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Opinion

Drought Adaptation Mechanisms Should Guide Experimental Design

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The mechanism, or hypothesis, of how a plant might be adapted to drought should strongly influence experimental design. For instance, an experiment testing for water conservation should be distinct from a damage-tolerance evaluation. We define here four new, general mechanisms for plant adaptation to drought such that experiments can be more easily designed based upon the definitions. A series of experimental methods are suggested together with appropriate physiological measurements related to the drought adaptation mechanisms. The suggestion is made that the experimental manipulation should match the rate, length, and severity of soil water deficit (SWD) necessary to test the hypothesized type of drought adaptation mechanism.

Trends

Much work has been done recently on improving crop water conservation through physiological assays for stomatal closure at high evaporative demand.

Advances in metabolomics technology have allowed physiologists to assess plant response to water stress through new eyes.

Advances in high-throughput phenotyping for physiological responses to water stress offer great promise in coupling abiotic stress tolerance with plant breeding efforts.

Despite recent experimental developments, the concepts of how to define drought adaptation mechanisms and the experimental protocols for measuring these have had less attention. A new focus on the experimental methodology will be necessary to more precisely control water stress in plant biology, metabolomics, high-throughput phenotyping, and breeding experiments.

What are Drought, Stress, and Damage?

Drought may be defined from the perspective of precipitation, soil or plant water status, or availability of human water supply [1]. Accordingly, the ideal definition for comparative physiological studies would be independent of the characteristics of a particular plant but be related to the local environment. If drought is independent of the plant, then it can be uniformly applied to any genotype or species present in an environment. Thus, we define drought as a decrease in water inputs into an agro/ecosystem over time that is sufficient to result in SWD [2]. This definition encompasses many forms of drought such as rainfall anomalies, irrigation failure, and annual dry seasons. Whether drought affects a plant is determined by the plant characteristics and environment. SWD is the key variable that links soil water with plant physiology, and is defined as a decrease in the available soil water, in other words water losses are greater than inputs. Alternative definitions of drought are often based upon conditions where soil water availability limits plant uptake [3]. However, these definitions are not useful when comparing genotypes/species where SWD can vary due to differences plant leaf area, roots, and physiology. Thus, we have chosen to employ the specific term ‘soil water deficit’ instead of ‘drought’ in the definitions of drought **adaptation** (see Glossary).

Stress may be defined as a negative change in the physiology of a plant away from a reference state as a result of the action of an external stress factor or internal stress ([4–6] for discussion). In physics, stress refers to an external factor such as temperature while strain is the response of the material [7]. However, the physiology literature generally uses stress in reference to physiological responses [4]. Therefore, we prefer to define ‘stress factors’ as external and ‘stresses’ as physiological responses. Note that physiological responses to daily ‘normal’ variation in potential stress factors such as light and temperature should not be termed stress, and should be considered as part of the reference state [5]. Drought-induced damage is a negative stress that persists for some time after SWD has ceased. Damage may be recoverable or irrecoverable and, in response to these deviations from unstressed conditions, acclimation or adaptation occurs.

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New Definitions of Mechanisms for Dealing with Drought

General terms used as objectives or mechanisms in drought research are: drought or stress tolerance, drought resistance, etc. (Figure 1). These terms are poorly specific of a plant characteristic or the drought phenomenon; therefore, demonstrating that these mechanisms occur in a genotype/species is difficult. For instance, the manner in which 'drought tolerance' is typically applied in the literature could mean that a plant tolerates stress, tolerates damage, or avoids water stress, thereby tolerating drought.

The basic terminology provided by the highly cited Levitt [7,8]–drought escape, avoidance, and tolerance–has not been widely adopted, and only 'drought tolerance' is widely used (Figure 1). Other excellent reviews provide examples of drought adaptation [2,9–11], but in practice little link is generally made between the proposed adaptation and experimental manipulation. Interestingly, the literature associated with plant biology tends to focus on 'stress tolerance' rather than 'water conservation', the greater focus of ecology and crop-related literature (Figure 1).

Clearly, nuanced definitions of plant mechanistic response to drought will be necessary to drive directed approaches to experimental design. We propose here four terms representing a hierarchy of adaptation mechanisms (Figure 2, Key Figure; Figure 3, diagnostic graphs of mechanisms; see also Figure S1, a flow chart, in the supplemental information online). For instance, a plant may avoid SWD despite a lack of water inputs (termed SWD avoidance; Figure 2). Examples include plants that explore deeper soils [12], or have slow root growth, leaving water for later in the season [13,14], as well as plants that conserve water through lower leaf area or transpiration [15–17] or match **phenology** to the wet season [18].

Plants that avoid SWD may have distinct physiological mechanisms from plants that encounter SWD but avoid physiological stress through **osmotic adjustment**, water storage in organs or root isolation from soil [19] (termed stress avoidance) (Figure 2). These mechanisms require specialized adaptations such as succulence [19] or are temporary because osmotic adjustment can only allow access to limited volumes of soil water [20].

Mechanisms that allow plants to tolerate SWD can include damage avoidance by preventing stresses from resulting in damage. Damage avoidance may also have a buffering effect whereby

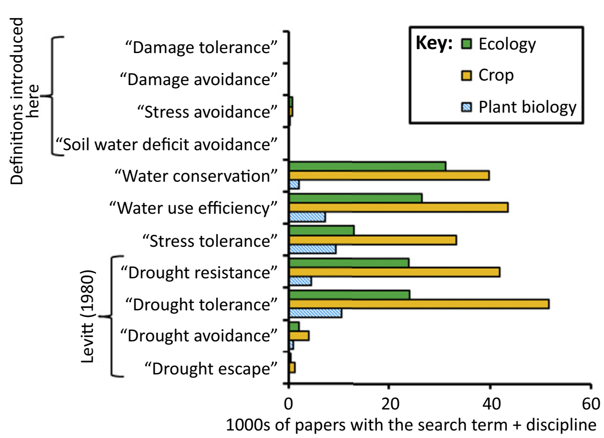

Figure 1. Use of Terms Related to Drought Adaptations in Scientific Literature by Discipline. The numbers of papers are results are from Google Scholar searches for the listed terms combined with +"drought" +"plant" and either +"plant biology", +"crop", or +"ecology". Terms promoted by Levitt [7,8] and those proposed here are indicated. Citations and patents were excluded.

Glossary

Adaptation: a general term that technically specifies an evolved trait that affects plant performance, but refers more broadly to added traits in transgenics or traits bred in crops.

Evaporative gradient: the gradient in water concentration between the inside and outside of the leaf, the driving force for transpiration.

Hydraulic conductivity: the ability of soil or a plant component to transport water over a pressure gradient.

Matric potential: a component of the water potential of soils owing to adhesion of water to the soil particles.

Osmotic adjustment: accumulation of osmolytes to allow greater solute potentials in cells.

Phenology: the timing of plant growth.

Potential evapotranspiration (ET_o): the combined soil evaporation and transpiration of an unstressed crop.