ABSTRACT

KHAN, GEORGE FEROZE. Single Nucleotide Polymorphism Discovery In Pines (Pinus) Species For Hybrid Analysis. (Under the direction of Ross W. Whetten, Ignazio Carbone, and Kevin Potter).

Understanding the genetic basis of population divergence and adaptation is an important aspect of forest genetic studies. Studies of genetic markers have contributed greatly to the understanding of gene flow, hybridization, population structure, and genetic movement within and between species. In the forest tree production industry, genetic markers may be very useful for selective breeding to improve productivity and quality of trees planted for the purposes of wood production. As marker technology has evolved, so has the depth of information. A Single-Nucleotide Polymorphism (SNP) is a DNA sequence variation occurring when a single nucleotide differs between individuals. These SNPs are potentially the best type of genetic marker in genetic screening application because of their abundance in the genome and their association with genes that affect adaptive traits and susceptibility to disease. This study compared sequences of genes in diploid genomic DNA extracted from 24 individuals of each of 16 Pinus species. The analysis targeted 10 genes in each species that covered a total of 2988 bp, and detected a total of 374 potential SNPs. The number of polymorphisms was highly variable among the different genes. This study shows that there is a potential for using SNPs markers as a tool for genetic screening of selective traits in forest tree breeding.
Single Nucleotide Polymorphism Discovery in Pines (Pinus) Species for Hybrid Analysis

by
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DEDICATION

To the love of my life Deval and our son Aden and also my parents for their love and support.
ACKNOWLEDGMENTS

I would like to express my appreciation to Dr. Ross Whetten for his guidance and support throughout my studies. I would also like to thank my committee members Dr. Ignacio Carbone and Dr. Kevin Potter for their encouragement, support and good suggestions.

I offer my sincere gratitude to Dr Steve McKeand, Jin Tong and Saul Garcia for helping me with the experiments and sharing thoughts and experience.

Last, I thank all graduate students and staff of the NCSU Tree Improvement Program for their help and support.
BIOGRAPHY

George Feroze Khan was born in Georgetown, Guyana on March 14, 1980. He attended Leguan Secondary School and graduated in 1996. After graduation he joined the staff at Leguan Secondary as a pupil teacher where he taught Mathematics to juniors and seniors. In 2000 he joined his family in the United States of America and continued his education at Tidewater Community College (TCC). After graduating from TCC with an AS in Science, he transferred to Norfolk State University (NSU) into the Biology program with a major emphasis in Molecular Genetics. At NSU, he joined the lab of Dr Camellia Okpodu where he gained his first experience in molecular research. Dr Okpodu’s research at the time focused on using RAPD (Random Amplified Polymorphic DNA) markers to distinguish between closely related Oak species. He continued working under Dr Okpodu until graduating with his B.S. in Biology in 2007. In the summer of 2006, while at NSU, he accepted a summer internship at North Carolina State University (NCSU) hosted by the AGEP (Alliances for Graduate Education and the Professoriate) program. It was through this internship that he first met Dr Ross Whetten, his future graduate mentor. Over the summer of 2006, he worked with Dr Whetten and members of the NCSU Tree Improvement Program and the Christmas Tree Genetics Program to look at the interaction between the fungus P. cinnamomi and three Fir species. This was an enlightening experience and he decided that NCSU had the program and people he would like to surround himself with in pursuing a graduate career. In the summer of 2007, after graduating from NSU, he accepted a bridging internship to again return to NCSU. This program acts to bridge the gap between undergrad and graduate
studies. This summer provided the foundation for the future master’s works. Following the summer internship, he joined the Department of Forestry at NCSU where his master’s thesis, under the direction of Ross Whetten, investigated the use of Single Nucleotide Polymorphism to identify closely related pine species. During his Masters program, his knowledge of genetics allowed George and his wife to produce a lovely son, Aden who was born on January 7, 2010. With the close of his master’s thesis work, George plans to continue his education by obtaining a Doctorate in Genetics and pursue a career in teaching. His current and future plans are to work for a year in the McKay Genetics lab at NCSU to gain valuable experience as he prepare to transition into the Genetic program PhD at NCSU. His future plans are to become a proficient biology/genetics teacher.
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Introduction

*Pinus* (Pinaceae), with over 100 widely recognized species, is the largest extant genus of conifers (Gernandt 2005). Pines are ecologically important as a major, often dominant component of boreal, subalpine, temperate, and tropical forests, as well as arid woodlands (Richardson et al., 1998). Economically, pines are an important source of wood, paper, resins, charcoal, food (particularly seeds), and ornamentals (Lambert, 2001). The natural distribution of the genus is confined to the Northern Hemisphere except for one population of *P. merkusii* located just south of the equator in Sumatra (Le Maitre, 1998). Species such as *P. caribaea*, *P. patula*, *P. pinaster*, and *P. radiata* are cultivated worldwide (Le Maitre, 1998). The taxonomic history of pines was reviewed recently by Gernandt (2005) who discussed evidence from morphology, anatomy, cytology, crossability, secondary metabolites, protein, and DNA comparisons. Gernandt group, also proposed a classification for the genus, recognizing 111 species in two subgenera, four sections, and 17 subsections. The species circumscriptions showed over 90% correspondence to a separate compilation by Farjon (2001), who recognized 109 species. Recent results from phylogenetic analyses of pine nuclear ribosomal DNA sequences and chloroplast DNA (Gernandt et al., 2003) provided refined hypotheses of interrelationships in the genus, and suggested the need for new circumscriptions and for a reduction in the number of subsections. These studies were based on sequences from less than half of the recognized species of pines, and did not always include representatives of all major lineages.
Genetic markers are important tools in the future of forest tree improvement. With improvements in technology, genetic marker analysis and mapping of forest trees have progressed through several stages, defined by the technology of the times, from isozymes, through restriction fragment analysis, and PCR, to genomics. Presented is a brief overview of the evolution and applications of molecular technology in tree improvement.

**Isozymes**

Early genetic mapping in trees was based on isozyme markers. Isozymes were used primarily to study genetic diversity in tree populations (Bousquet et al. 1988). Mapping of isozyme loci in conifers was carried out establishing several linkage groups, using the haploid megagametophyte tissues (Adams and Joly, 1980). Isozyme marker technology is based on separation of proteins according to differences in their charge-to-mass ratio. A crude protein extract is prepared from the plant tissue and the components of the extract are separated according to their charge by gel electrophoresis. The individual enzymes must then be identified using an assay that links their function to a staining reaction. Isozyme marker technology offers limited information and is very time consuming.

**Randomly amplified polymorphic DNA (RAPD) markers**

RAPDs (Williams et al. 1990) are based on PCR amplification of anonymous genomic segments using short primers of arbitrary sequence. Unlike traditional PCR analysis, RAPD (pronounced "rapid") does not require any specific knowledge of the DNA sequence of the
target organism: the identical 10-mer primers will or will not amplify a segment of DNA, depending on positions that are complementary to the primers' sequence. For example, no fragment is produced if primers annealed too far apart or 3' ends of the primers are not facing each other. Therefore, if a mutation has occurred in the template DNA at the site that was previously complementary to the primer, a PCR product will not be produced, resulting in a different pattern of amplified DNA segments on the gel. The technical simplicity and accessibility of RAPDs allowed for the generation of the first saturated genetic maps with broad genome coverage in forest species (Grattapaglia and Sederoff 1994). The drawbacks of RAPD markers for application in forest tree linkage mapping include their dominant mode of inheritance, which leads to reduced information content. RAPDs are highly sensitive to experimental conditions that include the genomic DNA concentration and the conditions of the reaction assay and their reproducibility has been challenged (Jones et al. 1997).

**Microsatellite or simple sequence repeats (SSR) markers**

Microsatellites are DNA sequences composed of variable numbers of short tandem repeats. These repeat number polymorphisms are detected by PCR amplification using primers that anneal to conserved flanking regions (Powell et al, 1996). High variability within populations and co-dominant inheritance make these markers highly informative in outbred forest tree pedigrees. The high information content of SSR markers also makes them the most powerful marker system for individual genotype discrimination, such as the identification of parents in tree breeding (Lambeth et al. 2001), and verification of genotype in clonal forestry (Rajora and Rahman 2003). The major drawback of SSR markers is the effort needed to select pairs
of working primers and the fact that only one locus can be sampled with each primer pair, although simultaneous analysis of multiple loci (multiplexing) can be achieved by analysis of SSRs of different size range and with different fluorescently labeled PCR products.

**Amplified fragment length polymorphism (AFLP) markers**

The AFLP technique provides a novel and very powerful DNA fingerprinting technique for DNAs of any origin or complexity. The AFLP technique (Vos et al. 1995) is based on the selective PCR amplification of restriction fragments from a total digest of genomic DNA. The technique involves three steps: (i) restriction of the DNA and ligation of oligonucleotide adapters, (ii) selective amplification of sets of restriction fragments, and (iii) gel analysis of the amplified fragments. PCR amplification of restriction fragments is achieved by using the adapter and restriction site sequence as target sites for primer annealing. The selective amplification is achieved by the use of primers that extend into the restriction fragments, amplifying only those fragments in which the primer extensions match the nucleotides flanking the restriction sites. Using this method, sets of restriction fragments may be visualized by PCR without knowledge of nucleotide sequence. The method allows the specific co-amplification of high numbers of restriction fragments. The number of fragments that can be analyzed simultaneously, however, is dependent on the resolution of the detection system. Typically 50-100 restriction fragments (Powell et al. 1996) are amplified and detected on denaturing polyacrylamide gels. Polymorphism is generated by sequence variation at the restriction sites and the sites of the selective nucleotides. AFLP markers have dominant inheritance and have limitations of information content similar to RAPD markers.
AFLPs have more total information per reaction (due to the higher multiplex ratio), but the procedure is technically more demanding, requiring a multi-step template preparation and resolution of fragments on sequencing gels. Furthermore, the AFLP technology is proprietary to Keygene of the Netherlands and requires licensing.

**Single-nucleotide polymorphisms (SNPs) in forest tree species**

SNPs are an abundant source of genetic variation and genetic markers that is only beginning to be exploited in forest trees (Kruglyak 1997). SNP detection and genotyping methods have improved in recent years due to the increased interest in the use of association methods for genetic dissection of complex human diseases, using either candidate genes believed to be involved in the disease or every gene in the genome (Risch and Merikangas 1996). SNP discovery typically requires confirmation of the polymorphism through PCR amplification and sequencing (Yen, 2006). One difficulty that arises for SNP discovery in forest tree species is that most individuals are highly heterozygous. This limitation can be overcome in conifers by the use of haploid megagametophyte tissue, which allows SNP haplotypes to be determined directly. In other woody species, sequencing from PCR amplified gene fragments requires the ability to discriminate between heterozygous nucleotides and sequencing errors. Even if discrimination of heterozygous loci is possible, linkage phase and haplotypes identity are more difficult to assign. Cloning remains the best approach to obtain accurate SNP haplotype and linkage phase recognition. This marker technology is the basis of this study.
Hybridization

Introgressive hybridization is an important evolutionary process. It has been defined as the selective incorporation of external genetic material as the result of repeated interbreeding (Anderson 1938). Recent molecular techniques have allowed detection of different mechanisms and dynamics of introgressive hybridization in natural populations of plants and animals, and exploration of its role in the evolution of new species (Vignal, 2002).

Introgressive hybridization seems to have been important in the evolution of Pinus species. In Mexico, Matos and Schaal (2007) reported events of ancestral introgression among natural populations of Pinus montezumae and Pinus hartwegii, while in Asia, Pinus densata may have been derived from the hybridization between Pinus tabulaeformis and Pinus yunnanensis. Hybrid zones have also been detected between Pinus pumila and Pinus parviflora var. pentaphylla (Samperdo, 2006). This process has also been detected in subsect. Halepensis in Europe and in some species in North America, Pinus strobes (Epperson et al. 2004) and Pinus taeda and Pinus echinata (Burke et al. 1997). Recent studies have analyzed introgression based on probabilistic approaches of maximum likelihood and Bayesian inference by organizing populations in a hierarchical way based on genetic criteria (Corander and Tang 2007). Another recent approach to detecting genetic barriers or areas where the rate of change in allelic frequencies is particularly high was developed by Dupanloup et al. (2008) and consists in defining groups of populations that are geographically homogenous and maximally differentiated. The history of genealogical lineages can also be traced in explicit evolutionary relationship with geographical
distribution of lineages to infer demographic scenarios (e.g., population expansion, colonization, and fragmentation (Templeton, 2003). This framework has the potential of straddling the interface between intra- and interspecific evolution. It is precisely at this interface that the process of speciation occurs (Templeton 2001).

**Sequencing Errors**

Ever since the advent of high-throughput sequencing with the Human Genome Project, investigators have faced a trade-off between data quality and cost of acquisition (Bouck et al. 1998; Olson and Green 1998). Fifteen years ago, Clark and Whittam (1992) recognized that sequencing error could be a problem for evolutionary analysis, and other groups tackled error in the context of alignments and genetic maps (States 1992). Error rate can vary from 0.1% to 3.1% depending on the platform and the level of coverage desired. For single pass sequencing, error rates can be as high as 3.1% (Hill et al 2000). Sequencing errors can have serious consequences for the current project and future research for at least three reasons. First, sequencing errors can cause automated annotation algorithms to fail to detect sequence features such as initiation and termination signals and introns. Second, sequencing errors can lead to spurious annotation of single nucleotide polymorphisms. Third, sequencing errors can lead to inaccurate or erroneous evolutionary inferences, such as in estimating the rate of nucleotide substitution or recombination (Clark and Whittam, 1992). The consequences of sequencing error will be most serious in intraspecific comparisons involving species with low natural genetic variability such as closely related Pine species or in interspecific comparisons
between closely related taxa. Although sequencing analysis software and technology have since evolved to now provide accurate estimates of the probability that a given base call is incorrect (Ewing and Green 1998), the problem is ever present.

SNP markers in pines would have value for applied breeding for analysis of parentage, including detection of hybrids, and as “candidate genes” for association studies of a variety of traits (Tabor et al, 2002). While a gene may be proposed as a “candidate gene” for a particular trait based on sequence similarity to genes of known function in other plant species, the real proof of gene function is based on finding or creating genetic variation in gene activity, and demonstrating a significant association with a change in phenotype. Analysis of naturally-existing genetic variation in populations can provide this kind of evidence, if cost-effective methods exist to detect and analyze genetic variation.

DNA sequence data from *Pinus taeda*, *P. pinaster*, and *P. sylvestris* support the hypothesis that it is possible to identify species-specific single-nucleotide polymorphism markers (SNPs) capable of resolving parentage of natural or experimental hybrids. Screening multiple pine species for SNPs will also allow identification of shared polymorphisms (markers that are variable in several species) as well as unique polymorphisms (markers that are fixed in most species but variable in one or two). These data will provide additional information regarding past speciation events, introgression in sympatric zones, and population structure. The goals of the current research are to survey fragments of 10 genes in 16 species of pine for DNA sequence variation. The 16 species to be analyzed will include: *P. taeda, P. elliottii, P. radiata, P. patula, P. tecunumanii, P. oocarpa, P. maximinoi, P.*
herrerae, P. leiophylla, P. teocote, P. greggii var. australis, P. caribaea var. hondurensis, P. jaliscana, P. pringlei, P. pseudostrobus, and P. greggii var. greggii. The expected outcome is identification of species-specific SNPs useful for hybrid testing. This test project will act as a launch pad to develop and test efficient methods for discovery and analysis of species-specific SNP variation, to understand relationships between genetic variation and phenotypic variation with groups of closely related species, and to characterize the extent of gene flow between related populations.
Materials and methods

Plant materials:

Plant materials and seeds were obtained from the CAMCORE (Central American and Mexico Coniferous Resources Cooperative) group. In cases where green tissue was not readily available, seeds were sown and young seedlings were harvested at 1 month of age. Tissues were collected and stored at -80°C until DNA extraction.

DNA Extraction

DNA was extracted using a modified CTAB based protocol developed in our lab by George Khan and Ross Whetten. The method was adapted for use with Nunc 96 well filter plates (Cat# 278010 Fisher Scientific) for high throughput. A detailed protocol is included in appendix 1.

Sequencing Reaction Template Production:

Primers were designed based on protein-coding sequences conserved between P. taeda and other related species, either pines when DNA sequences for other pine species were available or spruce if no pine species DNA sequences were available, to provide the highest probability of successful amplification from each of the target pine species. Primers were designed using Primer 3 V0.4.0 (Rozen 2000). Primers template are listed in (Table 14).

Sequencing

Sequencing templates were PCR amplified with Taq Polymerase (NEB Cat # M0273L) using a standard PCR cycle: Initial denaturation: 95°C for 30 seconds, followed by 25 cycles: 94°C for 15 seconds, 55°C for 30 seconds, 70°C for 35 seconds, followed by a final
extension of 72 for 5 minutes then hold for 4–10°C. Sequencing reactions were purified following Nunc-PCR purification method (Nalge Nunc). Quantification was done using Quant-iT™ PicoGreen® dsDNA Reagent and Kits (Invitrogen). Sequencing was carried out at the NCSU GSL (Genome Science Laboratory) on an Applied Biosystems 3730xl DNA Analyzer. The GSL performed the sequencing reaction set-up, reaction clean-up, capillary electrophoresis, and base calling.

**Data Analysis**

Data were formatted and cleaned using SNAP Workbench (Aryol 2006) and Sequencher 1.10.1 (GeneCodes Corp., Ann Arbor, MI, USA). Individual sequences were first catalogued by gene and species. First all the individual sequences for a specific gene from a species were imported into Sequencher. Sequences were then aligned and trimmed so that every individual had a representative sequence. The consensus sequence for that gene was further edited by hand to include ambiguity codes to represent within species variation. If more than two individual sequences supported a particular base call, and the trace files clearly supported that call, than an ambiguity code was entered to reflect that polymorphic site in the consensus. One consensus sequence for each of the 10 genes for each of the 16 species was then exported for further analysis. For the SNP analysis, individual genes were analyzed separately. The consensus sequence of each gene from each species was then realigned and further trimmed so that there is representation throughout the alignment for every species. Final alignment of the gene consensus sequence was carried out in SNAP workbench so that the information can be extracted for the species genotyping. Putative species specific SNPs
were identified as any sequence with a base different from the consensus of all species, whether it was an ambiguity code or a specific base. The ambiguity codes were maintained as a candidate inter-specific SNP.

**Phylogenetic analysis**

The consensus sequences for each gene representing each of 16 species were uploaded into SNAP workbench where each gene was analyzed separately. Sequences were realigned using ClustalW (Thompson, 1999) within the Workbench to ensure that all consensus sequences were trimmed so that a representative base was present at each position. Sequences were then collapsed into haplotypes removing indels and excluding infinite site violations. Haplotypes were then input into PAUP 4.0(Swofford 2002) for bootstrapping and maximum likelihood analysis. The unrooted most parsimonious trees were generated using a heuristic search with *Pseudostrobus* as the out-group. Heuristic search optimality setting was set to parsimony. Along with the phylogeny, tree with length, Consistency index (CI), Homoplasy index (HI) and Retention index (RI) values will be maintained to support the tree. Bootstrap support values were calculated based on the 50% majority rule consensus rule where gaps were treated as missing and trees were unrooted. Since the information content per gene differs significantly, phylogenetic analysis was conducted on genes 111, 112, and 113 as representative of genes with the highest information content.
Results

Sequencing of the 10 targeted genes across the 16 *Pinus* species resulted in a total of 2988 bp with sequence length varying from 248 bp to 366 bp per gene for the different species. For each gene in each of the 16 species, PCR products from 24 individuals were sequenced using a single reaction run per PCR product. Table 13 shows the number of recoverable sequence that contributed to the consensus for the targeted gene, because the number of individual sequences varied per gene per species due to sequencing error or reaction failure. When generating the consensus, if two or more individual sequences within a gene alignment supported a different base call that difference was be manually coded into the consensus using an IUPAC Nucleotide ambiguity code (Table 1).

The final sequence length of gene 101 was 366 bp, and yielded nine potential SNPs (Table 3). Of the 16 species, five accounted for the nine SNPs with 11 showing no variation. *P. greggii var. australis* and *P. greggii var. greggii* both shared SNPs at position 115 and 269. *P. oocarpa* was the most distinct species at this gene position with 33% of the polymorphism at this gene. Positions 200 and 219 were unique to *P. maximinoi* and *P. patula* respectively.

Gene 104 had a total of 302 bp with 16 potential SNPs (Table 4). Six of 16 species showed no polymorphism. Positions 157 and 251 were each conserved between four different species. *P. oocarpa* accounted for the 25% of the 16 polymorphisms. Six species shown in Table 4 had the potential of being identified by a single SNP. Gene 105 had a total of 355 bp with 17 potential SNPs (Table 5). Four of 16 species showed no polymorphism. Position 272
had a G nucleotide in 6 species and a T in the 10 others. *P. leiophylla* accounted for the majority of SNPs with 29%. At this gene position, three targeted species were separated by a single polymorphism. Genes, 106 had a final sequence length of 323 bp with 10 potential SNPs (Table 6) and, gene 107 had a total of 270 bp and 27 potential SNPs (Table 7). Gene 109 (Table 8) had a total of 271 bp with 9 potential SNPs at 6 positions. *P. leiophylla* was the most diverged with 44% of the polymorphism. 10 of the targeted species had no polymorphism at this position. Gene 110 (Table 9) had a total of 318 bp with a potential 61 SNP occurring at 35 positions. *P. maximinoi* and *P. leiophylla* shared 11 SNPs at 11 different positions.

Gene 111 (Table 10) had a total of 254 bp with 112 potential SNPs occurring at 51 positions (Table 12). At this gene, *P. pseudostrobus* and *P. radiata* accounted for 47% of the total variation. The phylogenetic analysis of this gene produces 12 haplotypes at 51 positions with H1, H2 and H12 comprised of multiple individuals. The phylogeny was based on 17 parsimony informative characters and 34 uninformative characters. Phylogeny was generated using *P. pseudostrobus* as the out-group, with a tree with length of 65, CI of 0.9077, HI of 0.0923 and RI of 0.8286. The 50% majority consensus tree was generated with bootstrapping values ranging from 26 to 100% (Figure 1). At gene 112, there was no usable sequence for *P. tecunumanii* after the sequences were trimmed to meet the analysis criteria. There was a length of 281 bp with 61 potential SNPs distributed over 26 positions (Table 11). Six of the targeted species can be identified by a unique polymorphism. *P. radiata* had the most conserved sequence, with only a single polymorphism relative to the cross-species
consensus. Phylogenic analysis was done based on 15 haplotypes containing the 26 positions with all targeted species in unique haplotypes. The generated tree had: length of 27, CI of 0.8519, HI of 0.1481, and RI of 0.8571 (Figure 2). The bootstrapping method using a heuristic search of the 26 characters found three positions to be constant, 13 variable sites were parsimony-uninformative, with 10 informative. The 50% bootstrap value was computed using *P. pseudostrobus* as an out-group varies from 38 to 68%. Gene 113 had a total of 248 bp with 41 potential SNPs occurring at 17 positions along the gene (Table 12). Positions 72 and 182 were the most conserved across the targeted species with *P. tecunumanii* accounting for 21% of the variation and six of 16 species had a unique SNP marker that could distinguish them at this gene position. The phylogeny was based on 11 haplotype and the 17 positions. Of the 11 haplotypes, H1 and H4 comprise multiple species, H4: *P. herrerae, P. maximinoi, P. greggii var australia, P. greggii var honduras, P. patula* and H1 *P. pringlei* and *P. jaliscana*. The tree had a total length of 18 with CI of 0.8333, HI of 0.1667, and RI of 0.7500 (Figure 3). Bootstrapping was done using the 50% majority rule consensus with bootstrapping support ranging from a low of 17% to a high of 64%. Again the analysis was based on 7 parsimony-informative sites.
Discussion

The use of SNPs as a marker technology is only beginning to be exploited in forest trees (Kruglyak 1997). This pilot study provides a snapshot of the use of SNP as markers for differentiating between closely related Pinus species for species identification or identification of hybrids. As detection and genotyping methods have improved in recent years, there has been increased interest in the use of association methods for genetic dissection of complex traits in forest trees. SNPs can be identified from sequencing projects like this one or from Expressed Sequence Tags (EST) databases that were derived from a mixture of genotypes (Somers et al. 2003). These databases will be the best source of nucleotide diversity data for association genetic studies or targeted gene identification in forestry, as more sequences and software that automate SNP discovery become available. Several substantial collections of ESTs are available for forest tree species. The completion of the poplar genome provided a resource for researchers interested in angiosperm trees (Tuskan et al., 2006), and the more than 45000 cDNA sequences and genes from pine (Samperdo 2006) available in GenBank provide a useful resource for researchers interested in conifers.

Analysis of sequences of fragments from 10 genes across 16 species showed significant levels of variation across the different genes. The length of sequence at different gene position also varies due to low sequence coverage and some PCR reaction failure. For each targeted species, PCR products from 24 individuals were sequenced using single Sanger
reads. Since the sequencing was done using PCR amplified gene products, multiple copies of a gene or heterozygous sites lead to poor sequence quality. Another area that leads to poor sequence was quantification of the sequencing products. Since some genes amplified better than others, the product yield varied considerably, making quantification of the over 4000 samples very challenging. Table 13 provides a snapshot of the different number of individuals that were used for the analysis. Another difficulty that arises for the SNP discovery was that pine species are highly heterozygous. This limitation can be overcome in conifers by the use of haploid mega-gametophyte tissue, which was not available for this study, which allows SNP haplotypes to be determined directly. Even if discrimination of heterozygous loci is possible, linkage phase and haplotype identity are more difficult to assign. Cloning remains the best approach to obtain accurate SNP haplotype and linkage phase recognition, however due to the number of samples involved in this study and time constraints, this was not an option.

After sequencing, the sequences were analyzed at each gene position separately. Since the number of individuals varied across the targeted species, it was difficult to look for within-species variation. We could not place enough confidence in a single sequence read as an accurate representation of an individual since there was no way to distinguish errors introduced during the PCR reaction or the sequencing reaction. Due to this concern, a decision was made to instead focus on between-species variation. For this analysis, all the individuals’ sequences at a gene position for each targeted species were aligned and trimmed to generate a consensus sequence. In generating the consensus, if two or more individual
sequences supported a different base call, an IUPAC nucleotide ambiguity code was hand edited into the consensus to reflect that change. Although the analysis of this dataset will focus on between-species sequence variation, there is some information about within-species variation.

Of the 10 genes surveyed, the level of genetic diversity varies considerably. Many of these species are believed to hybridize naturally in the sympatric zones, so allele-sharing among the species may be quite common. For this project, we were not able to take advantage of the latest high-throughput DNA sequencing methods due to financial constrains but this pilot project shows that the potential for SNP analysis using high-throughput DNA sequencing methods shows great promise as the field advances. Combining such surveys of genetic diversity with phenotypic analysis could prove very powerful in linking genetic variation to phenotypic or physiological variation between and within species.

Introgressive hybridization represents a possible cause for the presence of shared polymorphisms among closely related taxa (Machado et al., 2001), and while natural hybridization has been reported among closely related Pinus taxa, more or less recent interspecific gene exchanges appear highly likely between the 16 Pinus species analyzed. Contrary to closely related taxa in the genus, these species do cross naturally and there are questions as to their actual recognition as distinct biological species (Burke et.al 1997). Since some of these species are located within pollen dispersal distance and they can hybridize naturally, trans-species shared polymorphisms are likely to be of shared ancestry. It is clear
from Figures: 1, 2, and 3 that these genes all support different snapshot in the evolutionary history of these species. Since there is little support across the three phylogenies, this could be a scenario where these genes have different evolutionary histories in this set of closely related species. Gene 112 and 113 are both involved in wood formation while gene 111 is involved in drought resistance (Table 2). Based on this dataset, the three genes have different phylogenetic histories. One possible explanation is that the targeted genes being amplified are orthologs not paralogs. This is a hypothesis that could be addressed in more detail by a follow up study using next generation sequencing technology with deeper coverage. The presence of trans-species shared polymorphisms also calls for caution in interpreting gene genealogies. In plant and tree species suspected of large historical population sizes, non-monophyletic patterns of allelic variation should persist for tens or hundreds of thousands generations. In such cases, it has been pointed out that extreme caution should be exercised when inferring reticulate evolution from polyphyletic patterns at nuclear loci (Hare et al., 2007). Such patterns could also be caused by the long-term maintenance of trans-species-polymorphisms of shared ancestry. The level of polymorphism across the different genes was significantly different. Gene 101 (EST1147582 Normalized pine embryo library) was much conserved across the 366 bp and a potential nine SNPs. This is in contrast with gene 111 a cysteine protease gene which from 254 bp sequence analyzed, had a potential 112 SNPs occurring at 51 different positions. Based on the evolution of the woody and herbaceous growth habits, it is plausible that the genes for wood formation are functionally conserved. Wood is a primitive character, and the herbaceous habit is a derived state for angiosperms.
This hypothesis was not supported in this study; gene 112 and 113 both associated with lignin synthesis were more polymorphic that some of the other drought stress genes. The findings of this study will be a valuable preliminary dataset for a larger population survey of adaptive variation in North and Central American pines. These species repopulated North America after the retreat of the Pleistocene ice sheets beginning about 15,000 years ago, and have diversified into a wide variety of ecological niches. Migration and colonization processes could have a different impact on tree species compared with annual plants (Austerlitz et al. 2000).
Conclusion

The objective of this project was to develop efficient methods for discovery and analysis of species-specific SNP variation, to understand relationships between genetic variation and phenotypic variation with groups of closely related species. This study has implications for the practical applications of molecular markers in forest genetics. SNPs can be useful as a new class of molecular markers for tree improvement. Variation in SNPs could be correlated with important traits across families within species, based on phenotypic data obtained by traditional breeding and progeny trials. SNPs that predict mature characteristics would be especially valuable. It was clear that there is a high level of variation depending on the targeted gene. The findings suggest that some genes are more highly conserved than others. As a launch pad to use SNPs as a valuable marker technology in the selection and breeding of forest trees, this project shows that the potential is there and the level of information depends on the number of genes analyzed and the level of genome coverage desired. The gene sequences being released from this study will provide a useful public resource for tree breeders and researchers working with Central American and Mexican pine species, as they move into implementing SNP markers into their breeding and selection program. Lastly, we showed that nucleotide diversity of organisms can be sampled by multi gene sequencing in the absence of a full genome sequence.
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Figure 1. Maximum likelihood tree of gene 111 (254 bp) CI of 0.9077, HI of 0.0923 and RI of 0.8286. Branch lengths do not reflect sequence divergence. Many terminal polytomies are due to identical sequences. Bootstrap values over 50% are shown above branches.
Figure 2. Maximum likelihood tree of gene 112 (281 bp) length of 27, CI of 0.8519, HI of 0.1481, and RI of 0.8571 CI of 0.9077, HI of 0.0923 and RI of 0.8286. Branch lengths do not reflect sequence divergence. Many terminal polytomies are due to identical sequences. Bootstrap values over 50% are shown above branches.
Figure 3. Maximum likelihood tree of gene 113 (248 bp) length of 18 with CI of 0.8333, HI of 0.1667, RI of 0.7500. Branch lengths do not reflect sequence divergence. Many terminal polytomies are due to identical sequences. Bootstrap values over 50% are shown above branches.
## Appendix

### List of Appendices

<table>
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<th>Appendix</th>
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<td>Appendix I</td>
<td>Detailed Extraction protocol.</td>
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<tr>
<td>Appendix II</td>
<td>NEXUS formatted consensus alignment file of the 10 targeted genes.</td>
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APPENDIX I

The following is a detailed high throughput DNA extraction method for extracting DNA from Pines.

Reagents:

**Buffer 1:** 2x CTAB buffer

- 100 ml 1 M Tris HCl pH 8.0
- 280 ml 5 M NaCl
- 40 ml of 0.5 M EDTA
- 20 g of CTAB* (cetyltrimethyl ammonium bromide)
- Bring total volume to 1 L with ddH$_2$O.

*CTAB will only go into solution after the addition of salts.

RNase optional and no BEM required

Reagent Dx (Qiagen) optional and added before sample disruption to help minimize foaming.

**Buffer 2:** 5M Potassium Acetate pH 5.7

- Ph with Acetic acid

**Buffer 3:** 0.66M Guanidine HCl in 63% EtOH

Guanidine hydrochloride is a dangerous irritant and proper protective garments, gloves and eye protection must be worn. Guanidine hydrochloride is highly reactive with bleach and the waste from the following steps must be disposed of properly.

**Buffer 4:** 25 mM NaCl, 5 mM Tris pH 7.5, 75% Etoh, 0.05mM EDTA

Final pH should be about 7.5-7.6

**Detail Protocol:**

Things to do before starting:

- Preheat water bath or heating block to 65°C

Tissue disruption
Add about 50 mg to 100 mg of fresh or frozen tissue to microcentrifuge tube along with two ceramic beads.

- Place in this order: rounded bead on bottom followed by tissue then cylindrical bead on top.

Add 40 μl Buffer 1 and cap tube.

- Addition of RNase is optional but not required.

Place tubes in mixer mill and disrupt tissues for 25s. Dissemble assembly, flip the outer tubes to the inside and repeat.

- Flipping tubes is essential to ensure tissue is completely pulverized.

Remove tubes and add an additional 360 ul Buffer 1 and repeat the Mixer Mill procedure

**Note:**

1: examine tubes at this time for any leaking or tissue clumping. No tissue clumps should be visible. Vortex or pipette further to remove any clumps. Clumps of tissue will not lyse properly and will therefore result in a lower yield of DNA.

2: For Dry tissue, increase buffer 1 to 600 ul and adjust buffer 2 to maintain ratio.

Incubate the mixture for 15 min at 65°C to lyse cells. Invert tubes 2 or 3 times during incubation.

- Ceramic beads do not need to be removed.

Spin briefly to remove excess foam, and then add 150ul of Buffer 2. Cap, invert 5 times to mix then incubate @ -20°C for 30 min to overnight

- This aids in protein precipitation.

**Note** This is also a stopping point, as samples can be stored at -20°C. If stored overnight, thaw samples before proceeding.

Centrifuge for 15-20 minutes @ 13000 rpm or equivalent.

Transfer 400ul supernatant to a 96 deep well plate containing 600ul of Buffer 3. Cap and invert 5 times to ensure good mixing.
Some precipitate might be transferred but should not affect DNA yield.
If more than 400ul supernatant is transfer, adjust Buffer 3 accordingly.

Transfer 1 ml of the mixture to a Nalge Nunc glass fiber filter plate, centrifuge 2 minutes @ 5000rpm, using a deep well plate to catch flow through.

- Discard flow through and repeat with any remaining mixture.

Wash each well twice with 500ul of buffer 4.

- A third wash can be done if color is present in second wash.
- Excess washes will not affect DNA yield.

Empty flow through and spin 5 minutes to dry the Column.

- This drying is key as residual ethanol can affect downstream uses of the DNA

Elute DNA with 150ul Tris pH 8.0, let stand for 5 to 10 minutes before centrifuge to collect elute

- Elution can be done with water, TE pH 8.0, Qiagen Buffer AE or EB.
- Alternatively, elution can be done twice with 100ul each for maximum yield.
- DNA quality can be checked on a 1% agar gel.
APPENDIX II

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**P_teoc10**

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**P_ooca10**

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P_leio13
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P_Psue13
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P_radi13
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P_elli13
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P_herr13
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P_patu13
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P_ooca13
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P_tecu13
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End;