Plant responses to drought and rewatering

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Abbreviations: ABA, abscisic acid; $A_{\text{net}}$, net photosynthetic rate; $F_{\text{m}}/F_{\text{v}}$, maximum efficiency of PSII photochemistry; $g_{s}$, stomatal conductance;
MDA, malondialdehyde; PDL, pre-drought limitation; PSII, photosystem II; RGR, relative growth rate;
ROS, reactive oxygen species; RWC, relative water content; SOD, superoxide dismutase; WUE, water use efficiency

Plants would be more vulnerable to water stress and thereafter rewatering or a cycled water environmental change, which occur more frequently under climatic change conditions in terms of the prediction scenarios. Effects of water stress on plants alone have been well-documented in many reports. However, the combined responses to drought and rewatering and its mechanisms are relatively scant. As we know, plant growth, photosynthesis and stomatal aperture may be limited under water deficit, which would be regulated by physical and chemical signals. Under severe drought, while peroxidation may be provoked, the relevant antioxidant metabolism would be involved to annihilate the damage of reactive oxygen species. As rewatering, the recoveries of plant growth and photosynthesis would appear immediately through growing new plant parts, re-opening the stomata, and decreasing peroxidation; the recovery extents (reversely: pre-drought limitation) due to rewatering strongly depend on pre-drought intensity, duration and species. Understanding how plants respond to episodic drought and watering pulse and the underlying mechanism is remarkably helpful to implement vegetation management practices in climatic changing.

Under the climatic changing context, drought has been, and is becoming an acute problem most constraining plant growth, terrestrial ecosystem productivity, in many regions all over the world, particularly in arid and semi-arid area.12 Based on the fourth assessment report by IPCC, global surface average temperature will have a 1.1–6.4°C range increase by the end of this century.3 It is indicated that a warming above 3°C would eliminate thoroughly fixed carbon function of global terrestrial vegetation, shift a net carbon source. With global warming, it is expected that water deficit would be escalated by increasing evapotranspiration, increasing the frequency and intensity of drought with an increase from 1% to 30% in extreme drought land area by 2100;3 which would offset the beneficial effect from the elevated CO2 concentration, further limiting the structure and function of the terrestrial ecosystem. The global climate models may forecast the precipitation regimes including its distribution and amount, but the complicated responses of terrestrial ecosystem to climate change may adversely affect the predict accuracy.1,4

Plant would response to water stress by dramatically complex mechanisms from genetic molecular express, biochemical metabolism through individual plant physiological processes to ecosystem levels5,6 which may mainly includes six aspects: (1) drought escape via completing plant life cycle before severe water deficit. E.g., earlier flowering in annuals species before the onset of severe drought;7 (2) drought avoidance via enhancing capacity of getting water. E.g., developing root systems or conserving it such as reduction of stomata and leaf area/canopy cover;8,9 (3) drought tolerance mainly via improving osmotic adjustment ability and increasing cell wall elasticity to maintain tissue turgidity;10 (4) drought resistance via altering metabolic path for life survives under severe stress (e.g., increased antioxidant metabolism);11,12 (5) drought abandon by removing a part of individual, e.g., shedding elder leaves under water stress;2 (6) drought-prone biochemical-physiological traits for plant evolution under long-term drought condition via genetic mutation and genetic modification.13,14 The processes may be involved in multi-aspects simultaneously in responses of plants to drought stress and thereafter rewatering.

In the field context, there is always interval occurrence in drought and/or rewetting events, particular under climatic change conditions predicting more frequent drought and flooding events.3 The water cycle change may greatly impact plant growth, photosynthesis and many key metabolic functions, thereby ecosystem productivity and agricultural achievement.5,16-18 Actually, sporadic precipitation would become a critical issue for maintaining ecosystem structural stability and even it’s surviving in arid and semi-arid area. For example, a small rainfall pulse can induce a rapid response in a desert ecosystem, which quickly triggers plant growth so that the plants can survive.19 Thus, to highlight how plant and terrestrial ecosystem cope with adverse abnormal climatic change variables is, and always will be crucial research issue in practical management of plant growth and vegetation productivity. Here, we try to provide a brief insight into how
Plant responses to the pre-drought and rewatering in terms of the plant growth, gas exchange and key related-physiological processes such as reactive oxygen species (ROS) metabolism. Finally, a regulation path schematic is presented to try to explain the involved processes.

**Plant Growth and its Allocation**

Plant growth and its biomass allocation are two most fundamental processes of vegetable kingdom, being remarkably influenced by environmental variables including water changing factor.\(^2\)\(^{20}\) Plant growth and vegetation production were obviously restricted during 2003 European drought with hot summer, a remarkable recovery seem to appear following the 2004 wetted year.\(^3\)^\(^\text{31}\) The over-compensation for plant growth upon rewatering after drought also has been confirmed by many experimental investigations.\(^2\)\(^{22-24}\) For example, as plant individuals of *Leymus chinensis* have been subjected to a short-term drought, its leaf area was significantly stimulated by rewatering, which might transcend levels of control pants always in well-watered conditions.\(^7\)

However, in the Patagonian steppes, when water was applied again after pre-drought, the vegetation density (as an indicator of ecosystem structure) still not fully recovered, which would lead to annual net primary productivity lags of the response to rewatering following dry year,\(^2\(^\text{25}\) indicating so-called pre-drought limitation (PDL) could exist. Our reports also showed that the final biomass or leaf area in plants subjected to long-term or severe drought could not reach the level of the control treatment, highlighting that whether plant growth have the complete recovery following rewatering may depend on the pre-drought intensity or duration.\(^1\)\(^\text{7,24}\)

This pre-drought constraint after rewatering may ascribe to meristem limitation in plant tissues.\(^2\)\(^{5,26}\) Our recent study indicated that tillers’ numbers of *Leymus chinensis* still was lower relative to those control treated within 50 d after rewatering, but a full, even over-compensatory recovery occurred 70 after rewatering, implying the tiller meristems’ occurrence and development may play a critical role in the response to rewatering after an experienced pre-drought.\(^1\)\(^\text{7}\)

Plant growth of *Koeleria macrantha* had a great response to rewatering after a 20-d-long-term drought with lower tiller relative water content (RWC) of 13%.\(^2\(^\text{7}\) However, the response to rewatering could not be observed for *Briza media* plants. This may explained why *Koeleria macrantha* can be easily found in xeric calcicolous grasslands where severe episodic drought often occur, but *Briza media* did not exist in the same extreme dry conditions,\(^2\)\(^\text{7}\) even both *Briza media* and *Koeleria macrantha* grasses bear a similar and high drought-tolerant ability which was confirmed by that titters’ RWC can maintain a similar level even as soil moisture had been decreased by less than 9%;\(^2\)\(^\text{7}\) it is suggested that the different responses of the two species to recycle watering may play a critical role in their evolutionary processes under a certain environmental pressures, possibly involving a physiological plasticity to drought.\(^5\)

Many investigators have proposed using carryover and/or memory effects to describe the response of production to current environmental constraint from previous years as additional independent variables.\(^2\)\(^\text{8,20}\) In a semiarid grassland of South Africa, for instance, Wiegand et al.\(^2\)\(^\text{9}\) found that 33–68% of the unexplained variation is related to a memory index combining mean monthly temperature and a memory of past precipitations. The limitation to growth due to pre-drought may be portrayed one of plant memory behavior on past drought stress. In our work, PDL to plant biomass occurred under severe drought. However, PDL of relative growth rate (RGR) was not found, in contrast, pre-drought stimulation appeared.\(^7\) It is strongly suggested that the pre-stresses’ memory may play the central role in new parts’ growth rather than final production, which may derive from the re-trigger of the store resources such as soil nutrition besides the water reaplication.

Plants may try to obtain water in soil by enhancing its root system under soil drought. Many reports indicated that the increases in biomass ratio of root and shoot under water stress confirm this conclusion.\(^3\) However, under extreme soil drought, no root: shoot ratio increase was observed, implying that there would be a threshold of soil moisture in response to plant biomass allocation to water stress.\(^8\) When plant is subject to extreme soil drought, the regulation capacity through asymmetric growth approach may be also lost abruptly.

**ROS and Peroxidation**

Under environmental stresses such as drought, a rapid ROS accumulation including singlet oxygen (O\(^2\))\(^\cdot\), superoxide (O\(^2\))\(^-,\) hydroxyl (OH\(^\cdot\)) and hydrogen peroxide (H\(_2\)O\(_2\)) may occur, leading to negative impact on antioxidant metabolism, and consequently cell peroxidation damage.\(^2\)\(^\text{1,31-33}\) Generally, a ROS increase during pre-drought can be reversed following refilling water.\(^2\)\(^\text{34,35}\) There was a sharp decrease in H\(_2\)O\(_2\), with a better recovery of net photosynthetic rate ($A_\text{net}$) and net transpiration rate as *Prunus* plants were rewatered after a 70 d long-term drought stress, to which the degree reached severe water stress level of -4 MPa leaf water potential.\(^3\)\(^4\) When a pea tree was drought-treated for 20 d, leaf RWC fell to a severe drought status of 41–53%, H\(_2\)O\(_2\) contents significantly increased, thereafter they drastically decreased by rewatering.\(^3\)\(^5\) H\(_2\)O\(_2\) contents in bluegrass leaves increased by 67% with a low RWC of 68% under drought, but it could return to control level only one day after rewatering.\(^3\)\(^5\) In roots, however, both drought and rewatering led to remarkably H\(_2\)O\(_2\) accumulation,\(^3\)\(^3\) indicating the response mechanism would differ in different plant parts. As well reported, antioxidative enzymes such as superoxide dismutase (SOD) might play an central role in antioxidant metabolism in plants subjected to environmental stresses including drought possibly through regulating their gene expressions and/or activities.\(^3\)\(^\text{2,36}\) In the bluegrass leaves, although SOD activities did not change obviously under moderate drought and following rewatering, the gene expressions of FeSOD and Cu/ZnSOD were remarkably downregulated by drought, but can recover to the control level after refilling soil water.\(^3\)\(^\text{5}\) In Alfalfa nodules, however, FeSOD and CuZnSODc was upregulated by moderate drought, while the upregulation only in CuZnSODp was observed following rewatering relative to control level, but the expression of MnSOD for any of the treatments maintained relatively constant, implicating that the responses may differ
because of species and tissues.\textsuperscript{36} Thus, in fact, the ROS and their regulated metabolism might depend on species, cultivars/varieties, tissues, stress intensity and its durations.\textsuperscript{34,35}

In field-grown evergreen \textit{Phillyrea angustifolia} (Oleaceae) plants, even when leaf had a low RWC of 50% after 48-d drought treatment, malondialdehyde (MDA) contents did not significantly change, but the photoprotector zeaxanthin and the antioxidant ct-tocopherol accumulated more 200% compared to always well-irrigated plants, and leaf reflectance also had a corresponding change, indicating higher capacity of the photo- and antioxidative protection of this species through involvement of xanthophyll cycle and antioxidant promotions.\textsuperscript{12,37} In bentgrass species, Bian and Jiang\textsuperscript{33} reported that moderate drought and recovery only have a marginal effect on lipid peroxidation in bluegrass leaves. However, it was obviously provoked by a prolonged drought when plant leaves’ RWC fell to sever dehydration level of less than 40%;\textsuperscript{48} and as tee plants were subjected to a severe water deficit, MDA was significantly accumulated, which could be reversed drastically by rewetting,\textsuperscript{39} indicating that whether lipid peroxidation appears or recovers strongly depends on drought intensity/duration,\textsuperscript{33,38} and species/cultivars.\textsuperscript{35,39} In our research, cell ion leakage, an indicator of cell integration damage, was drastically attenuated by rewatering after a relatively long-term pre-drought (30 d), albeit no reaching the normal level in well-watered plants; moreover, this occurrence was only in young leaves of \textit{Leymus chinensis},\textsuperscript{38} implicating that the new parts of the plants might have a highly metabolically repairing capacity upon the rewatering following a pre-water-deficit stress.

**Photosynthesis and Stomatal Behavior**

Drought limitation to photosynthesis has been reported in many studies,\textsuperscript{2} of which a few documents covered the photosynthetic responses to cycled water deficit. As reported, full recovery of net photosynthetic rate ($A_{net}$) has been observed as drought stress is eliminated following rewatering.\textsuperscript{5,17} For example, after 15 d rewatering, \textit{Populus nigra} L. leaf $A_{net}$ can completely recover to the level recorded following water deficit in the plants rewatered to field capacity level of soil moisture after leaf $A_{net}$ fell to almost zero at lowest soil moisture (Fraction of available soil water, FASW 25%) at 35 d after starting drought treatment.\textsuperscript{30} In our recent report,\textsuperscript{17} severe and extreme drought caused light-saturated net photosynthetic rate ($A_{sat}$) to significant drops of 22% and 75% compared to the ample moisture treatment as a control, respectively. However, rewatering almost completely negated the difference between drought-treated and the control plants, indicating a complete resumption. The $A_{sat}$ and stomatal conductance ($g_s$) in summer drought-stressed \textit{Phillyrea angustifolia} plants were decreased by about 90% with a low leaf RWC of 50%, but the maximum efficiency of photosystem II (PSII) photochemistry ($F_{v}/F_{m}$) was not affected under the same drought condition,\textsuperscript{12} indicating the photosynthesis downregulation may mainly derive from stomatal limitation for this species. Based on recent study of Izanloo et al.\textsuperscript{5} for different wheat cultivars, PSII activities demonstrated different change trends as exposed to a cycle drought-treated regime even reaching wilting point of the soil moisture, that a drastic decline in $F_{v}/F_{m}$ (from 0.82 to 0.65) was found in Kukri plants, with no significant change for other two cultivars compared to well-watered treatment. Plants of \textit{Lonicera japonica} Thumb. with tetraploid chromosome have a higher drought-resistance during water deficit and more rapid recovery after rewatering in terms of gas exchange and chlorophyll fluorescence compared to those with diploid chromosome,\textsuperscript{39} showing the different responses from different genetic types. In our experiment, there was an obvious decline in $F_{v}/F_{m}$ of \textit{Leymus chinensis} leaves under severe soil drought, while a fully recovery appeared following refilling water. This is indicated that, compared to those gas exchange parameters, the functional activity of PSII photochemistry may contribute to both higher drought-tolerance and higher recovery capacity, which might not be independent of species and/or cultivars.

Stomatal regulation plays a key role in gas exchange between vegetation and atmosphere interface. Ninety percent loss of plants is from transpiration thought stomatal opening.\textsuperscript{41} On the other hand, stomatal limitation would be recognized a major factor for photosynthetic reduction when available water become scant, while non-stomatal limitation such as decreases in Rubisco activity, CO$_2$ availability in the chloroplast and PSII photochemistry efficiency is progressive gradually with water stress intensity and persistence duration.\textsuperscript{7,42,43} However, stomatal conductance would not be always associated with $A_{net}$ in some cases,\textsuperscript{44} which is still under debate. It is interesting, from the report by Flexas et al.\textsuperscript{42} that Rubisco activity is directly and closely linked to decreased $g_s$ and mesophyll conductance induced by abscisic acid (ABA) rather than leaf RWC, indicating that some signals such as ABA between stomatal behavior and CO$_2$ fixation in mesophyll cell might play a sensing role in regulating the relation between photosynthesis and stomatal movement. As reported, full recovery always co-occurred in both photosynthetic function and stomatal aperture when rewatering after an episodic drought,\textsuperscript{5} even a larger $g_s$ in pre-drought-treated plants appeared following rewatering compared to the control plants not underwent pre-drought experience, indicating a occurrence of over-compensation of gas exchange.\textsuperscript{45} However, in \textit{Leymus chinensis} leaves, $g_s$ only had a partial recovery after rewatering, no reaching the level of the well-watered treatment,\textsuperscript{46} being similar in hybrid Richter-110 (\textit{Vitis berlandieri}, \textit{Vitis rupestris}) plants.\textsuperscript{47,48} Flexas et al.,\textsuperscript{46} further indicated that the relative contribution of stomatal (SL) and mesophyll conductance (MCL) limitations rather than biochemical limitations would be responsible for the decreased photosynthesis during water stress and slow recovery after rewatering, and the former could mostly limit photosynthesis recovery after rewatering. The relative contributions from different limitation components during drought and after rewatering may need to be elucidated in future experiments using different species.

Moreover, based unequivocally on a recent report of Huang et al.\textsuperscript{49} H$_2$O$_2$ could also be a regulator for stomatal behavior in optimizing water use efficiency (WUE), which a drought and salt tolerance (DST) protein has been confirmed to be involved in the process by mediating H$_2$O$_2$ products. There is evidence that DST function loss can lead to a decrease in stomatal aperture and its density, increasing WUE and enhancing tolerance of rice plants.
to water deficit. Actually, the H$_2$O$_2$ produced by photosynthesis can act on the redox states of leaf antioxidant pools, implicating the possibility of photorespiratory H$_2$O$_2$ as a signal role under drought. It is implicated that stomatal movement and photosynthesis may link to ROS metabolism, signal cascade and photorespiration, which together needs to be investigated in the future.

**Signals and Other Biochemical Process**

Drought-sensed signals and their roles including physical and chemical types have already been well documented. Of them, a stress hormone, ABA usually is emphasized, being recognized as a key drought-sensed signal from root to shoot, although does not to do so in all species. The ABA produced in root would be transported to shoot which regulate the stomatal behavior. ABA may exist as an apoplastic component in the stem xylem that comes from root through apoplastic route, which may play a linkage signal role between shoot and roots. In *Glycine max* L. Merr. plants, a decrease in $g_s$ and an increase in xylem [ABA] may occur simultaneously before leaf turgor had a significant change, implying that seemingly root-originated ABA would regulate stomatal behavior at moderate drought. It is also suggested that the ABA accumulation in leaves induced by root physical or other chemical signals would directly regulate the stomatal movement. An evidence indicated that high ABA level can be eliminated when plant is rewatered to an optimal water condition, perhaps leading to re-opening of the stomata. Wheat plants with low ABA content, together with high osmotic adjustment, would have a rapid and complete recovery of function processes such as growth rate, photosynthesis and $g_s$ from drought-stressed limitation after rewatering, depending on different genotypes. However, there is evidence showing that some physical signals such as hydraulic press from roots may induce leaf stomatal closure when soil water deficit occurs. No ABA increase in some species was also observed as the plants subjected to rapid dehydration. An ABA application to leaves of *Craterostigma plantagineum* does not increase drought-tolerance. Thus, whether and how the stomatal aperture is controlled by ABA is still under debate.

Recent works showed the Cytokinins (CKs) can be as a regulator in response to water stress in tobacco transgenic plants with an increase in catalase inside peroxisomes and the CO$_2$ compensation point, indicating the cytokinin-mediated occurrence of photorespiration may play a beneficial role in protecting photosynthetic processes during severely restricted water condition. Water channel as an initial hydrostatic signal also is a critical component for plants to absorb water from soil and transport to shoot and up-leaf, undergoing a comprehensive biological process, which together needs to be investigated in the future.

**Conclusions**

The responses of plants to water changing conditions cover many aspects from genetic molecular level, biochemical and physiological processes, through whole individual to community levels. For example, as plant is exposed to moderate drought, a stomatal aperture may be decreased possible through sensing physical or chemical signals such as hydraulic press and ABA. A decline of the stomatal conductance may limit the net photosynthetic rate and water transpiration with progressive water stress, leading to increased WUE because the transpiration is inhibited more than photosynthesis. When drought intensity became severe even extreme, photochemical efficiency and Rubisco activity would be constrained, which may reduce $A_{max}$ to zero; at the same time, other adverse biochemical-physiological metabolisms including peroxidation may be exacerbated, together consequently reducing plant growth rate. The photosynthesis and plant growth may start to be stimulated immediately following an application of watering pulse. However, the extent and magnitude of the stimulation from rewatering may depend on pre-drought intensity.
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tus), and species/varieties, of which a compensatory/full/partial
recovery may appear (Fig. 1). Additionally, plants could accli-
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tant ecological significance because there is both aridifying and
warming trends in terrestrial ecosystems at global and regional
scales, particularly in many arid and semi-arid areas in terms of
climate change prediction. The underlying mechanisms of the
molecular and integrative responses to episodic drought would be
elucidated further.