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More from less: plant growth under limited water

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When subjected to abiotic stresses, plants actively re-program their growth by modulating both cell division and cell expansion. Growth decreases rapidly upon stress onset but it recovers and adapts once stress conditions become stable. Here, we review recent advances in understanding the mechanisms underlying both stress-induced growth repression and adaptation with an emphasis on drought and leaf growth and we briefly discuss how this knowledge can be translated into crops. It is now clear that stress response of growing and mature leaves is distinct and should be studied separately. Both cell proliferation and expansion are regulated by common signaling pathways involving gibberellins and DELLA proteins while down stream effector genes are stage specific.

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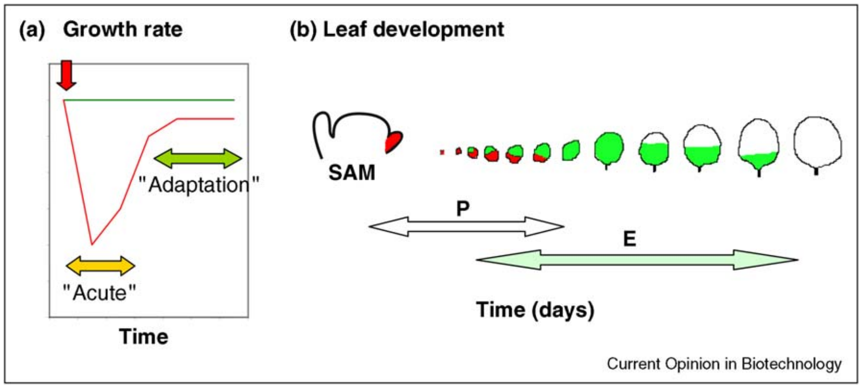
Introduction

To minimize the deleterious effects of stress and to complete their life cycle under adverse conditions, plants have evolved different adaptive responses that are summarized in the avoidance/tolerance model [1]. For example, during drought, plants close their stomata and accumulate compatible solutes to maintain a low water potential and to avoid dehydration. Simultaneously newly synthesized protective proteins, such as dehydrins and antioxidants, restrict damage to other proteins and cellular membranes and lower the levels of harmful reactive oxygen species (ROS) (see article by J.M. Pardo in this issue). Plants also reduce their growth as a way to save and redistribute resources that can become limited under extreme stress. Accordingly, growth reduction occurs rapidly after stress onset and independently of photosynthetic rates and plant carbon status [2,3•], arguing that growth reduction is not simply a secondary effect of resource limitation, but an important adaptive response. Counter-intuitively, plants exposed to mild drought stress even accumulate sugars and starch [3•]. Although growth retardation increases the survival rate, during moderate stress episodes when survival is not threatened, it can be seen as counter-productive with unnecessary yield losses and major consequences for agriculture. Therefore, new crop varieties in which growth would be less inhibited during sporadic spells of moderate stress would be extremely advantageous for plant productivity, particularly in mild climates. We might even speculate that in modern varieties, breeders have already selected for reduced growth sensitivity under mild stress conditions. Knowledge of the mechanisms underlying growth reduction under stress is an important prerequisite to further improve crop productivity. Whereas an enormous amount of information is available on the molecular mechanism controlling stress tolerance in mature leaves, our current understanding of stress-regulated growth is still very fragmentary, partly because studies combining detailed growth analysis and molecular characterization of growing organs are relatively scarce [3•,4•,5]. Most of the available stress data were obtained from mature tissues or whole plants, in spite of the fact that developmental stage and cell identity have a major influence on the observed stress responses [3•,6•]. Hundreds of genes and many metabolites were shown to change specifically in growing versus mature leaves and in different root tissues under osmotic and salt stress, respectively [3•,6•]. Additionally, in most studies the applied stresses are rather extreme, leading to plant death, a situation that is rare in modern agricultural practice. Related, while numerous screens identified mutants that cope better with extreme stress [7–9], often because of their inherent dwarfed stature [10,11], only a very limited number of studies report on plants that grow better under mild stress conditions that do not threaten plant survival although they restrict growth [12,13••]. This review will mainly focus on drought stress and its impact on *Arabidopsis thaliana* leaf growth, but key findings on other stress conditions, plant species, and organs will also be highlighted.

‘Acute and adaptation’ growth responses

Response of plant growth to stress onset is often characterized by a rapid and acute (‘acute response’) inhibition, followed by recovery and adaptation to the new condition (‘adaptation response’) (Figure 1A). In barley (*Hordeum vulgare*) leaves, the leaf elongation rate (LER) decreased close to zero within seconds after salt addition to the roots, followed by recovery of LER to approximately 46% and 70% of the non-stressed plants within minutes and days, respectively [14]. Similarly, in the shoot apical meristem

Figure 1



Growth response to stress. **(a)** Schematic representation of 'acute' (yellow arrow) and 'adaptative' (green arrow) growth response of plants subjected to stress. Red arrow marks stress onset. **(b)** Schematic representation of *Arabidopsis* leaf growth. Leaves initiate at the flank of the meristem (SAM). The number of recruited cells might influence the final cell number. Initially leaf growth is driven exclusively by cell proliferation (P, red shading). Within several days and starting from the leaf tip, cells exit the mitotic cell cycle and start to expand (E, green shading). After a few days, leaf growth is steered solely by cell expansion. Again starting at the tip, cells become mature (no shading), coinciding with growth cessation [63]. The final cell number and size might therefore depend on the length of the developmental windows of proliferation and expansion (white and light-green arrows), respectively, and/or the duration of single cell cycle (the shorter the cycle, the higher the cell production per unit of time) and rate of expansion.

(SAM) of salt-treated *Arabidopsis* plants [15], the cell cycle activity was reduced transiently (12 h and 36 h after stress onset) and subsequently recovered (4 days after stress onset). While the acute response prepares plants for possibly more severe conditions, the adaptive response can be seen as the establishment of a new steady state to prolonged and stable stress. This two-phase ('acute' and 'adaptation') growth response indicates that the mechanisms that govern growth repression upon stress sensing and those that allow growth adaptation are distinct and will be discussed in more detail below.

Drought reduces leaf growth by affecting cell division and expansion

In dicotyledonous plant species, such as *Arabidopsis*, leaf growth results from the proliferation and subsequent expansion of founder cells, recruited from the SAM. Consequently, the final leaf size depends on the number of recruited cells as well as the rates and developmental windows of cell division and expansion [16] (Figure 1B). Soil water deficit and relatively mild osmotic stress affect the leaf area by reducing both cell number and size, as shown in *Arabidopsis* and sunflower (*Helianthus annuus*) [3•,17••,18]. Importantly, the initial growth reduction can be compensated by a longer proliferation and/or expansion time, a phenomenon denominated 'growth extension'. In an extreme case, the final leaf sizes of the *Arabidopsis* accession An-1 grown under control and soil water deficit conditions were identical, but were reached in stressed plants only after an additional two weeks of growth [17••,18]. Interestingly, in *Arabidopsis* and sunflower leaves, exposed to a long water restriction period, epidermal cells retained some ability to expand, even though the leaf apparently had reached its final size [19] (Figure 1).

Root-to-shoot signaling in leaf growth regulation

In partial root drying experiments in which only part of the root system is subjected to drying, reduced leaf growth and stomatal closure occurred even when the remaining roots had enough moisture to fully supply leaves with water [20], leading to the conclusion that fast chemical signal(s) are generated in the drying roots mediating both leaf responses. Whereas the plant hormone abscisic acid (ABA) is a key regulator of stomatal conductance [21], results on leaf growth-regulating hormonal signals are still under debate and contradictory. For instance, because externally applied ABA represses growth, it is commonly viewed as a growth inhibitor [22], but a positive role of ABA through the inhibition of ethylene production has also been proposed on the basis of results obtained with ABA and ethylene mutants and ABA and ethylene inhibitors in maize (*Zea mays*), *Arabidopsis*, or poplar (*Populus trichocarpa*) [23–25]. Similarly to ABA, exogenously applied ethylene and its precursor 1-aminocyclopropane-1-carboxylic acid (ACC) inhibit growth [26] and accumulate under stress [27,28•], and ACC can be transported by the xylem from root to shoot [29]. Moreover, ethylene-deficient tomato (*Solanum esculentum*) plants subjected to soil drying were characterized by stomatal closure, without effect on their leaf growth, in contrast to wild-type plants [28•]. However, in maize plants grown under drought stress neither endogenous levels of ethylene nor ABA could be correlated with reduced leaf elongation [30]. Short-term