

My research program is centered on identifying the genetic and genomic mechanisms of ecological adaptations and how those adaptations contribute to the formation of new species (Lowry 2012). A primary focus of my research is to understand how differences in water availability between habitats drives adaptation in plant species. To this end, I am studying the genetic basis of adaptive divergence and reproductive isolation between coastal perennial and inland annual ecotypes of the yellow monkeyflower (*Mimulus guttatus*). This research revealed that a chromosomal inversion polymorphism plays a major role in evolution of ecotypes adapted to wet and dry habitats. Ultimately, identifying the connections between gene expression and plant physiology will be the key to understanding adaptations to drought stress. Therefore, I have developed a new research program in perennial *Panicum* grasses to understand these connections using a combination of classic plant physiology and genomic approaches. Research with *Panicum* grasses has also provided the opportunity to understand the genetic basis of adaptation over a large-scale latitudinal gradient, which contrasts to adaptation between adjacent habitats in *Mimulus*. I am very interested in how adaptation on such different geographic scales influences the evolution of species (Lowry 2010).

### **Adaptation and Speciation in *Mimulus***

Ecological adaptations can contribute to the formation of new species when they result in reproductive isolating barriers (Lowry et al. 2008a; Lowry & Hopkins 2013). However, we still know very little about how individual genetic loci contribute to ecological adaptations and reproductive isolation in nature. My PhD dissertation research at Duke University, with John Willis, was focused on identifying adaptive loci involved in divergence between ecotypes of *M. guttatus* and determining the contribution of those loci to fitness and reproductive isolation under natural field conditions. The *M. guttatus* complex is composed of many ecotypes and species, each endemic to different ecoregions across western North America and adapted to a suite of local environmental conditions. *M. guttatus* is an ideal model system for integrating ecology, physiology, and genetics. We now have a sequenced genome, a relatively reliable genetic transformation protocol, and extensive experience doing experimental manipulations in nature.

My research on coastal perennial and inland annual populations of *M. guttatus* contributed to a greater understanding of how divergent habitats drive the formation of reproductively isolated ecotypes and new species. I combined field and laboratory experiments to demonstrate that inland populations of *M. guttatus* have evolved a locally adaptive early flowering annual life-history in response to hot summer drought. In contrast, individuals in coastal populations are late-flowering perennials, adapted to year-round soil moisture and a low vapor pressure deficit maintained by coastal summer fog and cool temperatures (Lowry et al. 2008b). Through a series of crossing experiments, I discovered a chromosomal inversion that differentiates the annual and perennial ecotypes across western North America. The inversion polymorphism contributes to a suite of adaptive phenotypic traits including the perennial/annual life-history transition. Using field experiments, I demonstrated that the inversion has locally adaptive fitness effects in both habitats. This study (Lowry & Willis 2010) showed for the first time in nature that an inversion polymorphism contributes to ecological adaptation and multiple reproductive isolating barriers between ecotypes. In contrast, I found that three loci responsible for salt tolerance in the coastal ecotype only had detectable fitness effects in the coastal habitat (Lowry et al. 2009). This result suggests that some ecophysiological adaptations may occur without fitness trade-offs.

**Future research:** Despite the potential role of inversions in adaptation and speciation, the actual genetic mechanisms by which inversions contribute to these processes are unknown. Classic models of adaptive inversion evolution argued that suppressed recombination of chromosomal rearrangements could facilitate the evolution of epistatic coadapted gene complexes. In contrast, a recent theory has been advanced that inversions can become established if they capture additive alleles at multiple loci that were already involved in local adaptation to divergent environmental conditions. Further, adaptive inversions could arise from changes in gene function or expression resulting directly from the inversion mutation itself, especially if it resulted in the disruption of gene promoters or changes in chromatin patterning. While there are now many theoretical models of the evolution of ecologically adaptive inversions, conclusive empirical support for any of them is lacking. I plan to develop a research program to distinguish between these different theories of adaptive inversion evolution in *M. guttatus* with a focus on the inversion involved in the annual and perennial ecotype divergence. This research will involve the identification of the gene or genes underlying the phenotypic effects of the inversion through a combination of population genomic approaches, gene expression experiments, and functional validation.

**Environmental Adaptations and the Evolution of Gene Expression in *Panicum***

Water availability is one of the most limiting factors for crop production and the fundamental factor governing the composition of plant communities globally. The frequency and intensity of drought has long been known to be an important selective agent during the evolution of plant species. While *M. guttatus* is an excellent system to understand the genetic basis of drought escape through adaptive flowering-time evolution, understanding the evolution of actual drought tolerance is best suited to species that grow and reproduce during periods of low soil moisture availability. Furthermore, most of the adaptive genetic variation in *M. guttatus* is partitioned between populations and ecotypes. For many other species, the majority of adaptive traits vary continuously along environmental gradients. A more general understanding of adaptation in the wild will be achieved through parallel research programs on species with strong habitat divergences and those where a large portion of the trait variation is distributed along environmental gradients. My current postdoctoral research focuses on physiological adaptations in perennial *Panicum* grasses. I am conducting this research at the University of Texas at Austin with Thomas Juenger, who is a leader in the evolutionary genetics of drought physiology. Development of this research program has greatly expanded my understanding of plant ecophysiology and my bioinformatics skill set.

***How do individual loci contribute to adaptation along an environmental gradient?***

Experiments to understand how individual genetic loci contribute to adaptation in the wild have been limited to contrasts between pairs of strongly divergent habitats. Thus, we have a very limited understanding of how loci contribute to a clinal pattern in fitness across the landscape. For example, do alleles at adaptive loci have gradually changing fitness effects across environmental gradients or do their effects change in a step-wise pattern as environmental thresholds are crossed? To better understand adaptation along gradients, I have developed a research program in perennial C4 switchgrass (*Panicum virgatum*). Genomic resources for *P. virgatum* have expanded due to its potential as a biofuel feedstock and its dominant role in the Great Plains ecosystem. *P. virgatum* has a long history as an excellent system for understanding geographic adaptations. Classic field experiments and recent yield trials demonstrate strong patterns of local adaptation across climatic gradients (Lowry et al. *in revision*). In 2011, I was awarded a USDA postdoctoral fellowship to develop a genetic mapping population to understand adaptation over environmental

gradients. The mapping population is derived from a four-way cross among accessions collected at four latitudes over the Great Plains (North Dakota, Nebraska, and two accession from Texas). I am in the process of assembling a linkage map for this mapping population (N=400 individuals) with markers derived by Next-Generation sequencing of a reduced representation library.

**Future Research:** The four-way mapping population is ideally suited to understand how individual loci contribute to adaptation along a latitudinal gradient. I have now created four replicates of all the individuals in the mapping population through clonal division. I am in the process of forming collaborations to plant replicates of the mapping population at four locations across the Great Plains. This experimental design will allow QTL mapping in the field and direct tests of adaptive genetic effects across environmental gradients. I will coordinate physiological monitoring of plants at each field site to relate genetically based fitness differences among lines to responses to local environmental conditions.

***What are the connections between gene expression and physiology in response to drought?***

Classic field experiments suggest that drought and heat stress are the primary drivers of local adaptation for *P. virgatum* in Texas (Lowry et al. *in revision*). This presents an excellent opportunity to understand the physiological and genetic basis of drought tolerance adaptations. I am currently engaged in a collaborative effort to evaluate drought response across a diverse panel of *P. virgatum* accessions through experimental manipulation of water availability in the field. This study has already revealed strong genotype by environment interactions for physiological response to drought. To understand how gene regulatory network evolution contributes to this differential response, we conducted RNA-sequencing with Illumina, as well as the quantification of hormones and metabolites. To build an integrative model of the levels of drought response, correlations were assessed between gene expression level, hormone production, metabolite accumulation, and physiological status.

Understanding the causes and consequences of natural genetic variation in gene expression is of fundamental importance to biology. However, the mechanisms by which natural variation in gene expression are generated, maintained, and impacted by environmental conditions are still poorly understood. One promising avenue for understanding the evolution of transcriptional regulation is through expression quantitative trait locus (eQTL) mapping. Here, mRNA transcript abundance for each gene in the genome is treated as a trait for genetic mapping. Recently, I conducted expression eQTL mapping with a recombinant inbred line (RIL) population of *Arabidopsis thaliana* in wet and dry soil moisture treatments (Lowry et al. 2013a). This study revealed thousands of genes responding to the environment and identified hundreds of eQTLs. I also identified dozens of genotype by environment eQTL interactions that may be important for the evolution of natural variation in drought response among accessions of *A. thaliana*.

**Future Research:** Previous plant eQTL studies have all been conducted in the laboratory, which makes it difficult to assess the full impact that a stress like drought will have on a plant. Further, perennial plant species are likely to respond to drought differently than annuals, like *A. thaliana*, which have evolved life-histories to escape drought. To meet this challenge, I have been working to develop a rapid cycling (two month seed to seed) small perennial relative of *P. virgatum* as a model ecological and evolutionary genomic system (Lowry et al. 2013b). This diploid species, *P. hallii*, has a broad ecological range distributed

from wet eastern Texas to the driest deserts of Arizona. Since 2010, Dr. Juenger and I have collaborated with the Joint Genome Institute (JGI) to assemble the genome of *P. hallii*. I am also in the process of analyzing 45 genomes of *P. hallii* accessions collected from across a soil moisture gradient in the Southwestern United States. We have made major progress in developing a transformation protocol for *P. hallii* callus tissue as well, which will allow for tests of function of candidate genes. There are two very divergent varieties of *P. hallii*. The most widespread variety, *var. hallii*, is found primarily in xeric habitats, while *var. filipes* is primarily found in mesic habitats. To determine the genetic basis of divergence between the two varieties, I conducted QTL mapping on an F2 population that I genotyped by Next-Generation sequencing (Lowry et al. *in review*). Through this study, I identified loci contributing to both morphological and physiological gas exchange traits. One locus on chromosome 5 contributed to six different traits that are involved in divergence between the varieties. I am now in the process of using this F2 mapping population to understand natural genetic variation in gene expression through eQTL mapping in the field.

I planted the *P. hallii* F2 mapping population in the field in the fall of 2012. In the summer of 2013, I subjected the plants to two different soil moisture regimes. I have partnered with the JGI to conduct RNA-sequencing to quantify gene expression for samples from both treatments. This will allow for eQTL mapping and thus, the analysis of natural variation in transcriptional response to soil moisture under field conditions. I have already developed an analysis pipeline for this project through the eQTL study I conducted with *A. thaliana* (Lowry et al. 2013a). Comparisons of results from *P. hallii* and *A. thaliana* will allow me to answer fundamental questions about abiotic physiological stress tolerance. Is the differential response to drought mediated by constitutive differences in gene expression or genotype by environment interactions? Are *cis* or *trans* acting polymorphisms more robust to environmental perturbation? Which gene regulatory networks are primarily involved in the evolution of drought tolerance?

#### **Future Research Vision**

My vision is to establish a broad research program aimed at determining how environmental conditions across the natural landscape contribute to the evolution of populations and species. I am very interested in understanding how adaptive genetic changes contribute to the process of speciation. My research program is focused on adaptations to drought because soil moisture availability is likely the most important environmental factor driving the evolution of physiology, development, and speciation in plants. My extensive experience in ecology, evolution, plant physiology, genetics, and bioinformatics makes me well suited to answer fundamental questions of adaptation and speciation in a landscape evolutionary genomic framework.

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Statement of Research Interests

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