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Review Article

LEAF LONGEVITY IN PLANTS UNDER WATER STRESS – A REVIEW

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ABSTRACT

Global climate change during last couple of decades has caused a total shift in different environmental perspectives. One of the most important aspects affected by the climate change is the precipitation pattern, both temporally and spatially. Subsequently, plants experience either severe drought or water logging, collectively referred to as water stress. The effect of water stress is initially reflected in the leaves. It causes multifaceted impact on the leaves such as wilting, chlorosis, necrosis, hormonal imbalance, reduced leaf expansion, thickening of cuticle, leaf bud emergence, leaf area expansion, leaf mass and extension growth. A negative impact on all these phenomena leads to a decline in the active life span or longevity of leaf effecting overall growth and development of a plant. This review gives a comprehensive coverage to all these and other related aspects being faced by plants.

Keywords: Adaptations, chlorosis, drought, stomatal closure, water stress

INTRODUCTION

Leaves constitute the most important part of the plant body which have the potential to convert the solar energy into chemical energy by a process called as photosynthesis. The photosynthates synthesised are subsequently translocated to different parts of a plant including the seeds, where a part of it is stored. Therefore, growth and development and the productivity of a plant are greatly determined by the active lifespan of the leaf, which is called as leaf longevity. Leaf characteristics are known to vary along environmental gradients such as, altitude, soil fertility, moisture, precipitation, and light availability (Markesteijn, 2005). Moreover, foliage reflects the state of growth and health of the plant. Visibly green and spotless foliage, with species specific natural shape, size, texture, indicates a perfectly healthy state of a plant. The injuries and damage resulting from stresses due to abiotic factors viz. drought, water logging, malnutrition, light intensity (low or high) and temperature or due to biotic factors like microbes, pests, or herbivory are overall expressed in the leaves (Lowman, 1992).

During last couple of decades, there has been uncertainty and a total seasonal shift due to global climate change. Sometimes there is a scarce rainfall and sometimes there is excessive rain fall, which causes floods and subsequent water stress. It is one of the major environmental constraints that affect the overall metabolic state of the plant and subsequently the growth and development. Water stress can be experienced by the plants both under scarcity (drought) and excess water (water logging) (Pena-Rojas *et al*., 2005). Leaf is the first part of the plant that reflects the effect of water stress. Water stress affects the hormonal balance (Koshita and Takahara, 2004), decreases cell growth, stimulates stomatal closure, decreases chlorophyll content, causes necrosis, alters leaf shape and affects membrane permeability (Hopkins, 1995; Flexas *et al*., 2004; Fariduddin *et al*., 2009). All these altered processes lead to decline in the longevity of the leaf. Water deficit brings about substantial functional and structural changes in the photosynthetic apparatus. Several studies in the recent past have focused functional changes due to water deficit (Chen *et al*., 2005; Monclus *et al*., 2006). Water deficit alters a variety of biochemical and physiological processes which include photosynthesis, protein synthesis and solute accumulation (Ashraf and Foolad, 2007). The extent to which photosynthetic capability is maintained during periods of water stress and the ability of rapid recovery of photosynthesis after resuming normal watering may play important role in drought adaptation. To retain photosynthesis under drought conditions, some xerophytic plants evolved to maintain adequate tissue turgor and stomatal opening (Chartzoulakis *et al*., 2002; King *et al*., 2005). The varying stress interacts with the dynamic of structural and functional development in growing tissues of leaves and results in varying responses under different developmental situations.

Leaf Longevity

Visibly, the leaf longevity may be considered to be the period from the stage of fully expanded leaf blade till senescence. Physiologically leaf longevity has been considered as balance between lifetime carbon synthesis, assimilation and partitioning to other plant organs (Kikuzawa and Lechowicz, 2006). Cost-benefits analysis of leaf longevity in a wide range of species revealed that longevity increases with the ratio of construction cost to maximum photosynthetic rate (Escudero and Mediavilla, 2003). The longevity has been reported to increase with the increase in initial photosynthetic rate as the leaf ages (Matsuki and Takayoshi, 2006). However, water stress adversely alters these processes. Water stress reduces leaf area by early on setting of senescence or by accelerating its rate (Knapp *et al*., 1999).

Many tropical and deciduous trees and shrubs shed their leaves during dry season in coherence with the degree of drought and re-emerge before or after the monsoon (Khan, 1999). Lower leaf absorption reduces water consumption and extends leaf longevity. These adaptations may buffer against the unpredictability of growing conditions in some driest sites (Darren *et al*., 1998). Dry soil conditions may favour early leaf senescence to reduce water requirements and avoid low water potentials deleterious for normal xylem dysfunctioning (Casper *et al*., 2001). Similarly, leaf shedding in response to drought stress occurred sequentially from older to younger leaves in field grown clones of robusta coffee (*Coffea canaphora*)and leaf senescence was proportionate to sensitivity of the clone to drought level (Da Matta and Rena, 2001). In some Mediterranean plants leaf longevity and leaf mass per area ratio have been found to be higher than in plants from relatively more mesic environments. The sites with long dry period are characterised by drought resistant semi-deciduous plants with lower leaf mass per area ratios, shorter lifespan, and greater CO_2 uptake (Gratani and Varone, 2006). Similarly, drought enhanced leaf shedding up to 20% in *Phillyrea latifolia* (Ogaya and Penuelas, 2006). During growing season the effect of decrease in predawn water potential was more pronounced in the deciduous species, than in evergreens. This adaptation may increase leaf longevity by avoiding irreversible damage during the summer drought (Mediavilla and Escudero, 2003). The phenological behaviour of *Quercus ilex* growing at mesic site differed with those at xeric site. The trees at mesic sites, renewed their crown almost completely (Bussotti *et al*., 2003). Similarly, in *Phlomis fruticosa* L (a seasonal dimorphic shrub), the summer leaves developed during late spring and had about one year longevity but winter leaves developed during early winter shed massively by late June. The physiological variability in dimorphic leaves has also been recorded. During late spring, the winter leaves had relatively highest percentage of the assimilating surface with 25% higher net photosynthetic rates as compared to the summer leaves (Grammatikopoulos *et al*., 1995).

Mediterranean plants confront with unpredictable precipitation during wet period and long hot dry summer extending up to subsequent autumn. The native plants developed a range of physiological and morphological adaptations (Kummerow, 1973) to withstand such climatic conditions. The perennial species of this region have 3 major adaptations as evergreen sclerophyllous shrubs, drought deciduous shrubs and drought semi deciduous shrubs (Lange, 1988; Grammatikopoulos *et al*., 1995). The evergreen sclerophyllous shrubs possess compact small heavily cutinised leaves with well developed stomatal regulation to check excessive water loss (Lange, 1988). This adaptation, however, reduced photosynthetic efficiencies (Tenhunen *et al*., 1987), but had extended longevity (Grammatikopoulos *et al*., 1995). The drought deciduous shrubs of this region lack stomatal regulation against water loss and other xeromorphic features. These shrubs shed their leaves in dry season as a result of desiccation. The drought semi-deciduous groups have intermediate strategy. The leaf senescence in this group is drastic but not complete during summer. The extreme drought stress is avoided partially by leaf shedding and partially by withstanding drought through remaining leaves. The leaves of this group are seasonally dimorphic (Grammatikopoulos *et al*., 1995). Likewise, the evergreen leaf cover in *Croton megalocarpus* decreased during period of high rainfall (Broadhead *et al*., 2003). However, *Gliricidia sepium* reduced its leaf cover during brief regimes of rains (Broadhead, *et al*., 2003).

In the Amazonian flood plains, the onset of flooding led to chlorosis, epinasty and abscission thereby causing an increase in leaf senescence in trees (Armbruster *et al*., 2004; Parolin *et al*., 2005). The new leaf formation reduced in aquatic phase and the deciduous period lasted only for two months in most of species of the flood plains (Schongart *et al*., 2002). Leaf shedding under water stress has been documented to occur both in deciduous and evergreen trees which tends to reduce new leaf formation (Parolin *et al*., 2004). Flooding and drought in Amazonian flood plain caused leaf shedding in the seedlings of all tree species. When subjected to water logging, three evergreen species shed 30% and three deciduous species 20-25% of their leaves. All submersed plant shed 100% of their leaves (except *Nectandra spp*. with only 60%) while the seedling subjected to drought shed around 40-100% leaves (Parolin, 2001).

Leaf Emergence

Water stress reduces leaf formation, induces early abscission and senescence and cosequently reduces the overall leaf number (Slama *et al*., 2006). Similarly, Clark *et al*., (1999) observed that waterlogging slowed down the leaf appearance rates in *Trifolium repens, Holcus lanatus* and *Lolium perenne*. In another report, *Coffea Arabica* possessed fewer leaves were produced when irrigated twice a week. The plants showed higher rates of leaf senescence and produced considerably smaller leaves than the plants irrigated twice a day (Da Matta, 2004). Formation of leaves in water limited Ramla Handa plants was 32% lesser than well watered plants. Under adequate water treatment, the plants increased leaf production to 79% (Grant *et al*., 2005). With longer drought periods, the leaf number decreased in several plants (Da Matta and Rena, 2001; Slama *et al*., 2006).

The flooding initially reduced formation of new leaf in *Cecropia latiloba,* an evergreen species. However, the emergence of new leaves continued during prolonged flooding in Amazonian flood plains. Submerged leaves necroted faster and shed within few days (Parolin *et al*., 2004). The water logging phase has been documented to cause leaf shedding and reduced new leaf emergence in evergreen trees (Parolin, 2002). Dead leaf percentage under excess soil moisture was thought to be the best criterion for selection of plants tolerance to flood (Armbruster *et al*., 2004). Heavy water logging also reduced the total leaf number in *Citrullus lanatus* (Yetisir *et al*., 2006). Leaf production in *Pauteria glomerata* stopped completely at the beginning of waterlogging and symptoms of senescence became dominant (Armbruster *et al*., 2004). The decrease of leaf number and area was stronger in *Quercus ilex* which is less drought resistant and lose its competitive advantage under increasingly drier conditions in the Mediterranean Holm oak forests (Ogaya and Penuelas, 2006).

Leaf Area

Leaf area is an index of plant growth, productivity and stress. Certain characteristics like phenology, stem morphology, rate of leaf emergence and potential leaf size, number, dry or fresh weight of leaf influence and determine the total area of leaf in a plant. The drought or waterlogging may affect some or most of these traits and eventually modify the leaf area (Blum, 1996). Plasticity in leaf area is another important factor that facilitates the efficient water use under drought (Blum and Arkin, 1984). The leaf plasticity of *Acer ginnala* seedlings has been reported to be greater. The leaf size and total leaf area in this species also decreased significantly with the intensity of water stress (Cheng *et al*., 2003).

Water availability and temperature have also been found to influence the leaf area of *Eucalyptus* plants (Battaglia *et al*., 1998). Drought stress can alter leaf structure considerably. Leaves of stressed plants were observed to be of smaller size and their cytological structure was altered in comparison to controls (Schurr *et al*., 2000). Similarly, Casper *et al*., (2001) noted that drought exposure to *Cryptantha flava* affected both leaf area and leaf specific mass. The leaves of drought stressed individuals of this species were smaller (0.91±0.075 cm^2) than leaves of control plants (1.28 ±0.104 cm^2). The leaf area in *Quercus ilex* and *Phillyrea latifolia* decreased in response to simulated drought (Ogaya and Penuelas, 2006). In *Coffea arabica*, prolonged drought stress mediated smaller leaf area and altered carbon allocation to varying tree organs decreased crop yield (Da Matta, 2004). Water stress significantly reduced the total leaf area to about 12%, leaf size to 13% and dry matter production to 55% in some cultivars of *Vitis vinifera* (Gomez-Del-Campo *et al*., 2003). The water stress due to irrigation at 15 days intervals reduced the leaf area to 88% in *Burleria lupuli* (Paz *et al*., 2003). However, in *Acacia* species, reduction in leaf area caused by water stress was attributed to reduced leaf initiation, leaf growth rate and leaf size (Otien, *et al*., 2005). Unyayar *et al.,* (2004) also observed that drought treatment in sunflower genotypes had a significant inhibitory effect on the growth of the leaves. The drought stressed plants had a significantly lower leaf area than those of the control plants.

Leaf Area Expansion

Leaves expand to intercept with the larger quantity of light and CO_2 for photosynthesis and to transpire water for cooling. The extent of leaf expansion is determined partly by genetic factors and partly by prevailing environmental factors. The development of leaf area is an important factor that could affect the plant response to water availability. Leaf area expansion decreased in response to induced water deficit. The expansion and development of transpirational surface also decreased drastically. It was believed that such arrested growth, with limited investment in osmolyte production, assisted plants in attaining high productivity in environments with intermitted cycle of drought and watering (Alves and Setter, 2004). Leaf expansion process is sensitive to the water deficit. This sensitivity is expressed in terms of smaller cells and reduction in numbers of cells produced by leaf meristems (Alves and Setter, 2004). Some workers have emphasized the role of cell turgor or tissue water status in determining leaf growth rates (Munns *et al*., 2000).

A constant soil water deficit decreased leaf blade elongation rate in *Zea mays*. The loss in elongation of leaf differed with the positions of leaf under low evaporative demand (Franca *et al*., 2000). Leaf extension rate in grasses has been found sensitive to water stress even when turgor was maintained (Thomas *et al*., 1999), which could be due to altered rheology of elongating cells at the base of leaf and thereby affecting the extensibility of the cell walls (Bacon *et al*., 1997). Water stress is also reported to reduce the length of the growing zone and the distribution of cell expansion rate within the zone (Durand *et al*., 1995). Water deficit substantially reduced leaf area growth in four monitored Cassava (*Manihot esculenta*) genotypes. After 3 and 6 day of withholding consistent irrigation, the leaf area was only 27 and 11% of control plants owing to 5 fold and 21 fold decrease in leaf area expansion rates respectively. In a number of plants, the leaf area growth decreased in response to water stress and rapidly reversed on the withdrawal of stress (Alves and Setter 2000). This response limited the development of plant transpirational surface area during water deficit and kept the sink demand adequately balanced with plant assimilatory capacity. Accumulated evidences suggested that both chemical and hydraulic signals are operative and integrated in regulation of leaf growth and stomatal conductance when plants were grown under drought stress (Comstock, 2002; Hu *et al*., 2006).

Under Mediterranean conditions, plant leaf area, leaf production and leaf growth were noted to be severely affected by soil water deficit. These studies indicated that leaf growth and senescence is most sensitive to drought (Tardieu *et al*., 2000; Slama *et al*., 2006). Parolin (2002) observed that reduction in leaf area were caused by leaf senescence and subsequent loss of leaflets. The leaf size reduction in *Senna reticulata* was directly related to water stress. In this species, the newly produced leaves and leaflets during waterlogged months were smaller than those produced during terrestrial period (Parolin, 2002). Water logging also reduced leaf elongation, kernel number and final yield in cereals (Collaku and Harrison, 2002).

Leaf Mass Per Area Ratio

It has been observed that thickening and high concentration of mechanical cells with thicker cell walls give Mediterranean sclerophyllous leaves a high leaf mass per area ratio (LMA). Several studies in the past have shown an increase in the LMA under drought condition in a number of plants (Grant *et al*., 2005; Gratani and Varone, 2006). Low LMA values during the wettest periods have often been observed in *Quercus ilex* growing in Mediterranean plains. LMA can be enhanced by increase in leaf density and thickness. The factors appears to be related to a great tolerance to drought (Ogaya and Penuelas, 2006; Gratani and Varone, 2006).

Extension Growth of Main Shoot

Water stress including drought and waterlogging has a significant effect on the elongation of main shoot or branch. Grant *et al*. (2005) observed a significant difference in the extension growth of the main branch of *Cistus albidus* when subjected to varying levels of water treatments. The water limited plants had about 24% shorter branches than those of well watered plant. The main branch in well watered plant grew around 38% more than the water stressed plants. Similarly in another study, the simulated soil water deficits first reduced leaf and stalk extension rate, then leaves per stalk and thereafter biomass accumulation and finally the sucrose accumulation in sugarcane (Inman-Bamber, 2004). Drought is also reported to retard the stem and root growth in a number of plant species (Munns, 2002: Molnar *et al*., 2004). The plant processes including stem extension are sensitive to soil drying (Slama *et al*., 2006).

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