* and a divergent one in *C. dentata*, genes that differentiate the most resistant *C. mollissima* from more susceptible *C. mollissima* show elevated nucleotide diversity and heterozygosity in resistant trees.

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Session 3

Biotechnology

Tubulins, Rhythms and Cell Walls in Poplar Leaves; Timing Might Be Everything
Dr. Scott Harding 15

Capturing Loblolly Pine Chromosomes for Genome Sequencing Using Laser Capture Microdissection Microscopy
Dr. Nurul Faridi 16

A Novel Approach to Phenotypic Analysis of Forest Trees for Accelerating Breeding
Dr. Donghwan Shim 17

TUBULINS, RHYTHMS AND CELL WALLS IN POPLAR LEAVES: TIMING MIGHT BE EVERYTHING

***Scott A. Harding**, Hao Hu, Liang-Jiao Xue, Batbayar Nyamdari, and Chung-Jui Tsai*
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We have recently reported on transgenic poplars in which the cell wall structure of xylem was changed due to tubulin manipulation (Swamy et al., 2015). While pleiotropic effects on plant development or morphology were not observed, stomatal closure in response to drought, and stomatal opening in response to light were impaired. The present study was undertaken to measure the impact of tubulin manipulation on leaf primary cell wall composition. A model is discussed in which constitutive over-expression of tubulins interfered with diurnal control of pectin and hemicellulose accrual, thereby altering primary cell wall composition and flexibility.

Alcohol-insoluble cell wall residue of source leaf tissue was sequentially extracted with different solvents to remove pectins, hemicellulose-linked pectins, hemicellulose xylans and other more tightly bound hemicelluloses. The yield of oxalate-extractable pectins was highest in the transgenic line with the highest accumulation of ectopic tubulin protein. The apparent pectin increase in transgenic leaves occurred at the expense of xylose. RNA-Seq analysis revealed that the expression of key genes controlling the partitioning of UDP-glucuronic acid for UDP-xylose (hemicellulose) and UDP-galacturonic acid (pectin) was slightly reduced in the transgenic lines. Ratios of their transcript levels were significantly perturbed compared to the ratios in WT plants in a way that would favor UDP-galacturonic acid formation. The normally oscillatory pattern of changes in the expression ratio of these genes in *Populus* (Filichkin et al., 2011) suggests sensitivity of UDP-glucuronic acid utilization to circadian control. We hypothesize, and there is literature support, that tubulin protein polymers (microtubules) facilitate the delivery of pectic polysaccharides from the golgi network to the cell wall. We suggest that constitutive overexpression of tubulin subunits in the transgenic lines favored utilization of UDP-glucuronic acid for pectic polysaccharides during the day when hemicellulose biosynthesis is less active. As a result, the availability of UDP-glucuronic acid for UDP-xylose synthesis at night was reduced.

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CAPTURING LOBLOLLY PINE CHROMOSOMES FOR GENOME SEQUENCING USING LASER CAPTURE MICRODISSECTION MICROSCOPY

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The loblolly pine (*Pinus taeda*) genome (23 Gb/1C; $2n = 2x = 24$) has recently been sequenced, but the ~1.8 million scaffolds forming the most recent assembly are mostly unordered and unmapped on the known linkage groups. Genome assembly is especially challenging for such large and highly repetitive genomes as in conifers. Sequencing individual chromosomes, separately, obtained through Laser Capture Microdissection Microscopy (LCMM), promises to reduce the complexity of genome assembly and allow for the confident assignment of contigs and scaffolds to specific linkage groups. However, preparation of karyotype-quality slides (full complement of well-separated chromosomes) for LCMM is notoriously difficult in plants compared to animals, where chromosome-based sequencing has been done using LCMM (frog, *Xenopus tropicalis*, Seifertova et al. 2013; salamander, *Ambystoma mexicanum*, Keinath et al. 2015). Obtaining karyotype-quality mitotic spreads is the key for capturing of individually targeted chromosomes with LCMM. We have successfully developed a robust protocol for preparing high-quality pine chromosome spreads on pen-membrane slides for LCMM. As an initial test for individual chromosome sequencing, we selected loblolly pine chromosome 12 (Ch12) for its special characteristic as being the smallest and only sub-metacentric chromosome in pines, and thus it can be easily identified under a 40X objective. Loblolly pine Ch12 are currently being collected and will be amplified using a whole genome amplification technique and sequenced using next generation sequencing (NGS) platforms. We will report the progress of the project.

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A NOVEL APPROACH TO PHENOTYPIC ANALYSIS OF FOREST TREES FOR ACCELERATING BREEDING

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Genomic Selection (GS) is one of the accelerating breeding methods. With the advent of high throughput molecular technology, numerous molecular markers distributed throughout the whole genome can be produced to characterize many genetic entries involving new perspectives in methodology of selection. In tree breeding the GS could significantly reduce the cost of genetic improvement schemes by limiting the size and number of field experiments. In order to successful performed GS, not only the genetic analysis of trees but also accurate phenotypic analysis is very important. Here, we present a novel approach to automatically measurement of tree phenotypes using drone and ground-based scanner. The actual utility of this scanner depends largely on the efficacy of point cloud data (PCD) analysis. The quantified data of each tree was validated using laborious measurements. The results showed that the individual tree growth was accurately reproduced using our method from three dimension registered scans, with a relative deviation of less than 5%. Therefore, we want to apply this method phenotype analysis for accelerating breeding and management of large-scale progeny test site.

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Session 4

Wood Yield

Benefits of Loblolly Pine Genetic Improvement for the Upper Coastal Plain of Mississippi
Ms. Valerie West 19

Loblolly Pine Biomass Cropping Study
Ms. Jessie Maynor 20

Benchmarking Gains from Planting Genetically Improved Loblolly Pine
Ms. Melissa Shockey 21

BENEFITS OF LOBLOLLY PINE GENETIC IMPROVEMENT FOR THE UPPER COASTAL PLAIN OF MISSISSIPPI

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Across the southeast U.S. landowners who wish to plant loblolly pine (*Pinus taeda* L.) are finding they have more options than ever before. In the past, plantation establishment relied primarily on open-pollinated seedlings. As breeding programs have progressed the seedling marketplace has grown to include multiple generations of open-pollinated (OP) stock, full-sib family stock generated by mass control pollination (MCP), and varietal stock derived from somatic embryogenesis or hedging. These new and diverse reforestation options need to be tested for suitability to the non-industrial private landowner (NIPL). In 2007, a loblolly pine genetic level study was installed in northern Mississippi to examine differences in growth among second-generation OP seedlings, MCP seedlings, and varietal stock. Following eight growing seasons, the average height of the MCP material was significantly taller than that of the varietal and second-generation OP planting stock types. The second-generation OP stock was also significantly taller on average than the majority of the varietal stock tested, in respect to total height. The average DBH of the MCP material was significantly larger than that of either the second-generation OP or the various varietals tested. The current findings of this study indicate that for the upper coastal plain of northeastern Mississippi the use of loblolly pine MCP material will maximize both total height and diameter growth for the forest landowner.

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LOBLOLLY PINE BIOMASS CROPPING STUDY

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Loblolly pine is grown on millions of acres across the Southeast because of its rapid growth and responsiveness to silvicultural and management inputs. Considerable genetic differences within species exist for growth, stem form and wood quality traits that influence biomass/biofuel production. By planting genetically superior trees with desirable biomass/biofuel traits, it is possible to dramatically increase the amount of biomass produced at any given site.

As part of the NC Department of Agriculture & Consumer Services Bioenergy Research Initiative, the NC State University Cooperative Tree Improvement Program established a trial in the Piedmont of NC near Butner with 20 of the fastest growing families, each with different characteristics that influence their bioenergy potential. At age three years, there were significant differences in height and stem forking between Coastal and Piedmont families. Most Coastal families were substantially taller than Piedmont families but had a higher frequency of forking. Shortly after completing these measurements, there were two severe ice/snow storms and very cold temperatures at the site, providing a unique opportunity to assess differences in cold hardiness between provenances and families. On average, Coastal families experienced higher stem breakage (33%) than the Piedmont families (25%). Five-year measurements were recently collected and will be reported at the conference along with future plans for the study site, which includes a harvest/thin at age 10 years to evaluate biomass and sawtimber yields.

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BENCHMARKING GAINS FROM PLANTING GENETICALLY IMPROVED LOBLOLLY PINE

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As loblolly pine (*Pinus taeda*) is the most important commercial tree species in the southeast US, much effort has been placed on selecting progeny with improved growth characteristics. Stands with different genetic backgrounds will lead to different stand characteristics over time. Straighter boles, fewer forks, and improved rust resistance are just a few examples of the types individual tree characteristics that tree breeding programs seek to improve. Developing a benchmark for comparison of improved genotypes is of importance so it can be determined if improvement gains are being met. The early selection open-pollinated (OP) loblolly pine family 07-56 has been widely planted across the southeast due to its fast growth. As such, it is a good candidate to act as a benchmark across the range where it has been planted.

The objectives of this study are to characterize OP family 07-56 stands across a range of sites and ages by describing diameter distributions, stem volume, and variability in individual tree traits. Data used for this study comes from five different unthinned block-plot Plantation Management Research Cooperative (PMRC) research trials located in the upper and lower coastal plain of GA, and the lower coastal plain of FL and SC.

Initially, the Kolmogorov-Smirnov test was used to determine if a two-parameter Weibull distribution was an appropriate fit for the diameter distributions. It was concluded that indeed a two-parameter Weibull distribution was appropriate for the data; shape and scale parameters were developed on the plot level. Shape and scale parameters were estimated following Bullock and Burkhart's (2005) methods in which age, basal area and trees per hectare were used to augment the models. Summary statistics of individual tree heights and diameters were determined on the plot level. Defects such as presence of fusiform rust, forking, and crook/sweep, decrease the quality, quantity, and value of sawtimber. Knowledge of the proportion of trees impacted in OP 07-56 by quality/value reducing defects is important for land managers; it can also be used as a mechanism of comparison for other improved loblolly pine genotypes therefore variables for rust and sawtimber quality were included in modeling efforts.

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Session 5

Markers for Gene Identification and Tree Improvement

Metabolomics Approaches for Tracking Biotic and Abiotic Stress Performance in Tree Improvement Programs
Dr. Anna Conrad 23

Progress on Pine SNP Discovery and SNP Array Design
Dr. Fikret Isik 24

Improving the Association Mapping Pipeline in a Loblolly Pine Population with a Complex Pedigree through Increased Marker Coverage Validation Using Disease Resistance Data
Dr. Tania Quesada 25

Whole Exome Genotyping in Loblolly Pine Identified 2.8 Million Single Nucleotide Polymorphisms Used for Association Analyses
Dr. Carol Loopstra 26

METABOLOMICS APPROACHES FOR TRACKING BIOTIC AND ABIOTIC STRESS PERFORMANCE IN TREE IMPROVEMENT PROGRAMS

Anna Conrad[1], *Jared Westbrook*[2], *Tatyana Zhebentyayeva*[3], *Luis Rodriguez-Saona*[4], *Pierluigi Bonello*[4], *Joseph James*[5], *Steven Jeffers*[3], *Paul Sisco*[6], *Frederick Hebard*[6], *Laura Georgi*[2], *Margaret Staton*[7], *Jean-Marc Audergon*[8], *Veronique Decroocq*[9], *Zongrang Liu*[10], *Christopher Dardick*[10], *C. Dana Nelson*[1,11], *and Albert Abbott*[1]

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With the development of higher throughput platforms for qualifying and quantifying metabolite composition, it is now possible to obtain a snapshot in time and space of the general and/or specific metabolite composition of plant tissues. This information coupled with phenotypic evaluation of plant performance can be used to identify biomarkers that may have utility for rapidly monitoring plant stress performance in improvement programs. This is particularly relevant for tree species where improvement programs have expensive labor and space requirements; therefore, rapid earlier monitoring and elimination of potentially poor performers at the seedling stage is desirable. In this regard, we have initiated two studies designed to evaluate: 1) the utility of general metabolomic profiles for the identification of chemical fingerprints linked to pathogen resistance in American × Chinese chestnut hybrids, and 2) specific metabolic pathway components in the phenylpropanoid pathway as biomarkers for developmental progression (i.e. fruit tree flowering) linked to annual climatic cycling. Our results indicate that evaluation of metabolite composition can be used to develop chemical fingerprint-based models to predict pathogen resistance in chestnut although further evaluation is needed to confirm these results and test the applicability of this approach on a larger scale. In addition, we found that evaluation of metabolite composition can be used to identify phenylpropanoid intermediates associated with developmental progression and adaptive trait variation in the perennial tree species peach and apricot. These studies highlight the potential utility and applicability of metabolite-based assay methods for breeding trees resistant to biotic and abiotic stresses imposed by invasive pathogens and a rapidly changing climate.

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PROGRESS ON PINE SNP DISCOVERY AND SNP ARRAY DESIGN

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Genomic selection has the potential to revolutionize pine breeding. Our efforts funded by the USDA-NIFA aim to bring genomics to pine breeding, with the goal of greatly improving genetic gain per unit time. Our group is coordinating SNP discovery efforts to bring genetic resources together for multiple pine species and use consistent bioinformatics tools for selection of informative SNPs. The genomic resources will be organized in the TreeGenes database for public access. These genetic resources (informative SNP markers, annotation, and an improved loblolly pine genome assembly) will stimulate a new wave of novel research endeavors in pine breeding and conifer genomics. During the first year of our four-year project, we have improved the genome assembly of loblolly pine by aligning deep transcriptomic sequence (Illumina short reads and PacBio Iso-Seq) for scaffolding purposes. This resulted in a total of 11,951 linked scaffolds to create 4,545 new super scaffolds. This improved assembly (v2.01) has been released to the PineRefSeq project page and TreeGenes database. It reports an N50 of 111 Kbp across a total of 1.76 million scaffolds (~1 million of 1Kbp and longer). This release serves as the primary reference for an updated gene (29,213 models) and repeat (84%) annotation. The final gene selection totaled 29,213 full-length high-quality gene models with an additional 14,045 partial models. Genomic resources generated from the PineMAP project are currently being aligned against v2.01 and SNPs are being assessed via an in-house pipeline, which leverages Freebayes, Varscan2, and applicable filtering. Preliminary SNP calls will be validated based on sequence and mapping qualities and will be used to describe genome-wide patterns of diversity and linkage. Over the next two years of the project we hope to genotype large number of samples for genomic predictions and other research applications.

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IMPROVING THE ASSOCIATION MAPPING PIPELINE IN A LOBLOLLY PINE POPULATION WITH A COMPLEX PEDIGREE THROUGH INCREASED MARKER COVERAGE VALIDATION USING DISEASE RESISTANCE DATA

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Next-generation sequencing technologies enables identification and detection of a large number of sequence variants or molecular markers. This allows a better characterization of genomic regions of interest in search for candidate genes of interest. In loblolly pine, resistance screening of fusiform rust and pitch canker diseases is routine in genetic improvement programs, as deployment of susceptible material would result in high economic losses to the timber industry. The CCLONES (Comparing Clonal Lines on Experimental Sites) population at the University of Florida has been one of the best characterized loblolly pine populations at a phenotypic and genotypic level. This population consists of 71 full-sib families derived from a circular diallel mating design with 41 parents. Previous studies have used this population to identify significant associations with fusiform rust resistance, pitch canker, and other traits using over 4,800 polymorphic SNPs.

More recently we used next-generation sequencing to genotype this population and increased the genotypic data available to over 67,000 SNPs. Because of the large datasets, a script was implemented using R software to automate table processing and selection a subset of 400, 1000, and 5000 SNP markers based on differences between the homozygous classes for each SNP. Association analyses were then performed using BAMD (Bayesian Association with Missing Data), a program that evaluates all SNPs simultaneously, performs multiple imputations of missing SNP data and uses the posterior distribution to generate a confidence interval from which significant associations can be detected.

Phenotypic data from previous screenings for fusiform rust and pitch canker were used to test the table processing pipeline. Nine significant associations were obtained for both fusiform rust at confidence intervals of 90% or higher. Sequence comparisons between the contigs harboring the old and new sets of SNPs are in process to confirm common markers between the datasets and validate the location of the significant SNPs in the pine genome.

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WHOLE EXOME GENOTYPING IN LOBLOLLY PINE IDENTIFIED 2.8 MILLION SNPS USED FOR ASSOCIATION ANALYSES

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Until recently, the number of markers available for genomic studies of loblolly pine (*Pinus taeda* L.) was limited. A much larger number is needed to cover the enormous genome in order to facilitate the use of genomics to accelerate breeding. Sequencing of the loblolly pine genome combined with improved methods for whole exome capture and sequencing allowed us to identify and genotype much larger numbers of single nucleotide polymorphisms (SNPs) in 375 trees from the ADEPT2 population. Exome sequence capture oligonucleotide probes (Roche NimbleGene) were designed using 199,723 exons in 48,391 high quality tentative genes. The probes covered 46,206,684 bp of the target regions. Trees were multiplexed for sequencing and between 25.25 and 60.55 million sequence reads were obtained per tree. The reads were mapped to loblolly genome assembly v 1.01. When the SNPs were filtered using the criteria of at least 10X sequencing depth in at least 90 % of the individuals and a minor allele frequency ≥0.05, 972,720 SNPs were acquired for downstream analyses. When the criteria were relaxed to include sequences with at least 5X depth in 100 % of trees with a MAF ≥ 0.01, 2,822,609 SNPs were identified.

The SNP markers were used to test for single locus associations, SNP-SNP interactions and correlation of individual heterozygosity with phenotypic traits. A total of 36 SNP-trait associations were found after false discovery rate (FDR) correction for specific leaf area (5 SNPs), branch angle (2), crown width (3), stem diameter (4), total height (9), carbon isotope discrimination (4), nitrogen concentration (2), and pitch canker resistance traits (7). Eleven SNP-SNP interactions were found to be associated with branch angle (1), crown width (2), total height (2), carbon isotope discrimination (2), nitrogen concentration (1), and pitch canker resistance (3). Non-additive effects imposed by dominance and epistasis account for a large fraction of the genetic variance for the quantitative traits. Genes that contain the identified SNPs have a wide spectrum of functions. Individual heterozygosity positively correlated with water use efficiency and nitrogen concentration. Association analyses done using also expression data for 198 genes with putative roles in wood development or response to drought or disease identified 2,581 significant associations. Analyses done using concentrations of 82 metabolites identified 536 associations with 53 metabolite concentrations. In conclusion, multiple effects identified in this study influence the performance of loblolly pines. This study has provided resources for understanding the genetic control of complex traits that have potential value for assisting with breeding through marker assisted and genomic selection.

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Session 6

Seed Orchards

Role of Summer Fertilization in the Nutrition and Carbon Relations of Loblolly Pine Reproduction
Dr. Mary Anne Sayer and *Dr. She-Jean Susana Sung* 28

Use of Trunk Micro-Infusion Treatments for the Management of Specific Insect Pests of Seed Orchard and Plantation Trees
Dr. Donald Grosman 29

Pollination Bag Type Impacts Cone Survival and Seed Yield for Mass Production of Control Cross Seed in Loblolly Pine
Mr. Austin Heine 30

Cone and Seed Characteristics in the Second Generation Seed Orchard of *Pinus thunbergii:* Seeds are Significant Carbon Sink
Mr. Ki Won Kim 31

ROLE OF SUMMER FERTILIZATION IN TH E NUTRITION AND CARBON RELATIONS OF LOBLOLLY PINE REPRODUCTION

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A 4-year study of loblolly pine reproduction dynamics was initiated in January 2015 in a southwest Louisiana seed orchard 20 years after ramet establishment. The immediate goal of this study is to identify operational treatments that enhance the cone production and seed efficiency of desirable loblolly pine genotypes. We initially hypothesized that summer fertilization and irrigation influence ramet nutrition and carbon source-sink relations to ultimately affect female strobili differentiation, the retention of female strobili and conelets, and the production of cones with a high seed efficiency. Levels of fertilization are (1) operational fertilizer application (OFA) of essential macro- and micronutrients as recommended annually by the Western Gulf Forest Tree Improvement Cooperative, (2) OFA plus mid-summer application of P, and (3) OFA plus mid-summer application of both P and N. Levels of irrigation applied in 2015 were ambient rainfall and drip irrigation of 288 gallons of water per ramet each day between July 10 and September 21. Ramet observations and treatment responses in 2015 warranted omission of the irrigation treatment in 2016. Ramets of one loblolly pine clone (30 in 2015 and 24 in 2016) were intensively measured to quantify vegetative and reproductive phenology, shoot leaf area by production year and flush, seasonal foliar nutrition, fascicle-level photosynthesis, and cone and seed yields. Data have identified windows of time when the carbohydrate supply for reproduction may be jeopardized by the carbohydrate demand of developing sinks. In 2016, for example, dramatic female strobili abortion coincided with the simultaneous occurrence of high flush and immature cone carbohydrate demands and prolonged cloudiness. The influence of fertilization treatments on aspects of ramet physiology that are important to reproduction during these windows of potential carbohydrate stress will be investigated in 2017 and 2018.

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USE OF TRUNK MICRO-INFUSION TREATMENTS FOR THE MANAGEMENT OF SPECIFIC INSECT PESTS OF SEED ORCHARD AND PLANTATION TREES

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Cone and seed insects severely reduce potential seed yields in southern pine seed orchards that produce genetically improved seed for regeneration programs. Some of the more important insect pests include the coneworms (*Dioryctria* spp.) that attack flowers, cones and stems of pines and the seed bugs (southern pine seed bug, Leptoglossus corculus, and shield-backed pine seed bug, Tetyra bipunctata), that suck the contents from developing seeds in conelets and cones, scales, thrips and cone beetles. Without a comprehensive insect-control program, these pests commonly destroy 50% of the potential seed crop. Other scolytid beetles, such as Ips engravers (Ips spp.), black turpentine beetle (Dendroctonus terebrans) and southern pine beetle (*D. frontalis*), can cause extensive direct mortality to trees in seed orchards, progeny test sites and commercial plantations.

The efficacies of systemic insecticides emamectin benzoate and imidacloprid have been evaluated by the Forest Pest Management Cooperative in numerous seed orchards and plantation trials during the past 19 years for preventing damage and mortality to cones and/or trees by cone and seed insects, cone and bark beetles and other arthropods. Emamectin benzoate has been found to be consistently effective in reducing cone damage and mortality (80 – 95%) by coneworms and to a less extent damage caused by seed bugs and slash pine flower thrips in both slash pine and loblolly pine orchards for two years compared to untreated checks. In contrast, imidacloprid is effective against seed bug and pine needle scale, but less effective against coneworms. Additional trials also have shown that a single application of emamectin benzoate has good activity against several species of scolytid bark and cone beetles for two or more years.

Although micro-infusion treatments have been proven to be highly effective at reducing damage and/or mortality, single tree injection applications have the stigma of being somewhat time consuming. A recent development in application technology will serve to significantly reduce application time and costs. This new method will be described.

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POLLINATION BAG TYPE IMPACTS CONE SURVIVAL AND SEED YIELD FOR MASS PRODUCTION OF CONTROL CROSS SEED IN LOBLOLLY PINE

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In 2016, over 1.4 million pollination bags were installed by seed orchard crews for mass production of control crossed seed of loblolly pine (*Pinus taeda* L.). At these production levels, even modest increases in seed yields for these control crosses will have a significant impact on seed orchard profitability and returns on investment in tree improvement. In the spring of 2014, we installed a study to compare four pollination bag prototypes. Bags from PBS International were compared to the industry-standard Lawson pollination bag with and without a support wire. Open-pollinated flowers were included as a control treatment. Based on preliminary results from the 2014 installation, another round of prototype testing began in the spring of 2015. The main objective of both trials is to compare seed yields and seed efficiencies of cones produced from different pollination bags.

Members of the NCSU Tree Improvement Cooperative installed this study in their operational seed orchards throughout the southeast US. In 2014, each bag type was installed at 9 orchards with 3 clones per orchard and 10 experimental blocks per clone, the target being 270 observations per bag type. The 2015 installation was very similar in design with the main exception being that the number of experimental blocks per clone was reduced from 10 to 5.

To quantify the utility of each bag, cone survival and seed yield per bag were calculated following cone harvest. Seed efficiency per cone was also calculated by counting the number of fertile and infertile cone scales. The 2014 version of the study is now complete; for seed yield per bag and cone survival, significant differences were found between the industry standard Lawson pollination bag and the two prototype bags and Lawson with a support wire. Results from the 2014 study suggest that stiffer/stronger material or the addition of a support wire to Lawson pollination bags increases female strobili survival at least 15%. The 2015 analysis is underway, and preliminary results indicate that cone survival per bag is significantly different between the Lawson bags and some PBS prototypes.

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CONE AND SEED CHARACTERISTICS IN THE SECOND GENERATION SEED ORCHARD OF *PINUS THUNBERGII*: SEEDS ARE SIGNIFICANT CARBON SINK

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Seed orchards are established from selected trees (plus trees) by sexual or asexual propagation, and functioned as the bridge between breeding program and plantation establishment. They are designed and managed to produce genetically improved seeds as many as possible. *Pinus thunbergii* is a two needle pine and native along the coastal areas in Korean peninsula. Based on the genetic information of progeny tests, the second generation seed orchard of *P. thunbergii* was established to achieve further genetic gain by grafts propagated from the selected combinations. The main purposes of present study were to survey the variation of seed-cone production among combinations, to investigate the characteristic of cone and seed by cone analysis, and to estimate genetic parameters (variance component, heritability and correlation) of seed characters in the second generation seed orchard.

We collected three to five mature cones from all individuals for three consecutive years and selected five healthy cones from 26 parental combinations, which had been not suffered from insects or diseases. And then we measured the length (mm), width (mm) and fresh weight (g) of cones each year. After the measurement, the cones were placed at room temperature for cone analysis. The cones were completely open after four week drying and seeds were extracted. The scales were classified into fertile and infertile scales depending on their shape and the seeds were grouped into developed seeds and aborted ovules. Mature seeds were classified into filled seeds, empty seeds and damaged seeds. Aborted ovule was classified into first-year aborted ovule and second-year aborted ovule. One-way ANOVA was carried out for the characteristics of cone and seed, and variance component and brood-sense heritability were estimated. Pearson's and Spearman's correlation coefficients were calculated for the characteristics during the survey years (2014∼2016).

There was a large variation of cone characteristics among combinations. The morphological characters of cone were superior in 2016 but the difference among combinations was relatively larger than other years. The mean weight of cone was ranged from 18.1g in 2014 and 28.4g in 2016, which was 56.9% heavier for three years. The means of cone length and width were also increased as the seed orchard is matured. The cone analysis revealed that there was a large difference of seed characteristics among combinations and years. The numbers of developed seeds were 60.4 (2014), 65.0 (2015) and 71.0 (2016), and the percentage of filled seed per cone was increased from 77.6 (2014) to 90.1 (2016). The aborted ovule was highest in 2014 (24.9%) and the seed efficiency was improved from 2014 to 2016. The broad-sense heritabilities (H2) of seed characters were ranged from 0.25 (filled seed) to 0.54 (seed efficiency), and the H2 of cone characters were also high. These results imply that seed and cone traits are under strong genetic control. The correlation among cone characters was positive and highly significant for all studied years. As expected, there was a strong positive correlation between cone weight and yield.

Developing seed is a strong carbon sink. Under the increased ambient CO2 concentration, trees may mature reproductively fast and produce more seeds. The carbon sink by seed production is a natural reservoir that stores carbon-containing chemical compound for an almost indefinite period of tree life.

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Session 7

Quantitative Genetics

Acoustic Velocity and Drill Resistance Breeding Values and Genetic Parameter Estimates for Juvenile Loblolly Pine of the US Atlantic Coastal Plain
Mr. Trevor Walker 33

US Forest Service Longleaf Pine Progeny Test Review and Analysis
Dr. Dana Nelson 34

Genetic Parameter Estimates from a Large Cloned Population of Loblolly Pine
Mr. Mohammad Nasir Shalizi 35

ACOUSTIC VELOCITY AND DRILL RESISTANCE BREEDING VALUES AND GENETIC PARAMETER ESTIMATESS FOR JUVENILE LOBLOLLY PINE OF THE US ATLANTIC COASTAL PLAIN

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Historically, selection for wood properties has been lacking from US southern pine breeding programs due to the prohibitively high cost to measure these traits on a large number of trees. Relatively recent innovations with indirect measurement tools now enable non-destructive, rapid assessment of large numbers of standing trees. These innovations include tools that measure acoustic velocity (as a surrogate for wood bending strength) and drill resistance amplitude (a surrogate for wood density). The potential for these tools to rank families for selection from progeny tests has been demonstrated in previous studies; however, this study is the first to present results of assessments in an operational setting, including a large number of families (270) of deep pedigree origin (third generation parents), tested widely in the southeastern US.

Measurements were taken in seven-year-old loblolly pine (*Pinus taeda* L.) half-sibling progeny tests established as part of the 3rd-Cycle of breeding and testing for the Atlantic Coastal population by the NC State University Cooperative Tree Improvement Program. Eight progeny test sites were sampled, two sites each from four multi-environmental progeny test series. Each test site contained approximately 70 families, represented in single-tree plots in a randomized complete block design with 20 experimental blocks per site. The Fakkop TreeSonic was used to measure acoustic velocity and the IML PD-Series Resistograph was used to measure drill resistance amplitude. To avoid shaft friction (drillbit drag), the Resistograph profile was split in half and only the first half was retained.

Heritability estimates for acoustic velocity were high: narrow-sense heritability across multiple environments was 0.39 and the half-sib family-mean heritability was 0.89. Genetic correlations between velocity and growth traits (height, diameter, straightness) were low, except for a moderately strong genetic correlation (r_G = 0.60) with height to diameter ratio (i.e. tree slenderness). We conjecture that the genetic correlation between slenderness and wood stiffness is due to the requirement of stiffer wood for families that emphasize height growth over girth to avoid stem breakage. One family had an exceptional breeding value for acoustic velocity (4.3 standard deviations above the mean) and also had an outlying breeding value for height to diameter ratio. Genotype by environment interaction was minor (type-B genetic correlation of 0.84).

Drill resistance amplitude narrow-sense heritability was 0.28 and half-sib family-mean heritability was 0.67. Genetic correlations with growth traits were very low, with about one quarter of families being above average for both volume and drill amplitude. Interestingly, the family with the highest drill amplitude breeding value also had a very high volume breeding value, which was comparable to a widely-planted parent for volume production. Genotype by environment interaction for drill amplitude was negligible (type B genetic correlation of 0.94). he genetic correlation between drill amplitude and specific gravity (measured on a subset of test sites) was very strong (r_G = 0.97).

The local checklot consistently ranked very near the average for both acoustic velocity and drill amplitude, corroborating selection on growth traits has not negatively affected wood properties. These results suggest a large amount of gain is possible for wood stiffness and density for loblolly pine families of the Atlantic Coastal Plain region in the US by using rapid assessment tools.

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US FOREST SERVICE LONGLEAF PINE PROGENY TEST REVIEW AND ANALYSIS

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Longleaf pine (*Pinus palustris* Mill.) is an ecologically and economically important pine species native to the southern US coastal plain from southeast Texas to southeast Virginia, including some higher elevation areas in north Alabama and Georgia. It is a species of concern having lost 97% of its native habitat due to a preference for loblolly pine in artificial regeneration, a reduction in fire as a management tool, and various land-use changes. Interest in restoring a substantial amount of the longleaf pine ecosystems across the region has been underway since the late 1990s. To support this restoration effort, large-scale artificial regeneration efforts were initiated over a decade ago. Access to genetically diverse, well-adapted seed sources has been a challenge in support of this effort. Very few longleaf pine seed orchards have been maintained or even preserved because resources (funding, personnel) to support longleaf pine improvement programs were severely reduced more than 20 year ago. Arguably the most extensive longleaf pine genetic improvement program was implemented by the US Forest Service's Southern Region in the 1980s. Through the years a small but persistent effort has continued within the Southern Region to maintain the existing first-generation seed orchards (now comprising 75% of all longleaf pine orchards) and preserve more than half (34 of 55) of the associated progeny tests. In an effort to enhance and extend the seed orchard capacity for longleaf pine, all viable longleaf pine progeny tests have been located, are being maintained, will be groomed for seed production areas, and have been re-measured using a sub-sampling scheme to reduce costs. Analysis of the resulting data set will be used to provide information for first-generation orchard rouging as well as to identify selections for grafting to establish a series of second-generation orchards. These data include two to eight tests on National Forests within seven states-- Texas, Louisiana, Mississippi, Alabama, Florida, South Carolina and North Carolina. We will report results obtained from our analysis and also discuss development options for both first- and second-generation orchards.

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GENETIC PARAMETER ESTIMATES FROM A LARGE CLONED POPULATION OF LOBLOLLY PINE

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Cloned progeny tests provide the ability to test the same genotypes in multiple environments. Compared to seedling progeny testing, cloned tests are more expensive but provides more reliable prediction of the genetic merit of individuals. The aim of this study was to estimate genetic parameters and predict breeding values for a large clonal population of elite loblolly pine.

This study included a clonal population obtained from 51 full-sibling crosses made from 24 elite parents of loblolly pine from the US Atlantic Coastal Plain. About 45 full-sib progeny per cross were cloned via rooted cutting techniques and planted at eight locations in the southeastern US. Each clone had one copy per location. An incomplete block row-column experimental design was used. Tree height, diameter at breast height, stem straightness, and the incidence of fusiform rust disease (caused by *Cronartium quercuum* f. sp. *fusiforme*) and forking were measured at age six. Individual tree models were fit to partition observed phenotypic variance into genetic and environment effects. Several variance-covariance structures were evaluated to model the clone by environment interactions, including compound symmetry, heterogeneous genetic, and factor analytic structures. The residual variance structure was allowed to be heterogeneous by site.

Results for height are reported here. More complex genetic covariance structures generally improved model fit statistics, indicating that heterogeneity in the data was better explained. However, the effect of variance-covariance structures on the precision of the breeding value predictions was modest. Overall standard error of difference between predicted genetic merit of clones was 5.1 for the compound symmetry and decreased to 5.0 for the factor analytic model. Sites had large differences for additive genetic and residual variances. The ratio of additive genetic variance over the residual variance at sites ranged from 0.16 to 0.65, indicating substantial differences in test site uniformity. However, the estimated clone mean heritability estimate was very high (0.97).

The extended factor analytic structure proved to be the best fitting model. This model explained 92% of genetic variance within sites. Genotype by environment interaction was generally negligible between sites. Additive genetic correlations between pairs of sites was generally well above 0.75, with an exception between site three and five (0.58). These results showed a high efficiency of selection from cloned progeny testing in loblolly pine, especially when utilizing advanced variance-covariance structures to model tree measurements.

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Session 8

Disease Resistance

Persea Species Restoration in Laurel Wilt Epidemic Areas
Ms. Katherine Smith 37

Population Genetics of the Laurel Wilt Pathogen, *Raffaelea lauricola*
Dr. Tyler Dreaden 38

Fusiform Rust Resistance in an Atlantic Coastal Elite Loblolly Pine Population
Mrs. April Meeks 39

PERSEA SPECIES RESTORATION IN LAUREL WILT EPIDEMIC AREAS

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Since its introduction in 2002, laurel wilt disease has spread across the southeastern US causing significant losses to redbay (*Persea borbonia*) and swampbay (*Persea palustris*) populations and to the avocado industry in Florida. The causative fungus, *Raffaelea lauricola*, is a symbiont of the redbay ambrosia beetle, *Xyleborus glabratus*. Given that the fungus can incite disease on a wide range of *Lauraceae* species and that beetles can pick up fungal symbionts from other beetles, there is strong concern that laurel wilt will spread beyond the range of redbay. The disease poses widespread ecological threats to species that contribute to canopies throughout the tropics and subtropics. Survivor trees collected from five US coastal maritime forest locations were propagated for genetic studies and restoration efforts. Disease severity ratings of survivor tree ramets revealed six of sixty-six genotypes tolerant to artificial fungal inoculation. Inoculations of open pollenated seedlings of these genotypes are underway to help understand inheritance of fungal tolerance and susceptibility. In addition, microsatellite markers, developed to track parentage and test diversity in the redbay survivor population, are being used to access the genetic diversity and relatedness of the persea species redbay, swamp bay and silk bay (*Persea humilis*). These data add valuable information to restoration efforts.

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POPULATION GENETICS OF THE LAUREL WILT PATHOGEN, *RAFFAELEA LAURICOLA*

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Laurel wilt is an emerging disease of members of the Lauraceae plant family in the southeastern United States. The disease is characterized by systemic wilt and rapid mortality. It is caused by *Raffaelea lauricola*, a fungus in the Ophiostomatales that is vectored by the redbay ambrosia beetle (*Xyleborus glabratus*) that was likely introduced to the southeastern United States from Asia around 2002. It was hypothesized the disease resulted from a single introduction event and the fungus has clonally replicated in the US. To test this hypothesis and guide resistance screening efforts, a population genetics study of *R. lauricola* using isolates from Burma, Japan, Taiwan, and the southeastern United States, using 11 microsatellite loci was conducted. A single multilocus genotype and a single mating type was found in the US and multiple multilocus genotypes and two mating types were found in the Asian isolates. Our findings support the single US introduction hypothesis, aid in the development of resistance screening methods and highlight the need to prevent the introduction of additional *R. lauricola* genotypes.

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FUSIFORM RUST RESISTANCE IN AN ATLANTIC COASTAL ELITE LOBLOLLY PINE POPULATION

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Fusiform rust is the most critical disease affecting the health and productivity of loblolly pine (*Pinus taeda* L.), the most commercially important pine in the Southeast. An Atlantic Coastal Elite (ACE) breeding population was developed in the NC State University Cooperative Tree Improvement Program to assess the short-term genetic gain for the Coastal regions of the Southeast. Twenty-four elite Atlantic Coastal parents were mated to produce 76 crosses and were screened at the US Forest Service Resistance Screening Center (RSC) in Asheville, NC. About 9775 progeny of the 76 crosses were challenged with a broad-based inoculum from expected deployment ranges, at a spore density of 50,000 spores per milliliter, and assessed for gall presence or absence after six months. The overall rust incidence was 0.48. Full-sib family means ranged from 0.11 to 0.83. The combined additive and genetic dominance explained 9.9% of the phenotypic variance. The ratio of dominance over the additive genetic variance was 0.13 (± 0.07). The narrow-sense heritability of full-sib family means was 0.93 (± 0.03), suggesting strong genetic differences among families.

Selection for rust resistant progeny was conducted at age six months, after gall assessment. All seedlings with rust galls, as well as some entire full-sib families, were discarded based on the expectation they would also be susceptible in the field. The remaining 2362 seedling progeny of the 51 crosses (~45 per family) were clonally propagated via rooted cuttings. Ramets of the clones were planted across eight test sites using incomplete block row-column designs. A half-sib family that was not tested for rust resistance at the RSC was included in the test design as a checklot, and fusiform rust disease incidence was recorded for these seedlings in the field tests. Survival, height, diameter at breast height, incidence of fusiform rust galls, straightness, forking and ramicorn branching were assessed at ages four and six. At age four, the cloned ACE population had an overall rust incidence of 0.02. The checklot family had 0.19 rust incidence both at ages four and six. At age six, the overall rust incidence was 0.06, indicating screening at the RSC with subsequent field-testing of survivors was effective.

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Session 9

Genomic Selection

Optimization of Genomic Selection Models for Slash Pine Advanced Breeding Population
Mr. Rodrigo Furtado dos Santos 41

Variability of Genetic Response to Selection under GBLUP Evaluation
Dr. Jan Stejskal 42

Analyzing Growth and Oleoresin Productivity of Loblolly and Slash Pine Pseudo-Backcross Hybrids
Ms. Jennifer Lauture 43

OPTIMIZATION OF GENOMIC SELECTION MODELS FOR SLASH PINE ADVANCED BREEDING POPULATION

*Matias Kirst, **Rodrigo F. Santos**, Gregory L. Powell, Salvador A. Gezan and Patricio R. Muñoz*
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Productivity of Southern pines plantations have dramatically increased over the past decades in part because of the development of genetically improved materials (McKeand et al. 2003). Tree breeding cooperatives have played a major role in enabling and facilitating that effort. Among these, the Cooperative Forest Genetics Research Program (CFGRP) from the University of Florida has been breeding mostly slash and loblolly pine for a single breeding zone, encompassing the natural variation that exists in four million hectares of timberlands and using traditional breeding approaches (White et al. 1993). More recently, phenotypic prediction of growth and disease traits based on high-throughput genomic information has been proposed to increase the efficiency and accelerate pine breeding programs. Simulated and experimental data have suggested that genetic gains in selection efficiency can range from 50% up to 200% when using genomic prediction approaches (Resende et al. 2012a).

In this work we describe the comparison of accuracy of genomic selection models generated from different single nucleotide polymorphism (SNP) sets, obtained from sequence capture/next generation sequencing technology, and applying various SNP identification and filtering parameters. The genotypic information was obtained from two populations: (1) the CFGRP 3rd cycle slash pine full-sib progeny test, where 1000 trees from 60 different crosses among 37 parents were genotyped, and (2) the CFGRP 2nd cycle Florida loblolly pine test, with 2000 genotyped individuals, representing 45 full-sib families derived by crossing 28 parents. From a total of 80,000 probes previously designed for P. taeda by RAPiD genomics LLC, an optimized subset of 12,000 were selected based on quality of the SNPs obtained from the parental trees. Phenotypic data such as tree height and diameter was obtained by end of the fourth from slash pine population. Genomic selection models for growth traits were developed using Genomic-BLUP (VanRaden 2008), and estimation of prediction performance was done using a ten-fold cross validation. The SNP filtering parameters were additionally evaluated by genetic parameters (inbreeding, genetic gain and variance) of the selected populations obtained by each genomic selection model. The accuracy of genomic selection models will be presented, including the comparison to pedigree-based BLUP prediction models for non-genotyped families.

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VARIABILITY OF GENETIC RESPONSE TO SELECTION UNDER GBLUP EVALUATION

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Novel breeding methods including genomic selection are based on genome-wide predicted breeding values (GEBV). Recent development coincides well with the new single nucleotide polymorphism (SNP) technology that is high throughput, accurate and relatively inexpensive. Genomic best linear unbiased prediction (GBLUP) is a statistical method that has been used to estimate GEBVs of various complex traits in both agriculture and forestry, GBLUP and its variations have become commonly used for selection in crop breeding. GBLUP is not dramatically different from traditional BLUP approach (Henderson 1975), as standard software available for linear mixed models can be used to solve mixed model equations, which is a major advantage of such methodology for breeders. Genetic relationships derived from pedigrees (basis of BLUP) ignore the random sampling of the two possible alleles from each parent at each locus during meiosis - variation defined as the Mendelian sampling term. GBLUP is based on a so- called genomic relationship matrix or more often realized relationship matrix as it describes identity- by-descent (IBD) at SNPs. Exploiting this variance could be the major added benefit of GBLUP.

While previous studies described GBLUP theoretical efficiency in agriculture, forestry diametrically differs in terms of production system, where the emphasis is on the use of seed orchards. This study represents a potential role of genomics in launching the new breeding program. The main objective of this work was to assess, through simulations, the impact of selection strategy in conjunction with BLUP vs. GBLUP on the predicted selection accuracies of mentioned statistical methods in a real-world forest tree breeding context. We evaluated the impact of genetic architecture of the target trait on the predicted accuracy of both strategies and primarily on the response to selection in production population.

We discuss: (1) BLUP/GBLUP relative efficiency and show that GBLUP is not always superior to traditional phenotypic evaluation, (2) large sensitivity of GBLUP's efficiency to trait's genetic architecture, and (3) excessive variance of the predicted genetic response in seed orchards.

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ANALYZING GROWTH AND OLEORESIN PRODUCTIVITY OF LOBLOLLY AND SLASH PINE PSEUDO-BACKCROSS HYBRIDS

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The University of Florida's Cooperative Forest Genetics Research Program and the Forest Biology Research Cooperative established a slash pine (*Pinus elliottii* Engelm Var. elliottii) and loblolly pine (*Pinus taeda* L.) backcross hybrid test. The study consisted of one open pollinated slash pine (E63xMix), one open pollinated loblolly pine (LobxOP), and three pseudo-backcrosses between a single loblolly by slash F1 hybrid with two elite slash and one elite loblolly pine parents. The test has a low and high fertilizer treatment. The objectives of this study are to assess the introgression of alleles and the efficiency and genetic control of various phenotypic growth and productivity traits of the backcrossed loblolly and slash pine families. This study will also compare the short-term oleoresin production of pseudo-backcross hybrids, loblolly and slash pine trees.

After three years of growth, the height, diameter at breast height (DBH), crown width along and across the planting bed, stem form, and disease and mortality status was measured for all trees in the study. In addition, the number of primary and secondary branches at two nodes were counted for all pseudo-backcross hybrids above 6 feet in height and a representative sample of the parent species. In spring of 2017, all trees with measured branch characteristics will be tapped for a 24-hour period to collect oleoresin. This will allow us to assess the difference of oleoresin productivity between both species as well as the different pseudo-backcross families.

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Session 10

Broadening Genetic Diversity

Forest Service Southern Region National Forest System - It's All about GRITS
Ms. Barbara Crane 45

Performance of Sweetgum Varieties on Upland Sites in North Louisiana
Dr. Joshua Adams 46

Diversity of Non-Native Tree Populations in the Different Districts of Rwanda
Dr. Kabera Telesphore 47

FOREST SERVICE SOUTHERN REGION NATIONAL FOREST SYSTEM – IT'S ALL ABOUT GRITS

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The Southern Region's National Forests are home to some of the most biodiverse forests in the country. Over 140 tree species occupy coastal, piedmont and mountain landscapes. Southern ecosystems are extremely vulnerable to forest health issues and climate change impacts. Updated management strategies are therefore required to support and maintain healthy, sustainable, resilient and productive vegetation on the National Forests, for now and into the future.

Genetics programs play a key role in developing and supporting successful land management activities, which include reforestation, restoration and gene conservation. Being proactive and creative with current and future needs is critical, as is flexibility in developing and integrating new ideas and management strategies. Our Genetic Resource program is constantly evolving and transitioning (Genetic Resources In TranSition "GRITS") to hedge our bets for success in future predicted climate scenarios. Assessment tools, such as *Forest Tree Genetic Risk Assessment System* (FORGRAS 2010) and *Conservation and Prioritization of Tree Under Risk of Extirpation* (CAPTURE 2016) have been developed which rank the vulnerabilities of many of our tree species to current and future risks. Many tree species have been identified as imperiled and subsequent seed collections are ongoing. We have engaged in multiple partnerships, especially with Camcore, to increase awareness of tree conservation concerns and orchestrate seed collection efforts. Actions and tools for restoring or retaining multiple tree species on the landscape are in development, including 1/ tree conservation collection protocols, 2/ updated seed zones, 3/ guidance for mixing seed lots to match updated seed zones, 4/ updated planting range maps and 5/ protocols for establishing conservation banks and restoration seed reserves on our seed orchards.

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PERFORMANCE OF SWEETGUM VARIETIES ON UPLAND SITES IN NORTH LOUISIANA

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Hybrid sweetgum (*Liquidambar styraciflua x formosana*) has been successfully brought to operational forestry alongside of native, but improved, sweetgum (*L. styraciflua*). These complementing stocks may provide ready sources of fiber on an array of sites, including upland areas. In 2015, six sweetgum genotypes were planted at two sites in North Louisiana in Homer, LA (LSU Hill Farm Research Station) and Ruston, LA (Louisiana Tech University). Genotypes consisted of four elite hybrid clones and two superior native sweetgum half-sibling families. At both sites 25-tree square plot experimental units were established for the genotype treatments, which were replicated four times in a randomized complete block design. After the first growing season there were significant differences in survival percentage, with native sweetgum generally performing poorly relative to the hybrids. Only one hybrid clone had survival under 90% while both native sweetgum families were under 90% survival. Growth rates were also significantly affected by genotype. Ground line diameter (GLD) and height change for the first growing season mirrored survival trends, with both native sweetgum genotypes performing poorly relative to the hybrid clones. Furthermore, these differences among planting stock were generally stable across the two sites with only GLD being significantly affected by site in the first year. First year results indicate new hybrid clones may be superior to native sweetgum genotypes for upland site afforestation.

Testing height and ground line diameter growth of hybrid Sweetgum varieties in the first year after planting compared to native half-sibling Sweetgum families to be used as fiber source for pulpwood industry.

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DIVERSITY OF NON-NATIVE TREE POPULATIONS IN THE DIFFERENT DISTRICTS OF RWANDA

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This study describes the occurrence and the distribution of non-native trees in 30 Rwandese Districts. Rwanda has a total of 63 different species, of which 40 are non-native and 23 are native; only species of the *Alder* genus was found to be present in all 30 Districts. The Directorate in charge of forestry under Ministry of Natural Resources (MINERENA) lacks reliable and up-to-date information on forest and tree resources, such as their number, wood volumes, and growth. Although a national forest inventory is underway, it will only provide the volume and areas of forest productivity as well as the different stages of forests degradation, but will not highlight the number of trees. The insects *Leptocybe invasa* and *Thaumastocoris peregrinus* damage large areas of *Eucalyptus* plantations in Rwanda. The concluding recommendations of this study is that forest managers need to start finding a way to collect tree data and conduct comprehensive surveys before undertaking tree planting projects. They should also train communities on how to maintain trees.

Keywords: Rwandese Districts, Native and Non-Native species, *Alder* genus

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Plenary Session

Advances in Tree Improvement

Genetic Parameter Estimates of Height-Diameter Relationships in Loblolly Pine
Dr. W. Patrick Cumbie 49

Breeding without Breeding: Confirmation of Theoretical Concept Using Real-World Tree Improvement Program
Dr. Jiri Korecky 50

Conifer Terpenes: Manipulating an Ancient Plant Defense Pathway for Production of Renewable Chemicals and Biofuels
Dr. Gary Peter 51

GENETIC PARAMETER ESTIMATES OF HEIGHT-DIAMETER RELATIONSHIPS IN LOBLOLLY PINE (*PINUS TAEDA* L.)

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Gains in productivity for loblolly pine often focus on tree volume but a better understanding of the relationship between volume, height, and diameter is useful as foresters and land mangers incorporate genetic performance in to stand management and financial decisions. We will explore the relationship of height and diameter in a variety of provenances, populations, and geographic locations. A comparison will be made between selection on various growth measures and we will explore genotype-phenotype associations using a clonally replicated population.

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BREEDING WITHOUT BREEDING: CONFIRMATION OF THEORETICAL CONCEPT USING REAL-WORLD TREE IMPROVEMENT PROGRAM

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In traditional tree improvement programs, simple recurrent selection scheme has been adopted to capturing additive genetic variance through repeated cycles of controlled crosses, selection and testing. Traditionally, selection within breeding programs was based solely on phenotypic evaluation. Marker-based approaches have been proposed to speed up the delivery of genetic gain in forest tree breeding. While genomic selection is the robust and more promising alternative to MAS, it is associated with effective high-throughoutput genotyping technologies generating sufficiently high genome coverage. Since these strategies require whole genome scans, they are too expensive in operational forestry breeding programs under most circumstances. The Breeding without Breeding approach seems to be an appropriate alternative as it only requires a small set of neutral polymorphic marker loci (e.g., 10-20).

We demonstrate the practical utility of Breeding without Breeding strategy, which offers great opportunities for its wide application in many breeding or conservation programs worldwide. We demonstrate the application in breeding program of Scots pine in the Czech Republic. Two existing first-generation seed orchards and their corresponding half-sib progenies were used to demonstrate the concept. App. 10% superior offspring were genotyped. We tested two approaches of genetic analysis: (1) pedigree reconstruction (i.e. transformation of half-sib into full-sib progeny) when parental population is genotyped, and (2) selection based on relationship matrix when parental genotypes are unknown.

BwB allowed bypassing the most resource-demanding breeding activity, i.e. controlled pollination. Moreover, the estimated reduced contamination rate among superior offspring under prescribed effective population size confirmed our theoretical expectations.

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CONIFER TERPENES: MANIPULATING AN ANCIENT PLANT DEFENSE PATHWAY FOR PRODUCTION OF RENEWABLE CHEMICALS AND BIOFUELS

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Conifer terpenes were the first “industrial” chemical and today are feedstocks for the largest nonfood-based hydrocarbon industry. Terpenes are important defense compounds that help protect the stem against boring insects and their associated fungi. Conifers evolved specialized duct systems that synthesize and store oleoresin composed of monoterpenes and diterpenoids. In southern pines, sapwood typically contains 3-4% dry weight of terpenes. We are studying the genetics of resin duct formation and terpene synthesis in loblolly pine with the goal of increasing terpene content in the stem for improved resistance to southern pine beetles and as a better source of chemical feedstocks for renewable chemicals and biofuels. With loblolly pine, we are using three genetic engineering strategies to increase wood terpene content. The first strategy aims to increase flux through the plastid terpene biosynthetic pathway. We identified three genes that can increase wood terpene content 2-3 fold. The second strategy uses regulators of resinosis to promote terpene synthesis and resin duct formation. We have identified four genes that increase wood terpene content 2 fold. The third strategy is improve the activity of biosynthetic enzymes. We will report our progress towards increasing wood terpene content.

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Posters

Listed in Alphabetical Order by Last Name

Using Simple Sequence Repeat Markers to Identify Chestnut Species and Hybrids
Mr. Charles Burdine 54

Project CAPTURE: A U.S. National Prioritization Framework for Tree Species Threatened by Climate Change and Other Threats
Ms. Barbara Crane 55

Recent News - Longleaf Pine Genetics and Silviculture Activities on the Southern National Forests
Ms. Barbara Crane 56

DNA Markers to Identify Southern Pines and their Hybrids
Dr. Craig Echt 57

TIPRoot Database: A Tool for Managing Breeding, Testing, and Selection Data in the NC State University Cooperative Tree Improvement Program
Mr. Daniel Genung 58

Reproductive Biology of *Paulownia elongata*, a Multipurpose Tree
Dr. Nirmal Joshee 59

Genetic Diversity and Clone Structure of the Endangered Species of *Thuja koraiensis:* Conservation Strategy in Response to Climate Change
Mr. Ki Won Kim 60

Effects of Thinning Regimes on Genetic Variation of White Oak (*Quercus alba* L.) in Eastern Hardwood Forests
Ms. Rachel Landham 61

Optimum Neighborhood Seed Orchard Design - Software Package
Prof. Milan Lstiburek 62

Use of Recirculating Irrigation System to Contain Soilborne Pathogen *Phytophthora cinnamomi* in Operational Disease Resistance Trials
Ms. Sunny Lucas 63

New Advanced Generation Seedling Seed Orchards Use Methodology Developed for *Eucalyptus grandis* in Florida
Mr. Peter McClure 64

Development of an In Vitro Assay for Resistance to *Phytophthora cinnamomi* in Chestnut
Dr. Scott Merkle 65

Somatic Embryogenesis in Ozark Chinquapin
Dr. Scott Merkle 66

Soil Compaction in Loblolly Pine Seed Orchards and the Impacts on Tree Health and Cone Yields
Mrs. Serenia O'Berry 67

Pitch Canker Disease as a Model to Discover Biological Drivers of Pitch Canker Disease in a Changing Climate
Dr. Tania Quesada 68

A Novel Approach to Phenotypic Analysis of Forest Trees for Accelerating Breeding
Dr. Donghwan Shim 69

A Proposed Study on the Genetic Control of Fertilizer Response and Post-Senescence Nutrient Content Assessed Via Foliar Sampling in Loblolly Pine
Mr. Andrew Sims 70

USING SIMPLE SEQUENCE REPEAT MARKERS TO IDENTIFY CHESTNUT SPECIES AND HYBRIDS

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In the past, the American chestnut (*Castanea dentata*) was considered one of the most important forest tree species of the eastern North America, having a native range that extended from Mississippi to Maine and in to Canada. The once dominant species is primarily only found today as coppice-regenerated stump sprouts. The introduction of chestnut blight, an overwhelming stem canker disease caused by the fungal pathogen *Cryphonectria parasitica*, is the primary reason for the rapid decline in American chestnut across its natural range. American chestnut did not coevolve with chestnut blight, and thus little to no resistance to the pathogen exists in the native species. Resistance to chestnut blight exists in the Asian chestnut species, including Chinese chestnut, *C. mollissima*, as this species co-evolved with the fungal pathogen. Fortunately, the fungus does not spread to the root system of chestnut and this coupled with chestnut's ability to sprout from adventitious buds below the root collar has resulted in millions of sprouts of American chestnut still living across the native range. Young sprouts typically become infected after a few years and die back and are replaced by new sprouts that repeat the cycle. After many years the older stumps fail to thrive and eventually die thus decreasing the overall supply of sprouts. Numerous research groups are applying various techniques to develop resistant American chestnut that retain the native species characteristics while also providing resistance to the pathogen. Since the introduction of the pathogen, Asian chestnut species and selected hybrids have been introduced and widely planted. In addition, chinquapin chestnut, *C. pumilla*, shares a similar range with American chestnut and is also very susceptible to the disease. Unfortunately, due to the introduction of non-native species and inter-species hybrids, it is often difficult to determine if a sprout is an American chestnut, another related native species (chinquapin) or a natural hybrid with chinquapin or one of several introduced chestnut species based on leaf and stem morphology alone. For this reason, a set of simple sequence repeat (SSR) markers are being developed that would allow for chestnut species separation using statistical analyses. We will report on our progress in developing such a set of markers and discuss their application in chestnut breeding and restoration programs

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PROJECT CAPTURE: A U.S. NATIONAL PRIORITIZATION FRAMEWORK FOR TREE SPECIES THREATENED BY CLIMATE CHANGE AND OTHER THREATS

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A variety of threats, most importantly climate change and insect and disease infestation, will increase the likelihood that forest tree species could experience population-level extirpation or species-level extinction during the next century. Scientists and managers from throughout the United States Forest Service have cooperated to develop a framework for conservation priority-setting assessments of forest tree species. The Project CAPTURE (Conservation Assessment and Prioritization of Forest Trees Under Risk of Extirpation) framework is data-driven and guided by expert opinion, and allows for the quantitative grouping of species into vulnerability classes that may require different management and conservation strategies.

The first application of this framework uses trait data and predictions of expected climate change pressure to categorize and prioritize 339 native tree species for conservation, monitoring, management and restoration across all forested lands in the contiguous United States and Alaska. This categorization is based on risk factors relating to the species' (1) exposure to climate change, (2) sensitivity to climate change, and (3) capacity to adapt to climate change. We used K-means clustering to group species into seven classes based on these three vulnerability dimensions.

The most vulnerable class encompassed 35 species with high scores for all three vulnerability dimensions. These will require the most immediate conservation intervention. A group of 43 species had high exposure and sensitivity, probably requiring conservation assistance, while a group of 69 species had high exposure and low adaptive capacity, probably needing close monitoring. This assessment tool should be valuable for scientists and managers determining which species and populations to target for monitoring efforts and for pro-active gene conservation and management activities.

The Project CAPTURE framework is being applied separately for an assessment of the threats to North American tree species posed by pest and pathogen infestations, and for tree species in Hawai'i and Puerto Rico.

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RECENT NEWS – LONGLEAF PINE GENETICS AND SILVICULTURE ACTIVITIES ON THE SOUTHERN NATIONAL FORESTS

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National Forests in the Southern Region are home to over 800,000 acres of longleaf pine, which serves as critical habitat for numerous species. Annually over 5 million longleaf pine seedlings are planted and approximately 500,000 acres are prescribed burned. Maintaining, improving and restoring the longleaf pine ecosystem is a priority for the region. Reforestation and restoration have been underway for several decades, utilizing both artificial and natural regeneration methods as well as prescribed fire.

Multiple activities in both the Genetics and Silviculture programs to support longleaf pine restoration are ongoing. These activities include: management of longleaf pine seed orchards and progeny tests for seed production; establishment of longleaf pine seed production areas on multiple forests; a south wide survey to assess longleaf pine seed orchard and seed bank resources; research on suspected hybridization between longleaf and loblolly pines (e.g. *Sonderegger* hybrid); DNA fingerprinting of all seed orchard longleaf pine trees and longleaf pine seed inventory for purity; research on suspect *Sonderegger* hybrid seedling morphology and prescribing burning to weed out hybrids; assessment of climate change impacts to the future desired condition for longleaf pine; development of updated planting zone maps and seed source maps for longleaf pine; and drafting a Southern Region Longleaf Pine Accelerated Restoration Strategy.

Many partners are involved in the various activities, including Southern Research Station, National Genetics Lab (NFGEL), Dr. Jim Barnett et. al., State Private Coop Forestry and Forest Health Protection.

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DNA MARKERS TO IDENTIFY SOUTHERN PINES AND THEIR HYBRIDS

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The issue of pine inter-species hybridization is a growing concern for National Forest System (NFS) seed orchards that provide seed for reforestation on NFS lands in the Southern Region. Because NFS seed orchards also sell surplus seed to state nurseries, which in turn can sell the seedlings to private landowners, hybridization is becoming a concern for these stakeholder groups. Climate change may be increasing chances for hybridization among pine species and there is speculation that some superior performing trees selected in the early days of Southern Region seed orchard establishment may be inter-species hybrids. Because the Forest Service has an obligation to make sure that its seed supply is genetically pure (not hybridized), the NFS Genetics program in conjunction with the National Forest Genetics Laboratory (NFGEL) will DNA fingerprint all longleaf and shortleaf pine trees and seed lots in NFS seed orchards. The goal is to remove seed producing trees that are inter-species hybrids and provide a quality check of current and future seed lots for the extent of species hybridization that may arise from off-site pollen sources. Ensuring species integrity of longleaf pine and shortleaf pine seed supplies will go a long way in Forest Service support of restoration initiatives for these species.

Hybrid seed producing trees in seed orchards and seasonal hybridization of longleaf and shortleaf seed trees by loblolly pine pollen are the two major practical concerns for orchard seed integrity. Because chloroplast DNA (CP) is only inherited through pollen in pines, we set out to develop easy-to-use diagnostic CP markers that would be unique to loblolly chloroplast genomes. While the main intent was to identify first-generation hybrids, this type of marker system obviously could also identify backcross hybrids that have a loblolly paternal lineage, though such higher generation hybrids, expected to be rare, are not an immediate concern for seed orchard operations. As part of a project with the Pennsylvania Bureau of Forestry, we also evaluated CP markers to identify hybrids between shortleaf and pitch pines. All markers were based on comparisons of pine CP sequences found in GenBank.

From a number of new CP markers evaluated, we found two that appeared species-specific based on our limited testing completed to date. One, in the tRNA gene for leucine, appeared as a single allele (gene fragment) only in loblolly pine (n = 49) and was not found in longleaf (n = 133), shortleaf (n = 153) or pitch pines (n = 8). The other, in the ycf1 gene of unknown function, provided what appeared as species-specific size alleles: three alleles in loblolly (n = 27), four in longleaf (n = 82), one in shortleaf (n = 142), and two in pitch pine (n = 6). While both markers can discern loblolly hybrids, the later marker can also identify other types of species hybrids. The two CP markers together have identified a longleaf x loblolly hybrid seedling from a small sample of a longleaf pine seed lot, confirmed three known pitch x loblolly trees, and possibly identified several shortleaf x pitch and pitch x shortleaf hybrids from Pennsylvania. Additional sampling is underway for each species, plus slash pine, to estimate the extent of each marker's species-specificity. Even if not strictly species-specific, as long as the frequency of shared alleles is sufficiently low, these markers could still be used to estimate proportions of hybridization in seed lots and identify orchard trees that are likely hybrid.

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TIPRoot DATABASE: A TOOL FOR MANAGING BREEDING, TESTING, AND SELECTION DATA IN THE NC STATE UNIVERSITY COOPERATIVE TREE IMPROVEMENT PROGRAM

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The NC State University Cooperative Tree Improvement Program developed its online database (TIPRoot – Tree Improvement Program Rapid online output tool) to provide Cooperative staff and members a means for organizing and accessing breeding, testing, and selection data for loblolly pine.

The most utilized tool in the TIPRoot database is the PRSTM database that contains breeding values for each selection and genetic values for every possible cross. In addition to downloading data for all selections in a given geographic region, a user can create PRSTM Spec Sheets that can be used toinform landowners and foresters about the predicted performance for growth, fusiform rust resistance, and stem quality of specific open-pollinated or full-sib families and for marketing seedlings. Since the primary limitation to adaptability for loblolly pine seedlings is tolerance of cold temperatures, a map is generated for each Spec Sheet indicating the risk of cold damage using minimum winter temperature.

Other tools in TIPRoot will be described including the use and management of pedigree information, management of genomic data, and the enhanced uploading of test measurements that includes data quality checks. We have recently developed Breeding Logistic tools to manage all the breeding and testing activities that connects information about the status of each cross in field tests, seed and pollen inventories, conelet and flower counts, and need for continued breeding. We estimate that the Breeding Logistics database has more than doubled the efficiency of breeding activities during the very hectic breeding season.

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REPRODUCTIVE BIOLOGY OF *PAULOWNIA ELONGATA*, A MULTIPURPOSE TREE

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Paulownia genus is a group of fast growing trees that grow well in the southern United States. *Paulownia* (Paulowniaceae) is a genus of deciduous hardwood trees from China used for agroforestry, biomass production, land reclamation, and animal waste remediation. *Paulownia* (*Paulownia tomentosa*), or kiri, was introduced into the US during the 1800s. It quickly became naturalized over much of the eastern states. Except for its ornamental qualities, it was generally ignored as a non-native weed tree. However, since Japanese buyers have begun to buy US grown logs, *Paulownia* is now considered a premier timber species. Forestlands, an important source of cellulosic biofuels feedstock, are expected to play an important role in meeting the national biofuel target. Plants are improved continuously by using molecular or classical breeding tools and in both cases it is important to have a clear understanding of reproductive biology. Light, Fluorescent, and Scanning Electron Micrography was conducted to study pollination and subsequent steps. Variable Pressure Scanning Electron Microscopy (VP SEM: Hitachi 3400 NII) was conducted at Agricultural Research Station, Fort Valley State University. This work represents *Paulownia* floral and reproductive parts in various magnifications. Current research deals with the structure of male and female reproductive parts, pollen germination and subsequent pollen tube growth through style using fluorescent aniline blue and SEM methods. We also present freeze fracturing technique to show internal structures of reproductive parts. Results indicate a pore at the wide spindle shaped stigmatic tip followed by hollow style. Stigmatic pore opens into a cavity with internal surface lined with elongated cells that are secretory in nature. Pollen grains parachute through stigmatic pore filling up the cavity and crowding stigmatic tip. Pollen grains germinate readily and hundreds of pollen tubes with callose plugs can be visualized in the style region. Ovary contains numerous ovules attached to the placenta. Pollen tubes can be seen in the close vicinity of ovules to commence fertilization.

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GENETIC DIVERSITY AND CLONE STRUCTURE OF THE ENDANGERED SPECIES OF *THUJA KORAIENSIS*: CONSERVATION STRATEGY IN RESPONSE TO CLIMATE CHANGE

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Comprehensive studies on the genetic diversity and structure of endangered species are urgently needed to promote effective conservation and management activities. Preserving the genetic diversity of endangered species can significantly affect their long-term survival and evolution in changing environments. Therefore, knowledge of the genetic diversity and population structure of endangered plant species is crucial for their conservation and management. *Thuja koraiensis* exhibits a very limited distribution with a few populations found on the Korean peninsula. It is the endangered tree species that can be found through alpine zones of Baekdudaegan Mountain Range from Baekdusan to Taebaeksan in the southernmost part of Gangwon province. Study on the life history of endangered species provides the basis necessary to investigate the reason for crisis faced and to establish the strategy of conservation. Unfortunately, limited information is available regarding the population genetics of this species.

Therefore, we conducted the germination test of seeds to understand the mechanism of reproductive propagation from three natural populations and the analysis of clone structure to characterize the genetic diversity of the species within a population of *T. koraiensis*. Microsatellite marker was used for analysis of the clonal structure and genetic variation. The microsatellite marker is the codominant marker showing high polymorphism and it has been widely used for population genetics and clonal structure analysis.

The cones were collected from Hwaaksan, Seoraksan and Hambaeksan populations in 2015, and the morphological characteristics of cone were measured. After cone drying, seeds were extracted and placed in chambers for germination tests. Additionally, some seeds from the Hambaeksan population were stored in a refrigerator until genomic DNA was extracted, and targeted to analyze clone structure and genetic variation. For clone structure analysis, a plot with 15 m x 15 m was set and seed samples were collected in Hambaeksan and the diameter at root collar was measured for all individuals in the plot.

The mean of cone length was highest in Hwaaksan (10.4 mm) and lowest in Hambaeksan (8.8 mm). The averages of 1,000 seed weight were 0.85 g (Hwaaksan) and 0.81 g (Seoraksan and Hambaeksan). The averages of germination percentage were 28.2% in Hambaeksa, 19.4% in Seoraksan and 12.2% in Hwaaksan. The germination speed was also peak in Hambaeksa and low in Hwaaksan. We developed 10 microsatellite markers and applied for clone structure analysis. A total of 152 trees were found in the plot and they were classified into four genotypes. The mean number of alleles was 6.3 and the mean number of effective alleles was 3.8 in the Hambaeksan population. The observed and expected heterozygosities were 0.629 and 0.642, which is an intermediate level compared to the other *Thuja* species distributed in North America.

The *T. koraiensis* is vulnerable to the drastic change of environment. Our results will assist with the design of conservation and management programs, such as *in situ* and *ex situ* conservation, seed collection for germplasm conservation and reintroduction.

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EFFECTS OF THINNING REGIMES ON GENETIC VARIATION OF WHITE OAK (*QUERCUS ALBA* L.*)* IN EASTERN HARDWOOD FORESTS

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Artificial selection due to management practices and industry demands can produce significant effects on the nature and extent of genetic diversity in natural tree populations. White oak (*Quercus alba* L.), a keystone species of economic importance to eastern hardwood forests, is potentially subject to genetic degradation due to selective harvest of timber-type trees (i.e., phenotypes) by the forest industry. This research project assesses the effects of silvicultural thinnings on the allelic variation of white oak utilizing microsatellite DNA analysis, specifically genomic and transcriptomic simple sequence repeat (SSR) markers. Our research objectives are to: (1) understand if silvicultural thinnings significantly change the degree of allelic variation in white oak stands, leading to a loss in population diversity and (2) discover the spatial attributes of genetic variation of white oak within stands in light of past silvicultural practices. Existing long-term thinning experiments of a white oak dominated study site established by the USDA Forest Service, in 1961 and 1962 on the Daniel Boone National Forest (Jackson County, KY, USA), provided eight half-acre plots varying in thinning intensity and timing. Leaf tissue samples were collected for DNA isolation and SSR marker analysis from all mature white oaks within the study plots for a spatial analysis of genetic variation. Differences in heterozygosity (observed and expected), total and effective allele numbers, Hardy-Weinberg deviations, linkage disequilibrium (LD), mean repeat number, variance of repeat number, inbreeding coefficient (F) and Fst (total genetic variance) were calculated using GenAlEx, and spatial analyses were conducted with R Studio and Arc GIS. We will present the results of this study and discuss its implications for white oak sustainability and conservation.

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OPTIMUM NEIGHBORHOOD SEED ORCHARD DESIGN – SOFTWARE PACKAGE

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Seed orchards represent the link between operational forestry and tree improvement. When a new orchard is established, factors such as the census of contributing genotypes and their physical allocation must be considered. All these factors affect the realized response to selection and levels of gene diversity. Therefore, good design should promote random mating and minimize inbreeding. While the existing designs are primarily focused on minimizing levels of inbreeding, the objective of the Optimum Neighborhood Seed Orchard (ONA) design is to maximize panmixia. It is generally known that pollination efficiency is a function of distance and thus most frequent genetic exchange occurs among neighboring clones. Because of this, panmixia in seed orchards was defined as a situation where close neighborhoods of all possible combinations of clones occur with the same frequency within the orchard grid.

Here we present computer algorithm to implement the ONA scheme using realistic input parameters, we also discuss the user's interface, and provide link to the actual software, so that breeders can freely use it.

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USE OF A RECIRCULATING IRRIGATION SYSTEM TO CONTAIN SOILBORNE PATHOGEN, *PHYTOPHTHORA CINNAMOMI*, IN OPERATIONAL DISEASE RESISTANCE TRIALS

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The Resistance Screening Center (RSC), operated by the Forest Health Protection unit of the USDA Forest Service, Southern Region, State and Private Forestry, has traditionally screened conifer and hardwood seedlings for disease resistance to various aerial pathogens. Recently, through a partnership with the American Chestnut Foundation, the RSC has begun screening chestnuts for disease resistance to the soilborne pathogen, *Phytophthora cinnamomi*. Intentionally bringing a generalist soilborne pathogen like *P. cinnamomi* into a container nursery setting, where multiple hosts reside, requires careful consideration, planning, and precaution. In an attempt to contain the pathogen, and prevent unwanted spread of the disease, a recirculating irrigation system was constructed in the greenhouse. Chestnuts are grown for 12 weeks before being inoculated with *P. cinnamomi*. Trays of seedlings are kept in hydroponic flood tables. Pre-inoculation, flood table drain valves are kept open and irrigation water is allowed to drain directly to the greenhouse floor. After the seedlings are inoculated, the irrigation water is considered contaminated. At this point, flood tables are connected to a contained and recirculating plumbing system. For the first two weeks post-inoculation, seedlings are watered overhead to create a favorable environment for infection. Irrigation runoff is pumped from the flood tables to a holding tank inside the greenhouse, where it is treated with sodium hypochlorite (bleach). Treated water is then held in an outside tank where the chlorine is allowed to dissipate before being released into a gravel field. After the initial overhead watering phase, seedlings are subirrigated to further reduce the risk of pathogen escape. Seedlings are flooded for four hours three times weekly. To counteract nutrient leaching, soluble fertilizer is added to the irrigation water. The containment system is designed to allow for water to be recirculated and used several times before being treated with chlorine. This creates a more nutrient rich environment and reduces the number of chlorine treatments needed. Seedlings are subirrigated for the remainder of the study, approximately 5 months. This system can be used as a model for screening other plant species for susceptibility/resistance to soilborne pathogens in a nursery setting.

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NEW ADVANCED GENERATION SEEDLING SEED ORCHARDS USE METHODOLOGY DEVELOPED FOR *EUCALYPTUS GRANDIS* IN FLORIDA

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Two advanced generation seedling seed orchards (SSO) recently established in Florida followed a novel cost-efficient, effective methodology developed through four generations of E. grandis genetic improvement. Combining short generation time and rapid growth with provenance and progeny testing in one place at one time, early selection, large infusions of new, primarily single-tree accessions, and use of pedigrees to minimize inbreeding resulted in steady and often great genetic gains. Advancing from a 1st-generation genetic base population of 4,352 trees from only 13 accessions to a 4th-generation genetic base population (GPop77) of over 31,000 trees from 529 worldwide E. grandis accessions resulted in productivity gains of as much as 195%. While the 1,500 trees in the 4th-generation SSO GO77 also captured individual tree responses to severe freezes, thus further illustrating the benefit of continued selection and orchard establishment, additional progeny tests contributed to the calculation of breeding values for stand basal area, bluegum chalcid resistance, and/or freeze resilience. Applying similar methodology to the tropical species *Corymbia torelliana*, a 1st-generation genetic base population (TPop08) included 960 seedlings from 29 local trees of unknown sources. The 72 selected trees in SSO TO08 combine surprising freeze tolerance (as low as −5°C) with good growth and tree form.

A 5th-generation *E. grandis* genetic base population (GPop15) established at the UF/IFAS Indian River Research and Education Center near Ft Pierce, FL, from July to October 2015 consisted of 4,157 propagules from 42 up to 4th-generation, open-pollinated progenies with superior growth, freeze resilience, and/or chalcid breeding values and four UF commercial cultivars. Sixty trees of 10 progenies were replanted in April 2016, resulting in 20 60x90' replications (10x3' spacing) with 36 progenies/cultivars systematically assigned to six rows of six 5-tree row plots and four incomplete replications. Based on periodic growth, freeze, form, chalcid, and windfirmness measurements, GPop15 was rogued to the best tree in each plot in April 2017 to create SSO GO15. Using performance through 2018, each replication will be further rogued to approximately the best six trees, resulting in GO15 having ~150 trees when abundant flowering begins in Fall 2019. GO15 should produce large quantities of seed by Spring 2020 and provide fast growing, freeze resilient, windfirm, and chalcid resistant *E. grandis* seedlings for central and southern Florida and similar areas.

TPop12, the 2,027 tree 2nd-generation *C. torelliana* genetic base population planted October 2012 on former citrus beds near Ft Pierce, included 66 progenies: 10 TO08 progenies, 25 Australian single-tree seedlots, and 31 Florida "wild" progenies. Tree size, form, fecundity, windfirmness, and survival were measured periodically. Seedlings coming from the diverse 115 trees selected for retention in SSO TO12 representing 54 progenies (25 from 10 TO08 trees, 52 from 22 Australian trees, and 38 from 22 "wild" trees) may be deployed in central and southern Florida.

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DEVELOPMENT OF AN *IN VITRO* ASSAY FOR RESISTANCE TO *PHYTOPHTHORA CINNAMOMI* IN CHESTNUT

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While the story of the devastation of American chestnut (*Castanea dentata*) by chestnut blight is familiar to those who work with this tree, less well-known is the fact the another disease—Phytophthora root rot, caused by the oomycete pathogen *Phytophthora cinnamomi*—had already extirpated American chestnut from the Piedmont and Coastal Plain regions of the southeastern U.S. decades before the arrival of the chestnut blight fungus, *Cryphonectria parasitica*. The lack of resistance to *P. cinnamomi* may pose a major barrier to introducing the products of The American Chestnut Foundation's (TACF) breeding program to the southern portion of the American chestnut's original range. The integration of genes for *P. cinnamomi* resistance from Chinese chestnut into TACF's hybrid chestnuts is now proceeding, but it will take additional years of breeding and selection. Combining somatic embryogenesis-based propagation of chestnut hybrids with a reliable *in vitro* assay for resistance to *P. cinnamomi* would help to more quickly evaluate chestnut cultivars thought to carry these resistance genes—which in turn should accelerate the production of elite chestnut cultivars with resistance to both *C. parasitica* and *P. cinnamomi* for planting throughout the eastern U.S.

We tested different *in vitro* screening approaches to rapidly identify *P. cinnamomi*-resistant chestnut cultivars using embryogenic cultures, shoots, and whole plantlets of wildtype American chestnut, transgenic American chestnut carrying putative *P. cinnamomi* resistance genes, and Chinese chestnut. Inoculation of cultures of embryogenic callus grown in 48-well plates with two isolates of *P. cinnamomi* failed to distinguish between American chestnut and Chinese chestnut because embryogenic callus of both species failed to turn to the blue-black color described in previous reports for chestnut callus derived from cambium tissue; instead, callus of both species turned brown after 3-4 weeks. However, American chestnut shoots derived by axillary multiplication that were stuck into 6% water-agar gel and inoculated with *P. cinnamomi* developed obvious symptoms, including wilting and blue-black lesions on the stems, but the ultimate cause of death could not be determined because the shoots had no roots. Whole plantlets (i.e. rooted shoots) of American chestnut and Chinese chestnut grown in 2% low melting point agarose gel showed differential responses to *P. cinnamomi* inoculation. American chestnut plantlets rapidly wilted and stems blackened while Chinese chestnut plantlets remained symptom-free for at least 6 weeks; however, stem lesions eventually did appear on these plantlets. Some transgenic American chestnut plantlets expressing candidate *P. cinnamomi*-resistance genes showed evidence of limited resistance, but these still succumbed to root rot more rapidly than Chinese chestnut plantlets.

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SOMATIC EMBRYOGENESIS IN OZARK CHINQUAPIN

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Chinquapins (or chinkapins) are shrubs or small trees closely related to the American chestnut, commonly found throughout the southeastern U.S. The Ozark chinquapin (*Castanea pumila* var. *ozarkensis*), is a variety of chinquapin that in the Ozark Highlands of eastern Oklahoma, southwestern Missouri and Arkansas. Like America chestnut, Ozark chinquapin populations have been devastated by chestnut blight, and most individuals now exist as stump sprouts of variable size and age. Because Ozark chinquapin is closely related to American chestnut, some of the same biotechnological approaches currently under development to help conserve and restore American chestnut may be useful for conservation and restoration of Ozark chinquapin. Immature (green) burs were collected in August 2015 from five Ozark chinquapin source trees growing in the Nature Conservancy's Nickel Preserve near Tahlequah, OK, and shipped to UGA. Burs were opened and nuts were surface-disinfested and dissected to remove the immature seeds, which were cultured on semisolid chestnut induction-maintenance medium (IMM) supplemented with 4 mg/l 2,4-D. After one month, explants were transferred to IMM with 2 mg/l 2,4-D, and proliferating cultures were transferred to medium of the same composition every three weeks thereafter. Overall, 19 embryogenic cultures, representing all five source trees, were obtained from 1368 immature seed explants, for an overall initiation rate of 1.4 percent. Suspension cultures were initiated from the cultures, and these were subsequently size-fractionated and plated to produce populations of somatic embryos. Over 1000 somatic embryos were produced from 15 lines and given 12 weeks of pre-germination cold treatment at 8º C before being transferred to a lighted incubator for germination. To date, over 70 of the embryos have germinated *in vitro*. The first somatic seedlings were transferred to potting mix and are growing in the greenhouse.

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SOIL COMPACTION IN LOBLOLLY PINE SEED ORCHARDS AND THE IMPACTS ON TREE HEALTH AND CONE YIELDS

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Mass production of controlled crosses for loblolly pine (*Pinus taeda* L.) has resulted in substantial increases in heavy vehicle traffic and likely increases in soil compaction in seed orchards. In this study, we examined soil compaction and its association with tree health and cone production. Soil strength was measured using a penetrometer and is an indirect measure of soil compaction. Multiple measurements were taken per tree to characterize the compaction profile of each tree. Tree vigor and cone production were also assessed, and there was a significant range in values for trees in the five orchards sampled. The association between the soil compaction values and tree health and cone production is being investigated to determine if there is a negative impact of soil compaction.

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PITCH CANKER DISEASE AS A MODEL TO DISCOVER BIOLOGICAL DRIVERS OF PITCH CANKER DISEASE IN A CHANGING CLIMATE

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Natural and agricultural ecosystems are affected by climate change through increased temperature, humidity, and unusual weather patterns. They are increasingly threatened by invasions by non-native pests and pathogens. The fungus Fusarium circinatum causes pitch canker disease in several pine species, leading to high economic losses in the timber industry. Favored by high temperatures and humidity, future outbreaks may become more frequent under predicted changes in environmental conditions over the next 50-100 years. A better understanding of F. circinatum biology is needed to inform predictions of which pathogen variants would likely cause outbreaks in future climate settings. We evaluated growth, spore production and germination among F. circinatum isolates cultured at various temperatures (25, 28, and 31°C). Results show significant temperature effects ($p<0.05$) in mycelium growth and sporulation among isolates.

Disease screening experiments were performed at the USDA Resistance Screening Center (RSC) in Asheville, NC. Eight different isolates from Florida and Georgia, including those used for RSC routine screening, were tested on one resistant and two susceptible hosts. Significant differences among isolates were observed, suggesting differential host response to the isolates tested. Some of those isolates were even more virulent than those routinely used at the RSC. Incorporating these new isolates in the RSC screening protocols would aid in the selection and breeding of pitch canker-resistant material.

We also implemented spore trapping experiments in three north-Florida sites to survey spore release throughout the spring and summer of 2016, and to test if weather events trigger increased spore discharge. Though spore trapping experiments need to be followed across several growth seasons, we present preliminary trends on spore release in the environment. These experiments will be repeated throughout the growing season of 2017 to validate our results. The product of these findings will contribute as a baseline for future research on fungal diversity, spatial distribution patterns and disease prediction, aimed at mitigating adverse effects of climate change on forest health.

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A NOVEL APPROACH TO PHENOTYPIC ANALYSIS OF FOREST TREES FOR ACCELERATING BREEDING

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Genomic Selection (GS) is one of the accelerating breeding methods. With the advent of high throughput molecular technology, numerous molecular markers distributed throughout the whole genome can be produced to characterize many genetic entries involving new perspectives in methodology of selection. In tree breeding the GS could significantly reduce the cost of genetic improvement schemes by limiting the size and number of field experiments. In order to successful performed GS, not only the genetic analysis of trees but also accurate phenotypic analysis is very important. Here, we present a novel approach to automatically measurement of tree phenotypes using drone and ground-based scanner. The actual utility of this scanner depends largely on the efficacy of point cloud data (PCD) analysis. The quantified data of each tree was validated using laborious measurements. The results showed that the individual tree growth was accurately reproduced using our method from three dimension registered scans, with a relative deviation of less than 5%. Therefore, we want to apply this method phenotype analysis for accelerating breeding and management of large-scale progeny test site.

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A PROPOSED STUDY ON THE GENETIC CONTROL OF FERTILIZER RESPONSE AND POST-SENESCENCE NUTRIENT CONTENT ASSESSED VIA FOLIAR SAMPLING IN LOBLOLLY PINE

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Loblolly pine (*Pinus taeda* L.) is the most widely planted forest tree species in the Southeast region of the US, deployed in ~80% of all plantations across the entire range. The literature supports that loblolly pine growth is under moderate genetic control and is also highly responsive to silvicultural treatments, especially fertilization. However, fertilization is often neglected because the application of fertilizer is expensive, nutrient uptake rate is low, and tree growth response is uncertain. Although response to fertilizer has been rigorously studied, the genetic mechanisms are largely unknown.

In view of expectations of increasing demand for wood, maximizing the efficiency and productivity of pine plantations is vital. These plantations are, in practice, almost always established with progeny of a small group of elite genotypes with little consideration to site-specific response of a particular genotypes outside of temperature. A comprehensive study to examine these issues would require an immense amount of time and financial resources for sampling and measuring test sites and analysis of foliar samples.

The University of Florida Forest Biology Research Cooperative (FBRC) has established a multi-site trial to evaluate the response of fertilizer treatment to elite families across a range of environments. The Site Specific Interactions of Genetics, Nutrition and Soils (SSIGNS) study is designed with 30 full-sib elite loblolly pine families with 5 treatment levels of macro- and micronutrient fertilizers, replicated three times at each site.

In this pilot study, live foliage from a subsample of trees was analyzed for nutrient content and assessed for genetic parameters, then the same trees will be samples for dead foliage the following year after the needles senesce, but before they fall. Samples were collected from the highest and lowest level of fertilization and will be collected over two years so that foliage from the same cohort is compared directly. In this way we will able to execute the study recursively, making sure that the genetic control of traits exists before the study is extended. The overall objective of this study is to estimate genetic parameters including narrow-sense and broad-sense heritability and dominance of foliar nutrient concentration and retranslocation.

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