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Review

The evolution of drought escape and avoidance in natural herbaceous populations

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A B S T R A C T

While the functional genetics and physiological mechanisms controlling drought resistance in crop plants are well studied, less research has examined the genetic basis of adaptation to drought stress in natural populations. Drought resistance adaptations in nature reflect natural rather than human-mediated selection and may identify novel mechanisms for stress tolerance. Adaptations conferring drought resistance have historically been divided into alternative strategies including drought escape (rapid development to complete a life cycle before drought) and drought avoidance (reducing water loss to prevent dehydration). Recent studies in genetic model systems such as *Arabidopsis*, *Mimulus*, and *Panicum* have begun to elucidate the genes, expression profiles, and physiological changes responsible for ecologically important variation in drought resistance. Similar to most crop plants, variation in drought escape and avoidance is complex, underlain by many QTL of small effect, and pervasive gene by environment interactions. Recently identified major-effect alleles point to a significant role for genetic constraints in limiting the concurrent evolution of both drought escape and avoidance strategies, although these constraints are not universally found. This progress suggests that understanding the mechanistic basic and fitness consequences of gene by environment interactions will be critical for crop improvement and forecasting population persistence in unpredictable environments.

Contents

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1. Introduction

Q2 Climate models forecast an increase in both the severity and frequency of drought in the coming 50 years [1]. This change is especially difficult for sessile organisms such as plants, which must be able to respond to wide fluctuations in growing season conditions while still maintaining the ability to correctly time developmental processes in response to environmental cues. At a population level, increasing aridity and drought should lead to strong directional selection for plants with higher fitness under drought conditions (i.e., drought-resistant plants); however, a more nuanced understanding of genes and traits under selection is limited by an incomplete knowledge of the mechanisms that plants use to resist drought stress [2]. Without understanding the innate resistance mechanisms plants possess, it is difficult to accurately assess future population persistence. Determining the prevalence and variation in the mechanisms underlying stress resistance and adaptation is a key goal for plant biologists.

Unlike in natural populations, responses to drought stress have been widely studied in a few major crop plants [3–7]. This literature has resulted in an improved understanding of the physiological pathways involved in drought perception and response as well as identified major-effect genes controlling drought resistance [3]. However, wild populations often harbor large pools of genetic and phenotypic diversity that can provide insights into novel mechanisms of acquiring drought resistance. These insights can range from characterizing new phenotypes to identifying new roles for genes involved in abiotic stress-response pathways. While understanding the diversity and prevalence of mechanisms underlying drought resistance in natural populations clearly benefits evolutionary biologists, these results can also help agronomists more effectively improve or develop crops. Here I synthesize recent progress describing how drought resistance has evolved in natural populations of herbaceous plants. I focus on studies that identify the genetic basis of drought strategies as well as describe the evidence that these strategies are advantageous in natural populations.

Adaptation to soil water availability is common across the ranges of plant species and is associated with the formation of ecotypes [8,9]. Adaptations conferring drought resistance have historically been divided into three alternative strategies: drought escape, drought avoidance, and drought tolerance [10]. Each of these strategies may evolve as a constitutive response that occurs independently of environmental cues such as water deficit, or can evolve as a heritable plastic response that is dependent on one or more environmental cues. Drought escape occurs when plants develop rapidly and reproduce before drought conditions become severe. Cession of vegetative growth may or may not accompany a drought escape response. In contrast, drought avoidance occurs when plants increase water-use efficiency (WUE) by reducing transpiration, limiting vegetative growth, or increasing root growth, and avoid dehydration during transient periods of drought stress. Drought avoidance has also been referred to as dehydration avoidance in recent literature. Finally, drought-tolerant plants are able to withstand dehydration through osmotic adjustment and production of molecules that stabilize proteins (Fig. 1; [10]). These strategies are coordinated physiological syndromes that involve many physiological and structural traits [11]. For instance, drought avoidance through increased WUE is mediated by lowering stomatal conductance, which in turn can be influenced by a number of different potentially correlated traits such as leaf area, leaf lobing, succulence, or stomatal density. Here, I will focus on recent advances understanding drought escape and avoidance. These advances are largely limited to studies examining flowering time as a measure of drought escape and leaf-level WUE as a measure of drought avoidance as these are the traits that have received the most attention. Mechanisms of drought tolerance have been covered in detail elsewhere [3,12].

Although each of these strategies is predicted to evolve in areas of frequent drought stress, they are often viewed as alternative strategies or syndromes that can be optimally employed in specific seasonal contexts for plants with specific life history strategies (Fig. 1; [6,13]). For instance, drought escape may be optimal for annual plants in environments with short growing seasons that are ended by severe terminal drought; whereas drought avoidance may be more optimal if the growing season is punctuated by transient droughts. These strategies are unlikely to evolve together because plants devoting all of their resources to rapid reproduction need to have high rate of carbon fixation and thus also high stomatal conductance. However, plants typically avoid drought by lowering stomatal conductance to conserve water and thus reducing the rate of carbon fixation and growth. The literature has largely supported this view with the most detailed examples pointing toward the independent evolution of drought escape and avoidance strategies [14,15]. There is limited evidence in some systems that suggests that there are not genetic constraints to the concurrent evolution of both strategies within individual populations [16]. The environmental conditions that favor evolution of specific strategies is still an open topic and identifying the genetic constraints and fitness ramifications associated with each strategy is an area of strong interest.

While phenotypes associated with escape or avoidance strategies have often been studied (e.g., [14,17,18]), obtaining a detailed understanding of the genetic and physiological mechanisms that plants use to escape or avoid drought in natural populations has been challenging. Recreating realistic drought conditions in an experimental setting is difficult and may not necessarily reflect field conditions [19]. Drought can combine the effects of water deficit and possible heat stress. Manipulating water availability is complicated in dry-down experiments because water uptake is greater in bigger plants; a problem that can create heterogeneity in the timing of water deficits [20]. An additional challenge is finding species with populations that thrive across a range of aridity conditions and that also possess a genetic toolbox amenable to exploring the genes and pathways responsible for adaptive divergence in morphology and physiology. In model genetic species where the genetic basis of drought escape or avoidance has been characterized, there are often multiple QTL (quantitative trait loci), each of small effect that underlie variation in drought resistance. This makes it difficult to identify the phenotypic effects of a given locus [21,22]. Further, drought escape and avoidance can both be dependent on environmental context where a water deficit or other environmental cue may induce rapid flowering or changes in WUE [23,24]. This inherent plasticity can complicate linkage mapping and make it difficult to predict drought resistance and fitness consequences in a seasonal environment.

Nevertheless, development of new ecological model systems such as *Mimulus guttatus*, *Avena barbata*, and *Panicum hallii* as well as renewed efforts to study *Brassica rapa* and *Arabidopsis* sp. in ecological contexts has begun to provide new insights into the genetics underlying adaptive drought escape and avoidance strategies. Specifically, work in these systems has begun to address longstanding questions about ecophysiological traits regarding the prevalence, adaptive value, and genetic architecture underlying variation in these traits in natural populations [6]. Here I review the advances made in the last decade toward identifying the fitness benefits and genetic basis of drought escape and avoidance strategies as well as the constraints that limit concurrent evolution of both strategies. This large body of the literature establishes that variation in drought escape and avoidance traits is prevalent and adaptive, and highlights promising systems where QTLs and genes responsible for this variation are known. In addition, this review

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