Shifting the plant stress research paradigm in the post-omics era

Paxton Payton¹ and Diane Rowland²

¹USDA-ARS Cropping Systems Research Laboratory, Lubbock, TX USA ²Agronomy Dept., University of Florida, Gainesville, FL USA

The challenge

Water scarcity truly defines the nexus between the escalating effects of climate change and the limits to crop production worldwide. Water availability is likely to remain the most critical barrier to food and fiber production in both the present and future agroecosystems. Food security is further threatened by the fact that water scarcity often goes hand in hand with high temperature stress, with these two abiotic stresses accounting for significant yield and annual economic losses worldwide (De Boeck et al., 2010; Lobell et al., 2013; Lobell et al., 2015). Compounding reduced yields is growth in world population, expected to exceed 8 billion by 2030, requiring a significant increase in world food production. Most arable land is already under agricultural production which accounts for more than 75% of global freshwater consumption, a rate that is unsustainable with an increasing population (Shiklomanov and Rodda, 2003; Pimentel et al., 2004; Pfister et al., 2011). Achieving sustainability in global agriculture will ultimately be determined by the ability to provide adequate water resources to grow crops – whether through capture of adequate and timely rainfall, efficient irrigation application, and/or highly stress tolerant varieties for production under these limited water scenarios.

Over the past 2 decades, there has been abundant research conducted on crop genetic responses under a range of abiotic stress conditions, with a majority of studies focused on improving the overused and frequently undefined trait of "drought tolerance". Drought tolerance is particularly difficult to define and achieve in agroecosystems because it requires water conservation with a concomitant maintenance of yield. Therefore, drought tolerance defined only as survival under water scarce conditions has virtually no utility in production systems. However, the progress towards developing drought tolerant crops operational in field production environments has been slow (Skirycz et al. 2011; Tardieu 2011; Blum 2011), likely due to three primary missing features in much of this research: 1) the assumption that drought tolerance in agroecosystems is a single characteristic that is universally defined, understood, and applicable to most production scenarios; 2) few true cross-communicational projects and meaningful partnerships between whole-plant physiologists and molecular geneticists; and 3) primarily studying drought tolerance under dichotomous conditions normally encompassing only adequate water in comparison to severe drought. Therefore, we contend there is a significant need for drought research that uses a combined approach between whole-plant physiology, genetics, and management (G x E x M), with the primary focus being testing hypotheses in relevant production conditions. The ultimate goal of this paradigm is the identification

of environmental (E and M) drivers of plant growth and a focus on phenotypic plasticity across a range of water managed environments (Aspinwall et al. 2014). *How can phenotypic plasticity be used in crop production to mitigate yield loss from water stress, thus increasing resiliency in increasingly variable environments? How can we accurately and robustly analyze and identify the key environmental water stress factors (timing, intensity, duration) that define the limits within specific production environments?*

How to shift the paradigm

First, combining stress physiology, agronomy, and genomics is a powerful approach for first defining meaningful drought tolerant characteristics, and ultimately carrying out relevant genetic dissection of the stress response. The combination of field physiology and functional genomics brings powerful solutions based on molecular causal links to physiological responses. However, without the detailed context of the growth environment from sowing to harvest, the reliable identification of traits that are functional and pertinent for agroecosystems for ultimate crop improvement in water scarce environments is low (Tardieu 2011; Vadez et al. 2013; Aspinwall et al. 2014).

Recommendation 1. Create stable and adequate funding for true multi-disciplinary approaches combining agronomy, physiology, and genomic-based, basic research to create holistic, regionally specific management systems that utilize key physiological and phenotypic traits for sustainable crop production in variable environments.

Second, selection for abiotic stress tolerance should be done using more production relevant drought conditions. For example, part of the reason why selection efforts for drought tolerance in any crop have progressed slowly is that most of the conditions used to select genotypes rely on diametrically opposed water availability conditions: well-watered vs. severely water stressed. It has recently been demonstrated that enhanced survival under such severe drought conditions is not linked with performance under mild drought (Skirycz et al., 2011) as would be more representative of the conditions in the typical production environment. Therefore, basing accession selection on the ability to survive severe drought stress has led to a low rate of success in most research programs aimed at improving crop drought tolerance (Skirycz et al., 2011), no matter whether the emphasis has been on molecular, physiological, or agronomic approaches. More relevant selection could be done utilizing mild drought timed to certain developmental stages or more cyclical water scarce time periods that would be more typical of production conditions (Rowland et al. 2012).

Recommendation 2. Given the complexity of $G \times E \times M$ interactions, there is a need for comprehensive, meta-scale data analysis approaches (bioinformatics) that elucidate the often subtle differences in E and M that result in large phenotypic or yield and quality differences.

Lastly, once a relevant "drought tolerant" phenotype has been adequately defined, reaching this crop ideotype could be further maximized by selecting genotypes under management systems designed to maximize water-use efficiency. One current approach used by producers in water-limited regions to battle abiotic stress is through efficient irrigation scheduling. However again, it is critical not to define water-use efficient systems with a "one size fits all" approach, but to tailor these systems for regional specific limitations in climate, water management logistics, and crop rotation. Once these limitations have been incorporated within a holistic management system, selecting for genotypes that are adapted for maintained production within these systems is greatly simplified and provides more targeted solutions to water scarcity.

Recommendation 3. Adopt a "top down approach" to the development of "drought tolerant" genotypes by supporting research based on tested regional cropping systems proven to enhance water conservation that serve as real world selection environments for the development of regionally specific tolerant ideotypes.

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