

Populus Community Mega-Genomics: Coming of Age

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Plants, once germinated or transplanted, will live and die in the same location their entire life. And for woody perennial plants, this circumstance exists for many years, even millennia. As a result, woody perennial plants in natural ecosystems or in plantations uniquely create an environment that fosters, shapes, and preserves heterogeneous communities. That is, trees co-exist with other organisms such as microbial and fungal pathogens, endophytes, arboreal insects, and rhizospheric microorganisms. Moreover, over a life span, not only do trees have to respond to potential biotic interactions, they also have to respond to abiotic challenges such as seasonal changes from spring to summer to winter as well as interannual climatic changes. Despite such challenges, arboreal forms of plant growth thrive today and throughout evolutionary history (Groover, 2005). Still, our understanding of the mechanisms of how trees adapt to local conditions and cope with biotic and abiotic challenges remains largely obscure.

In the last ten years, *Populus* has emerged as the model tree for biological studies among all forest trees because of numerous attributes, including rapid growth, relatively short reproductive cycles, ease of vegetative propagation, general amenability to *in vitro* culture, regeneration and transformation, and extensive genetic and genomics resources such as breeding populations, genetic maps and large EST resources (Bradshaw *et al.*, 2000; Jansson and Douglas, 2007; Tuskan *et al.*, 2004; Wullschlegel *et al.*, 2002). The recent release of the reference genome of *Populus trichocarpa* (Tuskan *et al.*, 2006) has provided unprecedented opportunities to advance our understanding of *Populus* biology and subsequent interactions with associated organisms. This is evidenced by a drastic increase of refereed publications related to *Populus* in the past three years, which now triples that of its close relative, *Salix* (Yang *et al.*, 2009). Since the *Populus* reference genome was released, one of the important *Populus* pathogens, *Melampsora larici-populina* (Martin *et al.*, 2004) (<http://genome.jgi-psf.org/Mellp1/Mellp1.home.html>), has also been sequenced. The DOE Joint Genome Institute (JGI) has also sequenced the genome of a symbiotic fungal basidiomycete, *Laccaria bicolor*,

(Martin *et al.*, 2008) that is able to engage a mutualistic ectomycorrhizal association with the roots of *Populus* (Kohler *et al.*, 2008). Likewise, many other *Populus*-associated pathogens and endophytes have recently been sequenced (<http://genome.jgi-psf.org/stema/stema.home.html>). Simultaneously, advanced “omics” tools have been developed, such as transcript profiling using high-throughput short-read sequencing and proteomic and metabolomic profiling via advance GS-MS. Thus, *Populus*, as a model, provides vast opportunities for studying *Populus*/biotic, *Populus*/abiotic, and *Populus*/climatic interactions, particularly at the molecular levels.

Beyond summarizing the relevant fields of research, our main intention with this special issue is to further stimulate thinking from the perspective of *Populus* as an entire living community, a community that contains a “mega-genome,” from both abiotic and biotic aspects. We certainly hope that this special issue will inspire more research in this area, not only by those who have long been involved in *Populus* genomics, but also by those who have not.

STATE OF THE SCIENCE

In this special issue, we solicited seven reviews with a theme of *Populus* community genomics. These reviews have been grouped into three areas: an update on *Populus* genomics, *Populus* interactions with the biotic organisms, and *Populus* interactions with the environment.

The first review provides an overview of *Populus* genomics. Yang *et al.* (2009) offer a comprehensive review of the state-of-the-science in *Populus* experiment-based functional genomics and computational genomics. These authors also summarize applications of various classical and “omics” technologies toward advancing *Populus* genetics and functional genomics. A major portion of the review also covers current progress in sequence-based discovery, from predicting gene function to comparative analysis of gene families to development of genomic databases and studies of the evolutionary dynamics at both the gene and genome level.

The next four reviews offer detailed progress and associated challenges in understanding *Populus* interactions with biotic organisms: insects, pathogenic organisms, endophytes, and rhizospheric microorganisms. Ralph (2009) provides an overview

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of emerging research strategies designed to target defense genes that directly mediate insect resistance in *Populus*, including the use of transgenesis to functionally characterize candidate defense genes, identify novel defense mechanisms through mutant population screening, and linked genetic/genomic approaches to study changes in gene expression. Duplessis *et al.* (2009) assess *Populus*-pathogen interactions at the molecular level for both the host and the pathogen. The availability of the *Populus* genome sequence has allowed comparative analyses with other sequenced plant genomes in an effort to reveal gene families that play key roles in defense response. One of the striking findings is that the NBS-LRR resistance (*R*)-gene family has expanded in *Populus* compared with other plant genomes, including *R*-gene subfamilies not previously reported in plants. This article also provides details on interactions of *Populus* with *Melampsora*, a rust disease that causes considerable damage in *Populus* plantations. Studies in this pathosystem have been advanced by sequencing of the *Melampsora larici-populina* genome, facilitating the reciprocal study of host response to pathogen attack and pathogen's reaction to the host at comparable genomic levels. Transcript profiles derived from compatible (susceptible) and incompatible (specific host-resistance) *Populus-Melampsora* interactions demonstrate that defense responses in perennial *Populus* are similar to those of annual plant species such as up-regulation of transcripts encoding pathogenesis-related proteins.

In addition to the traditional host/pest or host/pathogen interactions, this special issue also reviews the state-of-the-science related to the interactions of *Populus* and its endophytes. Endophytes are microorganisms that create complex and long-lived associations within plant tissues. Unlike many pathogens, endophytes typically have a beneficial effect on their host. Despite this benefit, the role of endophytic bacteria in growth and development of their host plants remains unresolved. Van der Lelie *et al.* (2009) review the interaction between *Populus* species and their endophytic bacteria and point to potential breakthroughs in our understanding of improvements in the productivity of *Populus*. The authors summarize direct and indirect mechanisms of improving host plant growth and development via endophytic inoculations, including applications of custom endophyte-host partnerships in *Populus* for improving productivity and establishment of *Populus* on marginal soils and phytoremediation of contaminated soils and groundwater.

An even less studied field of *Populus* community genomics is *Populus* interactions with its associated soil microbiome. Podila (2009) provides new insights gleaned from genomic-level studies involving *Populus* and its soil community, especially mutualistic and symbiotic ectomycorrhizal interactions. Special focus is given to the communication and signaling that occurs in the soil between tree roots and mycorrhizal fungi and the effect that root exudates and fungal enzymes exert on the turnover and translocation of nitrogen, mineral nutrients and soil organic matter.

The final two reviews deal with *Populus* environmental interactions with Wullschleger *et al.* (2009) reviewing light, tempera-

ture and moisture responses and Chen *et al.* (2009) emphasizing metabolic responses to biotic-abiotic factors. Although research focused on understanding the molecular processes that underpin the *Populus* growth and development has steadily increased over the last several decades, the ability to examine the basic mechanisms whereby trees respond to a changing climate and resource limitations has benefitted greatly from the recent release of the reference genome of *P. trichocarpa*. Wullschleger *et al.* (2009) summarize the literature with focuses on integrating transcriptomic, proteomic, and metabolomic analyses related to *Populus*' response to its climatic and edaphic environment. These authors highlight instances where two or more omic-scale measurements confirm and expand our inferences about mechanisms contributing to observed patterns of response. Chen *et al.* (2009) cover the genomics-level secondary metabolism in *Populus* that is involved in interactions with biotic and abiotic environments. To ensure its survival and reproduction in complex biotic and abiotic community environment, *Populus* produces a myriad of secondary metabolites as adaptation mechanisms. These authors also review how these compounds relate to certain biological/ecological processes such as defense against insects and microbial pathogens or adaptation to abiotic stresses.

CHALLENGES AND FUTURE ADVANCES

The landmark event of the release of the reference genome of *P. trichocarpa* along with the genomic sequences of some of its biotic associates has greatly elevated research activities in *Populus* and its associated communities. *Populus* biologists are now able to take a systems approach to quantifying the diversity of genes, proteins and metabolites that govern the growth and development of *Populus*. While substantial advancements have been achieved in *Populus* genome-based science, many challenges remain. To meet these challenges, a coordinated effort amongst the diverse set of research communities will be required.

The interactions between *Populus* and other biotic organisms and/or the abiotic environment are complex, involving multifaceted signal transduction networks and many genes expressed in spatial-temporal manners. As more "omics" tools become available and the costs come down, massive amount of "omics" data (e.g., transcriptomics, proteomics, metabolomics and phenomics) will be generated in an effort to deconvolute the processes and links between phenotypic responses with gene expression. Concomitantly, high-performance computational pipelines will be needed in order to handle data generation, storage and analysis. This vast amount data will need to be integrated into functional systems biology platforms which are designed to reveal the underlying mechanisms controlling *Populus*' response to biotic organisms and/or abiotic conditions. Based on the reviews in this special issue, it is anticipated that a network of interactomes will be produced in the near future.

Finally, *Populus* is considered a woody bioenergy crop and is one of the two primary bioenergy crops studied within the

three DOE bioenergy science centers (BioEnergy Science Center, <http://bioenergycenter.org/>). *Populus* also plays a critical role in maintaining healthy natural and managed ecosystems, contributing to carbon sequestration (Tuskan and Walsh, 2001), and providing raw materials for pulping, paper and other forest products (Tuskan, 1998). As such, there is one outcome we can surely predict, i.e., *Populus* will continue to gain importance in production forestry, environmental stewardship and renewable energy production. This popularity will demand more of systems-biology-based research, embracing both functional genomics and community mega-genomics. We anticipate that *Populus* and its associated mega-genome will continue to be a model for the study of other forest tree species as well as a new model for the study of host-microbe interactions among all plant species.

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