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# The Conifers: Genomes, Variation and Evolution

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David B. Neale • Nicholas C. Wheeler

# The Conifers: Genomes, Variation and Evolution

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## Foreword

Conifers, and related gymnosperms, are among the world's oldest groups of organisms. I learned that in my first year at university while training as a forester, and even now, as a forest geneticist nearing the end of my scientific career, I still find this fascinating. Conifers evolved during the era of the dinosaurs and continue to dominate large expanses of forest around the world, even after the subsequent evolution of the angiosperms, which are exceedingly more species-diverse. What was in the DNA of conifers that made them so durable? In *The Conifers: Genomes, Variation, and Evolution*, David Neale and Nicholas Wheeler review and synthesize findings from traditional genetic studies and the most recent molecular genetic research that helps elucidate why conifers may have persisted for millions of years.

Humans have long valued conifers for their exceptional wood properties. Straighter in form, and possessing stronger yet lighter wood than most angiosperms, they have been important construction materials throughout the world for thousands of years. Today, conifers are an important forest resource in many countries. Early in the twentieth century, scientists recognized the significance of conifer genetics to the practice of forestry. Common garden studies by pioneering geneticists showed that many conifer species had considerable levels of genetic variation, making them highly suitable to “improvement” using classic breeding techniques developed on domestic plants and animals. Many traditional conifer breeding programs were subsequently initiated, practicing recurrent selection in order to improve desired traits — such as growth, resistance to disease and insects, and, more recently, adaptability to changing environments. In the 1980s, molecular genetics studies of forest trees also became a key element to understanding their basic biology. Using the technique of protein electrophoresis, these molecular approaches enhanced our knowledge of conifer genetics and became instrumental to understanding conifer mating dynamics, informing seed production practices, and developing forest tree genetic resource management programs.

As molecular biology techniques improved through the 1990s and onward, significant resources were invested in molecular genetics and genomics research due, in large part, to the progress and promises of the human genome project. While traditional forest genetics and tree breeding research waned around the world, largely due to fundamental shifts in the economics of forestry investments, forest tree molecular geneticists were keeping pace with the genomic advances occurring in most other organisms (e.g., *Arabidopsis* and humans). During the turn of this

century, study objectives changed to more scholarly questions, along with divergence in the terminology and vernacular used by forest tree breeders and forest tree molecular geneticists. To address this, Neale and Wheeler have neatly clarified the terms used in modern molecular genetics of conifers and, more importantly, have presented the most recent information of conifer genetics in a modern synthesis that integrates many aspects of their quantitative and population genetics. The book is presented in an understandable way, highlighting recent breakthroughs in gene structure and gene families, comparative genomics, phylogenetics, and landscape genomics, for example, but also identifies the interesting challenges ahead in genomics research of these marvelous organisms. Any new forest geneticist must now be versed in both classical and modern population genetics and quantitative approaches, as well as molecular genetics terminology, techniques, and bioinformatics of genomics. *The Conifers: Genomes, Variation, and Evolution* provides a much needed unification of these topics and should be required reading for new students of conifer molecular biology and genomics.

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## Preface

The study of the genetics of forest trees began more than 100 years ago, coincident with the rediscovery of Mendel's classic works. For three quarters of the twentieth century, conifer genetics was dominated by the study of phenotypic variation in provenance trials (Chap. 8), species hybridization trials (Chap. 15), disease and insect resistance (Chap. 14), and development of tree breeding methods, all of which suggested most traits in trees were quantitatively inherited. Furthermore, many traits were adaptive and varied in response to environmental factors such as temperature and moisture.

Forest genetics research approaches, funding sources, and personnel began changing significantly in the mid-1970s as biochemical and DNA marker development allowed for population genetic and mating system investigations. These neutral markers were subsequently used to characterize the genetic basis of quantitative traits (Chaps. 9 and 11) and enhance our understanding of conservation genetics (Chap. 13) and phylogenetics (Chap. 16). Recent developments in high-throughput genome sequencing technology have resulted in a quantum leap in our knowledge of conifer genomes (Chaps. 2, 3, 4, 5, 6, 7, 12, and 17). We anticipate this knowledge will continue to increase rapidly, as it has for so many other organisms. A review of the state of knowledge in conifer forest genetics therefore seems appropriate.

In this monograph, our goal is to summarize and synthesize this body of work, specifically for conifers, in a manner that would be useful for practicing professionals in conifer genetics and genomics research but also for those from other fields of forestry and plant biology who might be curious as to what has been learned over 100+ years in this small discipline. The monograph is organized into three major parts, Genomes, Variation, and Evolution, and we have tried to synthesize and cross-reference across all chapters and sections. We have not included the very extensive literature in applied conifer breeding and tree improvement research, and instead refer readers to other important works in this area (Wright 1976; Namkoong 1979; Zobel and Talbert 1984; Mandal and Gibson 1998; Kumar and Fladung 2004; White et al. 2007; Plomion et al. 2011). While our search and summary of the relevant literature is certainly not exhaustive, we have sought to provide a comprehensive view with a modest (over 1600) number of exemplary citations.

Finally, the authors of this monograph have enjoyed and been rewarded by our years of making small contributions to this discipline of forest genetics working

individually and for much of our careers together. We have benefitted from knowing and working with a substantial number of the scientists, past and present, who have defined the forest genetics discipline. We are using this moment to give a little something back to the discipline that has given us so much. It is our perspective on the evolution of our discipline over the last 100+ years (Wheeler et al. 2015) that has shaped our final chapter (Chap. 18).

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