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# Natural variation and genetic constraints on drought tolerance

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Drought is a central abiotic stress for both natural plant populations and agricultural crops. Substantial natural genetic variation in drought resistance traits has been identified in plant populations, crop species, and laboratory model systems. In particular, studies in *Arabidopsis thaliana* have discovered variation in a number of key physiological traits involved in plant–water relations that may underlie evolved drought stress responses among accessions. Despite this abundant variation, we still know little about the complex genetic architecture of drought tolerance or its role in constraining evolution. Unfortunately, few natural allelic variants have been cloned for drought related traits — progress cloning QTL, the use of RNA-sequencing methods for evaluating gene expression responses to soil drying, and improved methodology for exploring complex multivariate data all hold promise for moving the field forward. In particular, a better understanding of the molecular nature of pleiotropic gene action and the genetics of phenotypic plasticity will give insight into local adaptation in plants and provide new avenues for improving crops.

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Drought can have dramatic and devastating effects on plants, plant communities, and agricultural crops. For example, the US has recently experienced a shocking period of drought. In 2010–2011, the state of Texas experienced the driest and warmest 12-month period on record [1]. The drought in Texas alone has resulted in an estimated US\$7.5 billion in agricultural losses [2]. Although extreme, these events are by no means unusual when viewed from a geologic or evolutionary perspective, and many climate change models forecast increasing frequency and severity of drought [3]. As such, drought has been, and will continue to be, a strong and important selective regime in plant populations. Has drought influenced standing

genetic variation and driven local adaptation in plants? Can studies of natural populations help direct efforts to breed new drought tolerant crops?

As sessile organisms, plants are faced with an enormous challenge. They cannot flee local conditions, and so must cope with them through physiological acclimation and evolutionary adaptation. As a result plants are exquisite in their ability to sense, respond, and survive a variety of abiotic stresses. Plants are thought to cope with water stress through escape, avoidance, and tolerance mechanisms [4,5]. Escape involves evolved or plastic shifts in phenology such that major periods of growth and reproduction do not coincide with periods of water-deficit, while avoidance strategies are adaptive responses that maintain plant–water status even in the face of a drying environment. Dehydration tolerance mechanisms protect plant cells and tissues from water deficit when it occurs, allowing recovery following periods of dehydration and drought. Importantly, these are not mutually exclusive strategies and likely play differing roles across species and stress of varying duration, intensity, and timing. A number of recent reviews have discussed the many plausible biochemical, metabolic, physiological, and morphological traits likely involved in drought adaptation [6–8].

Evolution requires standing genetic variation. Is there evidence for heritable variation in drought resistance or its composite traits? The answer is a resounding yes. Quantitative genetic variation has been observed in a host of natural populations, in crop species, and in laboratory model systems. The literature is too large to adequately review here — nevertheless, a few examples are illustrative. In *Arabidopsis thaliana*, substantial genetic variation among natural accessions has been observed in many measures of water relations (relative water content, leaf water and osmotic potentials) [9,10<sup>••</sup>], instantaneous gas exchange ( $A$ ,  $g_s$ , water and transpiration use efficiency) [10–16], guard cell responses to environmental signals [17], gene expression responses to soil drying [10<sup>••</sup>,18], metabolite production under water deficit [19,20<sup>••</sup>,21<sup>•</sup>], and root and shoot growth under water deficit [10<sup>••</sup>,22–24]. Similar results have been observed in natural populations of *Arabidopsis lyrata* [25], *Boechera hoelboelli* [26], *Brassica rapa* [27], *Avena barbata* [28], and *Brachypodium distachyon* [29] to name but a few. The crop literature is replete with examples of responses to selection to improve drought tolerance as well as considerable support for standing genetic variation in drought related traits [30–32]. In a number of cases, genomic regions harboring this variation have been identified through quantitative trait loci (QTL) mapping [32–34] and many

genome-wide association studies (GWAS) are underway. The major gaps in the field are that most studies focus on annual herbaceous species, rarely test explicit hypotheses concerning local adaptation, and are completed in controlled or artificial environments. As such, we still know little about drought tolerance in longer-lived perennial plants or performance under natural drought regimes, especially where drought interacts with other abiotic stresses. Furthermore, in only a handful of cases have drought-related QTL been cloned and the molecular mechanism of their action revealed.

Natural populations are mutant pools that can give insight into plant function, are a vital resource for plant improvement [35,36], and can harbor novel alleles that are not accessible through forward or reverse molecular approaches. The majority of traits that have been studied are heritable [37] and evolution is now thought to rarely be limited by a lack of genetic variation. Rather, quantitative geneticists and breeders argue that the genetic architecture or the structure of genetic variation plays a more important role [38,39]. Here, I use the term genetic architecture to describe the pattern and nature of allelic effects underlying a set of phenotypic traits, including their emergent properties such as pleiotropy, modularity, and ultimately evolvability.

### Genetic architecture and constraints

As plant biologists, our attention often focuses on single phenotypic traits, molecular processes, or genetic pathways. However, organisms do not function so simply and instead comprise complex suites of layered traits (e.g. molecular → cellular → metabolomic → physiological → developmental) that interact with each other and the environment. It is important that we embrace this complexity when we discuss genetic variation and constraints. In 1955, Dickerson [40] provided a simple but elegant example of how misleading a focus on single traits can be. He showed that a set of traits could all display equal genetic variance and yet a response to multivariate selection to increase each trait was not possible. In this case, the pattern of genetic correlation ( $r_g$ ) among the traits resulted in an axis in multivariate space that lacks genetic variation and thus constrained the system from evolving. A major challenge in modern plant biology is to identify these types of constraints on plant growth, especially under stress, and through an understanding of mechanism manipulate them for crop improvement.

### Genetic correlation, pleiotropy, and constraint

The structure of the genetic variance/covariance matrix (the 'G-matrix') is a central determinant of the pathways of possible phenotypic evolution [37] (Box 1). A major contributor to the structure of the G-matrix is pleiotropic gene action. Are there examples of genetic correlation and pleiotropy in drought adaptation traits? One striking example is the strong link observed between plant

#### Box 1 Quantitative genetic analysis and genetic architecture

There are a number of statistical methods that can be used to explore natural genetic variation. In the simplest case, the relative contribution of genetic and environmental influences on phenotypes can be partitioned into respective variance components using family-based studies. These center on patterns of resemblance among relatives (e.g. fullsibs, halfsibs, parents/offspring) to estimate well-known parameters like the additive genetic variance ( $V_a$ ), environmental variance ( $V_e$ ), total phenotypic variance ( $V_p$ ) and the narrow-sense heritability ( $h^2 = V_a/V_p$ ) [37]. These parameters can be used to model responses to natural or artificial selection with the breeders equation ( $R = h^2s$ :  $R$  = response to selection, change in trait mean from generation 1 to 2;  $h^2$  = narrow-sense heritability,  $V_a/V_p$ ;  $s$  = selection coefficient). An emerging view is that it is the multivariate structure, or genetic architecture, of suites of traits that ultimately restricts or constrains responses to selection and phenotypic evolution. Quantitative genetic approaches are easily expanded to include the genetic covariances between traits [50]. The estimation of the genetic variance/covariance matrix (G-matrix) for sets of traits is at the core of the modern quantitative genetics.

The elements of the G-matrix describe the genetic architecture for pairs of traits, but it is the multivariate geometry of the entire matrix which ultimately determines evolutionary response [38]. This geometry can be better explored by decomposing the eigenvectors and eigenvalues of the matrix, as may be familiar in multivariate tools such as Principal Components Analyses (PCA). These methods facilitate the identification of combinations of traits along axes (eigenvectors) and the amount of genetic variation associated with each (eigenvalues) [51]. Axes with large eigenvalues represent so called 'evolutionary lines of least resistance' while eigenvectors with zero eigenvalues result in so called 'forbidden trait combinations'. New methods have been developed for assessing the rank or dimensionality of the G-matrix [52], or the number of eigenvectors with zero eigenvalues. Alternative methods can be used to explore the structure of genetic covariance functions among traits and across environments [53] or the genetic structure of the plasticity of multiple traits [54]. These tools may be especially helpful for assessing structure and in identifying molecular mechanisms driving patterns in abiotic stress responses through genome-wide tools including microarrays, RNA-sequencing, and metabolomics profiling.

life-history, phenology and whole-plant physiology observed in many species. This is an especially clear pattern in the model plant *Arabidopsis*, where McKay *et al.* [11] have found a large positive genetic correlation ( $r_g = 0.65$ ) between date of first flowering and measures of water-use efficiency (WUE). Early flowering accessions display low WUE and late flowering accessions display high WUE (Figure 1). In this case, there is reduced genetic variation in the bivariate space for early flowering/high WUE and late flowering/low WUE trait combinations. Selection for these trait combinations would show little or constrained evolutionary response as they lie perpendicular to the major axis of variation. Natural pleiotropic gene action at a number of flowering time candidates (e.g. *FRI* and *FLC*) has been implicated as driving this genetic correlation [11]. This architecture may explain the predominance of spring and winter annual life histories in *A. thaliana*, possibly related to drought escape (early flowering/low WUE) and avoidance (late flowering/high WUE) strategies evolving along lines

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