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REVIEW

Plant responses to drought, acclimation, and stress tolerance

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Abstract

At the whole plant level, the effect of stress is usually perceived as a decrease in photosynthesis and growth. That is why this review is focused mainly on the effect of drought on photosynthesis, its injury, and mechanisms of adaptation. The analysed literature shows that plants have evolved a number of adaptive mechanisms that allow the photochemical and biochemical systems to cope with negative changes in environment, including increased water deficit. In addition, the acquisition of tolerance to drought includes both phenotypic and genotypic changes. The approaches were made to identify those metabolic steps that are most sensitive to drought. Some studies also examined the mechanisms controlling gene expression and putative regulatory pathways.

Additional key words: chlorophyll; fluorescence induction; high temperature; net photosynthetic rate; photosystem 2; ribulose-1,5-bisphosphate carboxylase/oxygenase; stomatal conductance; water stress; water use efficiency; xanthophylls.

Introduction

In the field, plants are often exposed to various environmental stresses. Usually, several stress factors act simultaneously on the plant, such as combined heat, water, and high irradiance at dry, sunny, and warm summer periods. In the frame of "physiological window", mild drought induces in plants regulation of water loss and uptake allowing maintenance of their leaf relative water content (RWC) within the limits where photosynthetic capacity and quantum yield show no or little change. Larcher (1987) defines stress as a "state in which increasing demands made up to an initial destabilisation of functions, followed by normalisation and improved resistance... If the limits are exceeded and adaptive capacity is overworked, the results may be permanent damage or even death... Stress contains both destructive and constructive elements and is a selection factor as well as a driving force for improved resistance and adaptive evolution." Lichtenthaler (1996) extended the Larcher's stress concept of plants by differentiating between eu-stress and dis-stress. Eu-stress is an activating, stimulating stress and a positive element for plant development, whereas dis-stress is a severe and real stress that causes damage, and thus negatively affects the plant and its development. Repair processes and adaptation not only lead to a restitution of the previous physiological functions, but also to hardening of plants by establishing a new physiological standard, which is an optimum stage of physiology under the changed environmental conditions. There exist many stress-coping mechanisms, which show up depending on the type and strength of stress.

Drought is a multidimensional stress affecting plants at various levels of their organisation. The plant response to drought at the whole plant and crop levels is complex because it reflects the integration of stress effects and responses at all underlying levels of organisation over space and time (Blum 1996). The dehydration process of drought tolerant plants is characterised by fundamental changes in water relations, biochemical and physiological processes, membrane structure, and ultrastructure

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Abbreviations: ABA - abscisic acid; Ax - antheraxanthin; Chl – chlorophyll; DCIP - 2,6-dichlorophenol indophenol; DGDG - digalactosyldiacylglycerol; F_0, F_v, F_m - initial, variable, and maximal Chl fluorescence; g_s – stomatal conductance; HT - high temperature; IAA – indol-3-yl-acetic acid; LWC – leaf water content; MGDG - monogalactosyldiacylglycerol; P_N – net photosynthetic rate; PSA - photosynthetic apparatus; PS2 - photosystem 2; RCs - reaction centres; RuBPCO - ribulose-1,5-bisphosphate carboxylase/oxygenase; RuBP - ribulose-1,5-bisphosphate; RWC - relative water content; Vx - violaxanthin; WUE - water use efficiency; Zx – zeaxanthin; ϕ_{PS2} - quantum yield of photosynthetic electron transport of PS2; ψ_w - leaf water potential.

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of subcellular organelles (Gaff 1989, Tuba *et al.* 1993, 1994, 1996, Sarafis 1998, Stevanovic *et al.* 1992). Depending on the differences in behaviour of the photosynthetic apparatus (PSA) during desiccation, two groups of desiccation tolerant (DT) plants were distinguished—homochlorophyllous desiccation tolerant (HDT) and poikilochlorophyllous desiccation tolerant (PDT) (Bewley 1979, Gaff 1989). The most essential difference between HDT and PDT plant during desiccation is that the PSA of the HDT plants is retained in a recoverable form, while in PDT plants the chlorophylls (Chls) and thylakoid systems are degraded and need to be fully reconstituted and revived (Tuba *et al.* 1996). Water deficit results in growth inhibition, accumulation of abscisic acid (ABA), proline, manitol, and sorbitol, formation of radical scavenging compounds (ascorbate, glutathione, α-tocopherol, *etc.*), stomatal closure and reduced transpiration rates, decrease in water potential of plant tissues, photosynthetic rate, and synthesis of new proteins and mRNAs. The majority of new proteins belong to dehydrin-like proteins, which are abundantly induced during embryo maturation of many higher plants as well as in water stressed seedlings (Pelah *et al.* 1997). Besides these physiological responses plants undergo also morphological changes. One of the largest is the adaptation of plants and chloroplasts to high (sun) and low (shade) irradiance. This sun-type or shade-type chloroplast adaptation is also induced by many other stress factors including drought. The adaptation processes essentially determine the rate of photosynthesis (Lichtenthaler *et al.* 1981).

Improving drought tolerance of cereal species is a major goal of most breeding programs (Blum 1988). Advances in breeding for drought tolerance have been made possible by progress in elucidation of physiological and biochemical mechanisms responsible for stress tolerance.

The present review surveys current knowledge about the effects of drought on photosynthesis based on physiological, biochemical, and biophysical information as well as about oxidative stress and antioxidant defence systems. It concerns only oxygenic organisms, predominantly higher plants. The interactions of water deficit with other environmental stresses are also discussed.

Effects on photosynthesis

At the whole-plant level, the effect of stress is usually perceived as a decrease in photosynthesis and growth, and is associated with alterations in carbon and nitrogen metabolism (Cornic and Massacci 1996, Mwanamwenge *et al.* 1999). Contents of photosynthetic pigments (Chl *a* and *b*, and carotenoids) in the leaves diminish. The rate of CO_2 assimilation in the leaves is depressed at moderate leaf water deficits or even before leaf water status is changed in response to a drop in air humidity (Bunce 1981) or in soil water potential (Gollan *et al.* 1986). Yordanov *et al.* (1997a, 1998) followed gas exchange and Chl fluorescence in bean plants during water and high temperature (HT) stresses and recovery. Water deficit (17–20 %) caused a significant decrease in rates of CO_2 uptake and oxygen evolution, and its combination with HT (40–44 % water deficit and leaf temperature of 45 °C) led to an almost complete inhibition of both processes, but these were capable to recover. The dynamics of recovery of CO_2 uptake and oxygen evolution were different in plants that experienced water deficit or in combination with HT. The carbamide cytokinin 4-PU-30 (10^{-6} M) protects in some extent photosynthesis during applied stress as well as the chloroplast ultrastructure and enhances the recovery (Stoyanova and Yordanov 1999). Todorov *et al.* (1998, 2000) found that application of plant growth regulators such as 4-PU-30 or some phenyl amines alleviated to some extent the plant damage provoked by polyethyleneglycol application. The accumulation of free proline, malondialdehyde, and H_2O_2 was prevented. Cytokinins induce the formation of sun type chloroplasts that are more tolerant against water and temperature stresses (Lichtenthaler 1981). The phytochrome, indol-3-yl-acetic acid (IAA), and kinetin induce the formation of chloroplast types with different morphology, chemical composition, and net photosynthetic rate, P_N (Straub and Lichtenthaler 1973, Buschmann and Lichtenthaler 1977). Sun type chloroplasts contain low amount of LHCPs (Lichtenthaler *et al.* 1984, Sarafis 1998) and reduced pigment antenna. IAA and even better kinetin promote the light-induced formation of pigment systems and electron transport chains.

Water loss leads to a progressive suppression of photosynthetic carbon assimilation in both desiccation tolerant [*Frullania dilatata* (L.) Dum.] and desiccation intolerant [*Pellia endiviifolia* (Dicks) Dum.] plant species (Deltoro *et al.* 1998). Drought caused a more pronounced inhibition in growth and P_N in the more sensitive cv. Adamello than the relatively tolerant cv. Ofanto of *Triticum durum* Desf. (Loggini *et al.* 1999).

During a slow desiccation of photosynthetically fully active leaves of PDT monocotyledon *Xerophyta scabrida,* the CO_2 assimilation, thylakoid activity, and respiration rate decline and Chl and carotenoid contents are successively broken down. The initially slow rate of leaf water loss is related with the large reduction in leaf area. Chls are broken down faster than carotenoids. The decline in P_N in desiccated leaves is largely caused by stomatal closure. The complete cessation of CO_2 assimilation, however, is due to the breakdown of Chls and thylakoids (Tuba *et al.* 1996). In contrast, in HDT plants the decline and cessation of P_N is due to a slow desiccation, and results not from a degradation but from inactivation of the thylakoid system, which is preserved during desiccation in the non-functional but easily recoverable form (Bewley 1979, Schwab *et al.* 1989). In HDT plants stroma enzymes are apparently only inactivated (but not degraded) since they are able to fix CO_2 even at extremely low osmotic potential (Nash *et al.* 1990).

Recovery of the photosynthetic system is obviously promoted by a complex of signals comprising metabolites produced during rehydration and appropriate leaf water relations, turgor, and maximal leaf water content (LWC). For example, in *Xerophyta scabrida* reaccumulation of Chl ($a+b$) started when leaves reached about 91 % of their maximal LWC which needed about 10 h. Water uptake through the leaf surface upon rehydration was of prime importance for recovery. This process preceded the development of new adventitious roots. *De novo* Chl and carotenoid syntheses began just before the leaves reached their maximum water content and specific leaf area and maximum pigment content were reached about 72 h after rehydration (Schwab *et al.* 1989, Tuba *et al.* 1994).

Revival in re-moistened HDT plants begins with intensive respiration ("rehydration respiration") (Farrar and Smith 1976). The recovery of the PSA starts during this rehydration respiratory phase and is completed within a few hours to 1 d (Meenks *et al.* 1991).

Osmotic adjustment and elasticity parameters help maintaining both pressure potential and volume of cell under water deficit (Peltier and Marigo 1999). The osmotic adjustment is attributable to the change in photosynthetic apparatus, in which both stomata and plastids are involved (Shangguan *et al.* 1999). The drought tolerant barley genotypes (*Hordeum vulgare* L.) Albacete and Alpha showed higher osmotic adjustment than drought susceptible genotypes Express and Mogador. The genotype Albacete exhibited also higher P_N than the others at low water potential. However, Kubiske and Abrams (1994) found no relationship between gas exchange and osmotic and elastic parameters in other plant species. Flagella *et al.* (1996) could not detect a relationship between the maintenance of quantum yield of photosynthetic electron transport of PS2 and osmotic adjustment under water deficit. Hence, to which degree osmotic adjustment may contribute to the acclimation of photosynthesis at a low leaf water potentials (ψ_w) remains unclear (Ludlow 1987, Flagella *et al.* 1996).

Stomatal and non-stomatal limitations

A decrease of photosynthesis due to water deficit has been attributed to both stomatal and non-stomatal limitations (Graan and Boyer 1990, Ort *et al.* 1994, Shangguan *et al.* 1999). Stomatal response is probably the most important factor controlling carbon fixation. Stomata closure is the first line defence against desiccation since it is much quicker than, *e.g.*, changes in root growth, leaf area, chloroplast ultrastructure, and pigment-proteins. The more drought-tolerant species control stomatal function to allow some carbon fixation at stress, thus improving water use efficiency (WUE) or open stomata rapidly when water deficit is relieved.

The relative part of stomatal limitation of photosynthesis depends on the severity of water deficit. At mild stress it is a primal event, which is then followed by adequate changes of photosynthetic reactions (Cornic and Briantais 1991). They found in three cultivars of *Phaseolus vulgaris* that stomatal conductance (g_s) declined before leaf RWC was affected. P_N was largely dependent on stomatal aperture. Farquhar *et al.* (1989) concluded that stomatal factors are more important than non-stomatal factors in affecting photosynthesis under water deficit, mainly because of leaf stomatal heterogeneity. ABA is possibly a major modulator of these effects (Blum 1996). Long-term water deficit leads to both stomatal and non-stomatal limitation of photosynthesis in leaves of sunflower plants grown in the field (Panković *et al.* 1999). Water deficit might decrease the sensitivity of stomata to low ψ_w (Farquhar and Sharkey 1982). Stomatal closure usually occurs before inhibition of photosynthesis and restricts CO_2 availability at the assimilation sites in chloroplasts.

Although stomatal closure generally occurs when plants are exposed to drought, in some cases (severe stress) photosynthesis may be more controlled by the chloroplast's capacity to fix CO_2 than by the increased diffusive resistance (Faver *et al.* 1996, Herppich and Peckmann 1997). Non-stomatal limitation of photosynthesis in sunflower leaves has been attributed to reduced carboxylation efficiency (Wise *et al.* 1992), reduced ribulose-1,5-bisphosphate (RuBP) regeneration (Gimenez *et al.* 1992, Tezara and Lawlor 1995), or to a reduced amount of functional RuBPCO (Kanechi *et al.* 1995). Shangguan *et al.* (1999) reported that non-stomatal factors are responsible for decline in photosynthetic capacity when plants experience a severe water deficit. Inhibition of chloroplast activity at low ψ_w decreases the capacity to fix available CO_2.

The initial inhibition of P_N, g_s, activities of the photosynthetic enzymes, and contents of Chl and total soluble protein were observed in sugarcane from leaf water potentials of -0.37 MPa. During water deficit, P_N and g_s decreased in a non-linear way, activities of the five enzymes investigated and contents of Chl and total soluble protein decreased linearly with decreasing ψ_w (Du *et al.* 1996). Non-stomatal responses of carbon fixation such as PS2 energy conversion and the dark reactions of RuBPCO carbon fixation are resistant to water deficit (Chaves 1991, Dickson and Tomlinson 1996). In addition, stomatal closure occurs before inhibition of photosynthesis and restricts CO_2 availability at the assimilation sites in chloroplasts.

There is an important role for a chemical signal, probably ABA originating from roots, in stomatal control in droughted plants. Tardieu (1996) suggests that in anisohydric species such as sunflower, stomatal control depends on chemical signals alone and that ψ_w behaves as a consequence of g_s and water relations, without a controlling effect. In contrast, ψ_w has an effect *per se* in stomatal control of isohydric species such as maize, in interaction with chemical signals.

In drying soil, a root signal is transmitted to the leaf causing stomatal closure before the plant water deficit increases. This signal is produced in the root tips, which presumably sense the drought when they lose turgor. Zhang *et al.* (1987) showed that total mass flow of xylem sap, but not the actual ABA concentration within the sap, controls the stomatal aperture.

Drought stress and PS2 activity

PS2 is highly drought resistant as found in investigations on the impact of various environmental stresses (drought, heat, strong irradiance), applied separately or in combination (Havaux 1992). At the same time water deficit markedly modified its responses to superimposed constraints. The existence of a marked antagonism between physicochemical stresses (*e.g.*, between water deficit and HT) was established, with a water deficit enhancing the resistance of PS2 to constraints such as heat and strong irradiance, that are usually associated with drought in field. Similar results were received with bean plants (Yordanov *et al.* 1999). Flagella *et al.* (1998) show that quantum yield of PS2, as related to Calvin cycle metabolism, is reduced only under drastic water deficit.

Extreme stress, such as 40 % decrease in RWC, caused a 50 % reduction in O_2 evolution and 25 % inhibition of 2,6-dichlorophenol indophenol (DCIP) photoreduction by PS2. In addition, the inhibited DCIP photoreduction by PS2 could not be reversed by 2,2-diphenylcarbazide, a typical exogenous electron donor to PS2, suggesting that water deficit did not affect electron donation to PS2 (He *et al.* 1995). The effects of water deficit applied separately and in combination with HT on parameters characterising the functional state of PS2 reaction centres in bean plants were less expressed than on CO_2 photoassimilation (Yordanov *et al.* 1997b).

Munné-Bosch and Alegre (1999) observed that water deficit did not cause an additional decrease in F_v/F_m ratio (photodamage). Drought decreased the pigment composition in *Melissa officinalis* leaves. Thus the degradation of pigments can be regarded as a regulation that allows water stressed plants to reduce the risk of over-excitation and photooxidative damage.

Cona *et al.* (1995) suggest that the water deficit syndrome is a combination of two components. One, water deficit effect, enhanced by irradiation, leads to a disassembly of a part of the PS2 core. Second, mild drought induces reorganisation processes that rebuild and maintain the remaining PS2 functional to counteract the depletion of PS2 core. The importance of these two drought consequences depends on the specific growth conditions and irradiance, offering an explanation for the conflicting results observed in water deficit experiments carried out in a growth chamber *versus* those carried out under field conditions.

Long-term drought reduces water content in a wide range; this leads to considerable depletion of pea PS2 core. The remaining PS2 complex was functional and reorganised with a unit size (LHCP/PS2 core) two fold larger than that of well irrigated plants and enhanced degradation of CP43 and D1 proteins (Girardi *et al.* 1996). The depletion of PS2 core was essentially reversed when water stressed plants grown at low visible irradiance were watered. The syndrome caused by long-term water deficit on photosynthesis may be a combination of at least two events: a reduction in the number of active PS2 RCs caused by a physical destabilisation of the PS2 core, and a PS2 re-organisation with enhanced D1 turnover to counteract the core depletion.

Declines in the photon yield of photosynthesis during desiccation can be due either to damage of the photosynthetic apparatus or to PS2 down-regulation (Calatayud *et al.* 1997). Deltoro *et al.* (1998) found a fast recovery of Chl fluorescence parameters when *Frullania dilatata* was re-hydrated which suggests that the decline in PS2 efficiency is regulatory, serving a photoprotective role. Chl fluorescence is a good indicator of dehydration effects in lichens (Jensen *et al.* 1999) or higher plants (Pol *et al.* 1999).

Enhanced non-photochemical fluorescence quenching (q_N) suggests that the observed photoinhibition (decrease in the ϕ_{PS2}) is due to photoprotective energy dissipation processes (He *et al.* 1996, Schindler and Lichtenthaler 1996). Increased energy dissipation may help to protect PS2 from over-excitation and photodamage. However, it brings about a decline in the effective quantum yield of PS2 photochemistry (Mattos *et al.* 1999).

RuBPCO and other photosynthetic enzymes

Kanechi *et al.* (1995) found a close relationship between RuBPCO content and maximal O_2 evolution rate measured at high photosynthetic photon flux density (PPFD) during leaf dehydration. The primary site of limitation of maximal O_2 evolution rate, measured at high PPFD, seemed related to significantly reduced RuBP content, not to the amount of Chl or RuBPCO, because of little changes in them by water deficit, nor in the activation state of RuBPCO or its specific activity. Water deficit may inhibit the capacity of RuBP regeneration by loss of both ATP and reducing power productions in photochemical reaction.

Prakash and Rao (1996) found in two cultivars of maize that below -2.0 MPa the inhibition of photosynthesis is in part attributed to g_s but mostly to the decreased activities of carbonic anhydrase, phosphoenolpyruvate carboxylase, and RuBPCO. The recovery studies revealed that the phosphoenolpyruvate carboxylase activity was mainly responsible for normal P_N after re-watering.

In two wheat (*Triticum aestivum* L.) cultivars Trakia (drought sensitive) and Slavianka 196 (drought tolerant), exposure to water deficit of different strength showed that RuBPCO activity was almost unchanged under mild stress, while under severe stress it was reduced by about 27 % (Kicheva *et al.* 1994). According to Lal *et al.* (1996) decreased supply of CO_2 to RuBPCO under both mild and severe water deficit is primarily responsible for the decrease in CO_2 fixation. According to Holaday *et al.* (1992) RuBPCO is not a prime target of water deficit and is not limiting P_N of leaves submitted to desiccation. The suggestion that CO_2 concentration inside chloroplasts during a mild drought is low is supported by the fact that the proportion of photosynthetic electrons allocated to the reduction of O_2 *via* the oxygenase activity of RuBPCO increases during desiccation. This is only possible if the CO_2 concentration in dehydrated leaves decreases with time. Consequently, the decline of photosynthesis during leaf dehydration may be due to the decline in CO_2 caused by stomatal closure.

Initially, intercellular CO_2 decrease was of little effect on CO_2 fixation (indicating the CO_2 pump provides sufficient CO_2 for carbon assimilation), and an eventual inhibition of photosynthesis by water deficit was caused by limited supply of CO_2 to RuBPCO. As CO_2 fixation decreased during water deficit, the PS2 activity per CO_2 fixed increased, a phenomenon observed when well-watered plants are provided with very low atmospheric concentrations of CO_2. At the same time both the ratios RuBP pool/RuBP-binding site on RuBPCO and RuBPCO activity/CO_2 fixation increased, which suggests that neither RuBP regeneration nor RuBPCO capacity limit photosynthesis (Lal and Edwards 1996). Panković *et al.* (1999) observed a decreased slope and a plateau of the CO_2 response curves that indicate decreased carboxylation efficiency (slope) and RuBP regeneration (plateau) in water-deficient leaves.

Drought stress and specific proteins

These proteins have particular structural features such as the highly conserved domain that may be involved in hydrophobic interaction leading to macromolecular stabilisation (Close 1996). Dehydrins are synthesised by the cell in response to ABA, low temperature, or any environmental influence that has a dehydration component, such as drought, salinity, or extracellular freezing (Ingram and Bartels 1996, Giordani *et al.* 1999). Dehydrins may stabilise macromolecules through detergent and chaperone-like properties and may act synergistically with compatible solutes (Close 1996). Ouvrard *et al.* (1996) isolated from a drought tolerant sunflower line R1 six cDNAs corresponding to dehydrin transcripts up-regulated by water deficit. Three of those transcripts, HaElip1, HaDhn1, and HaDhn2, were differently accumulated in tolerant (line R1) or sensitive (line S1) plants during water deficit. In leaves of R1 plants the accumulation of the last two transcripts correlated with the drought adaptive response. Progressive drought lead to accumulation of HaDhn1 and HaDhn2 transcripts reaching higher levels in R1 than in S1 plants (Cellier *et al.* 1998). In drought resistant sunflower leaves, dehydrin transcript accumulation is associated with tolerance mechanism leading to the maintenance of cellular turgor, suggesting that dehydrins might also be involved in preventing cellular dehydration. Dehydrins may also protect cytosol structures from deleterious effects of cellular dehydration

(Baker *et al.* 1988, Dure *et al.* 1989, Close 1996). A correlation was found between drought adaptation and dehydrin accumulation in wheat and poplar (Labhilili *et al.* 1995, Pelah *et al.* 1997).

He *et al.* (1998) suggest that water deficit affects the expression of the *psbA* and *psbD* genes, possibly at the transcriptional level. Southern and DNA dot blot analyses consistently showed that water deficit did not affect the template levels of either *psbA* or *psbD* genes. This suggests that the decreased abundance of *psbA* and *psbD* transcripts under water deficit is not due to limited gene templates but likely a result of lowered gene transcription activity and/or changed mRNA stability.

Urea-SDS-PAGE and Western blot analysis showed that the steady state concentrations of major PS2 proteins, including the D1 and D2 proteins in the PS2 reaction centres, declined on a Chl basis with increasing water deficit, possibly as a result of increased degradation. *In vitro* translation experiments and quantitative analysis of chloroplast RNAs indicated that the potential synthesis of chloroplast proteins from their mRNAs was impaired by water deficit. Thus its effects on PS2 protein metabolism, especially on the reaction centre proteins, may account for the damage to PS2 photochemistry (He *et al.* 1995).

34 kDa chloroplast drought-induced stress protein (cdsp) was found in the thylakoids of potato plants subjected to a progressive water deficit (Pruvot *et al.* 1996). From immunoblot analysis the cdsp 34 protein appears to be an extrinsic protein preferentially located in unstacked stroma thylakoids. Based on the abundance and on its location within thylakoids, a putative role for this chloroplast protein is discussed in relation to the tolerance of the PSA of higher plants to dehydration.

Drought stress and lipids

Strong water deficit leads to a disturbance of the association between membrane lipids and proteins as well as the enzyme activity and transport capacity of the bilayer (Caldwell and Whitman 1987). Lipids are, along with proteins, the most abundant component of the membranes and they play a role in the resistance of plant cells to environmental stresses (Kuiper 1980, Süss and Yordanov 1986).

An efficient repair and full reconstitution of membrane integrity during re-hydration would be a prerequisite to cell survival. Water deficit resulted in variations of the chloroplast fatty acid composition, particularly in an increase of the percentage of fatty acids having less than 16 carbon atoms, and in a marked decrease in the percentage of linolenic acid (18:3), beyond -1.8 MPa, associated with an increase in the percentage of linoleic acid (18:2). The increase of C18:2, which markedly parallels the decrease of C18:3, is in favour of the hypothesis of an inhibition of the desaturase activity (Pham Thi *et al.* 1982).

Fatty acid composition of desiccation tolerant mosses changed during drought as well as the activity of several enzymes involved in lipid metabolism. Two different enzymatic pathways were proposed to explain tissue defence against the uncontrolled loss of unsaturated fatty acids (Dhindsa and Matowe 1981, Stewart and Bewley 1982). In higher plants, water deficit leads to a decline in polyunsaturated fatty acid content of leaves, particularly in glycolipid fractions (Chetal *et al.* 1981, Pham Thi *et al.* 1982, Monteiro de Paula *et al.* 1990). It also results in a profound overall drop in MGDG, the major leaf glycolipid.

At least at sufficiently severe stress, the content of polar lipids decreases (Martin *et al.* 1986, Navari-Izzo *et al.* 1989, Pham Thi *et al.* 1990). In leaves, this decrease was first due to changes in glycolipids (Chetal *et al.* 1982, Ferrari-Iliou *et al.* 1984). Stevanovic *et al.* (1992) found a decreased content of polar lipids in *Ramonda* leaves. Similar results were obtained by Stefanov *et al.* (1992) in *Haberlea rhodopensis* and *Ramonda serbica.* They found that lipid and sterol composition changes more drastically at 50 % water deficit, while at 87 % (air-dried plant) it is similar to that in fresh plants. All discussed changes, according to the authors, can lead to the stabilisation of the cell membrane and may have adaptive values. Similar phenomenon was observed in other plant species (Chetal *et al.* 1981, Monteiro de Paula *et al.* 1990). Finally, the lipid composition of desicated *Ramonda* leaves is profoundly modified: the ratio phospholipids (PLs) to galactolipids (GLs) increased and relative proportion of MGDG to DGDG drastically decreased. An increase in the PLs relative to GLs in leaves indicates a preferential degradation of chloroplast membranes (Öquist 1982). In two cultivars of *Vigna unguiculata* water deficit provoked a decrease in the leaf content of polyunsaturated molecular species of polar lipids, especially that of galactolipids (Monteiro de Paula *et al.* 1990). After severe water deficit a decrease in unsaturation and linolenic acid as well as a loss of lipolytic antioxidants took place in sunflower plants (Sgherri *et al.* 1996). The interactions among membrane components change in relation to a changed chemical composition. Such changes are probably among the causes for modified conformation of proteins and for the position of various molecular species in lipid bilayer, so that they become more exposed to molecular oxygen. 18:3/18:3 MGDG and 18:3/18:3 DGDG are the molecular species most susceptible to water deficit and the phenomenon is particularly marked in the drought sensitive cultivar. According to Monteiro de Paula *et al.* (1990) this decrease in lipid content may be due to a slowing down of the biosynthetic processes as well as to an acceleration of the degradative phenomena.

In drought sensitive seedlings of *Lotos corniculatus* the ratio of MGDG/DGDG declined 3-fold, while the relative part of MGDG was 12-fold lower. In contrast, in relatively drought tolerant seedlings of *Cerastium fontanum* no changes of this order were recorded in the days immediately following rehydration (Olsson *et al.* 1996). Thylakoids from drought tolerant wheat plants that experienced water deficit showed an increase in lipid to protein ratio in comparison with the control, whereas this ratio remained unchanged in the sensitive wheat cultivar (Quartacci *et al.* 1995). In both cultivars water deficit determined different arrangements in the composition of individual thylakoid polar lipids, but their unsaturation level remained unaffected, with the exception of MGDG. The fatty acid composition of major phospholipid of coconut palm was markedly enriched in linolenic acid in response to water deficit, suggesting slowing down of MGDG biosynthesis and/or an adaptation to drought stress (Repellin *et al.* 1997).

The deleterious effects of water deficit on the biosynthesis and degradation of leaf polar lipids were less pronounced in the drought-tolerant variety, and this indicates a greater stability of cell membrane (Monteiro de Paula *et al.* 1993). They demonstrated that the activities of MGDG-hydrolases increased under water deficit and the susceptibility of leaf lipid extracts to peroxidation increased in drought-stressed leaves. Drought-induced degradation of polyunsaturated galactolipids is no doubt responsible for the disorganization of chloroplast membrane (Vieira da Silva *et al.* 1974) and free fatty acids inhibit electron transport during photosynthesis (Mvé Akamba and Siegenthaler 1980). Moreover, modifications in the lipid composition, as well as changes in their fatty acid unsaturation, could have dramatic consequences on the physical properties of cell membranes (Liljenberg 1992).

Drought stress and saccharides

Mild water deficit (-1.0 MPa) caused in bean plants a decline in the starch/sucrose partitioning ratio indicating that starch synthesis was inhibited more than sucrose synthesis (Vassey and Sharkey 1989). Thus the reduced rate of photosynthesis is caused by stomatal closure and the restriction of CO_2 supply leads to a reduction in the capacity for both starch and sucrose synthesis.

According to Quick *et al.* (1989), partitioning changed markedly at moderate water deficit: more sucrose and less starch were made. Increasing water deficit led to a large increase in content of fructose-2,6-bisphosphate. This is explained in terms of a simultaneous increase of fructose-6-phosphate and inorganic phosphate contents as the cell shrinks. The high fructose-2,6-bisphosphate content led to the accumulation of triose phosphates, and a potential significance of this for protection against photoinhibition is proposed. There was an increase in the extractable activity of sucrose-phosphate synthase. Its activation may be one of the first sites at which spinach leaves respond to a rising water deficit.

Water deficit stimulates conversion of starch to sucrose in sugar beet leaves at the CO_2 compensation concentration (Fox and Geiger 1986). This increase in contents of soluble sugars will presumably play a role in osmotic adjustment (Morgan 1984) and may also contribute to maintaining the size of metabolic pools of the photosynthetic carbon reduction cycle. According to Massacci *et al.* (1996) sugar accumulation is less sensitive to drought than photosynthesis, irrespective of drought conditions. Monosaccharides accumulate markedly under water deficit, and gibberellic acid may further stimulate such accumulation (Alhadi *et al.* 1999).

Interactions between water deficit and other environmental factors

Drought is associated with enhanced heat tolerance of photosynthesis, *i.e.*, water deficit shifts the temperature threshold towards higher value. Water-stressed leaves placed at 42 °C exhibited a much smaller decrease (15 %) in the photochemical efficiency of PS2 than those of control. An increase in heat resistance of a few degrees can be extremely important for a plant's survival because heat induced inactivation of photosynthesis occurs in a very narrow temperature range (Havaux 1992). The PS2 thermotolerance acquired during leaf dehydration is reversible upon re-hydration of the leaves. At elevated temperature (above 40 °C) the photoinhibitory irradiation induced less damage in water-stressed leaves, indicating that water deficit counteracts the negative effects of HT (Havaux 1992, Yordanov *et al.* 1997b). These results suggest the existence of an antagonistic interaction of stresses, with one factor enhancing the tolerance to another factor.

Water deficit alone did not modify the amplitude of F_v in leaf but showed slight decrease in photosynthetic electron transport. However, interaction with light caused significant decrease in the efficiency of photosynthesis. It was greater when plants were photoinhibited at 30 than 10 °C. Water deficit alone does not lead to significant damage to the primary photochemistry but photoinhibition causes inhibition of both electron transport activity and Chl fluorescence. The damage was further enhanced by the combination of water deficit and HT (Sharma and Singhal 1993). Yordanov *et al.* (1997a) showed that when the Chl fluorescence was measured at 47 °C, the F_v/F_0 ratio in sunflower was considerably higher in plants that endured combined stress (water deficit + HT) compared with control plants. In maize plants such changes were not observed. The combined action of water deficit and HT led also to noticeable (in sunflower) or weaker (in maize) increase of stability of LHC2 at HT and decrease of the F_v (25 °C)/F_v (47 °C) ratio (an indicator for the tolerance of photochemical activity and O_2 evolving system).

Drought-induced changes in thermal optimum of leaf photosynthesis at normal CO_2 and limiting irradiance can be substantial, such as a decrease from 22 to 15 °C for French bean (Cornic and Ghashghaie 1991). These changes in leaf photosynthesis in response to temperature are correlated to similar changes in g_s.

In intact plants, thermotolerance of PSA increased significantly when the ψ_w was decreased to -1.0 MPa; it attained maximum at -1.5 to -2.0 MPa (Li *et al.* 1996). However, the thermotolerance decreased when water potential was further lowered to -4.0 MPa. When intact cucumber plants were re-irrigated after 3 d of water deficit treatment, the thermotolerance of PSA increased temporarily during the first 2 h, and then within 24 h sharply decreased to the level of the irrigated control leaves. Exogenous ABA applied to leaves of irrigated plants caused an increase in thermotolerance of PSA depending on its concentrations. Leaves treated with 1 mM ABA showed a nearly complete tolerance of PSA within a day; this high tolerance level was maintained for at least 6 d. Thus the enhanced thermotolerance of PSA in water-stressed cucumber leaves was probably mediated through a water deficit-induced increase in endogenous concentration of ABA.

P_N of *Trifolium repens*, *Plantago lanceolata*, and *Paspalum dilatatum* increased (approximately by 50 %) by exposure to elevated CO_2 under well-watering and further increased to over 300 % when soil moisture decreased (Clark *et al.* 1999). Drought diminished photosynthetic down-regulation to elevated CO_2 in *Larrea tridentata* resulting in seasonally transient patterns of enhanced carbon gain (Huxman *et al.* (1998). These results suggest that water status may ultimately control the photosynthetic response of desert systems to rising CO_2.

The water status of plants significantly improved under elevated CO_2 concentration possibly by decreasing g_s and/or by increased root growth (Uprety *et al.* 1995). Significant interactions between CO_2 and water suggest that elevated CO_2 concentration compensates for low water availability in loblolly pine and in whole seedling stands regardless of stand type (Groninger *et al.* 1996). Elevated CO_2 decreased water loss rate and increased leaf area development and P_N in both well-watered and drought-stressed soybean (*Glycine max* Merr.) plants. However, elevated CO_2 did not improve plant water relations and thus did not increase water deficit tolerance of cherry seedlings (Centritto *et al.* 1999).

The positive combined effects of CO_2 enrichment and water deficit on WUE resulted in P_N stimulation, while transpiration rate in CO_2 enriched plants resembled that of unenriched plants under water deficit (Liang and Maruyama 1995).

According to Chaves (1991), an optimum balance between water loss and uptake of intercellular CO_2 exists, and an alteration in these rates represents an adjustment in g_s to match the intrinsic photosynthetic capacity rather than a causal relation.

Oxidative stress and antioxidant defence systems

In optimal conditions, leaves are rich in antioxidant enzymes and metabolites and can cope with activated O_2, thus minimising oxidative damage. Antioxidant metabolites are present in chloroplasts at very high concentrations (10-20 mM ascorbate and 1-4 mM glutathione) (Iturbe-Ormaetxe *et al.* 1998). Apart from their obvious role as enzyme substrates, they can react chemically with almost all forms of activated O_2 (Halliwell and Gutteringe 1989). Drought stress can result in an increased production of reactive oxygen species and therefore requires elevated levels of antioxidants for stress compensation. The ability of plants to overcome the effects of different stresses and to sustain their productivity may be related to the scavenging of stress-induced toxic oxygen species, such as H_2O_2, $OH^\bullet$ (hydroxyl radical), and $O_2^{-\bullet}$ (superoxide radical). The hydrophilic antioxidants ascorbate and glutathione are effective chemical scavengers of oxygen radicals. Enzymatic detoxification systems involved in the action of superoxide dismutase (SOD), peroxidases (POX), and reductases either quench toxic compounds or regenerate antioxidants with the help of reducing power provided by photosynthesis (Polle and Rennenberg 1994).

In shoots of rice plants water deficit induced lipid peroxidation, Chl bleaching, and loss of molecular antioxidants including ascorbate (Asc), glutathione, [α]-tocopherol, and carotenoids. During water deficit the activities of enzymes processing active oxygen, such as SOD, ascorbate peroxidase (APOX), and POX decreased slightly (SOD, APOX, and POX) or substantially (catalase, CAT). In contrast, monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR) showed significantly increased activities in water-stressed shoots (Yong and Jin Jung 1999).

Pea plants that experienced mild drought (-1.3 MPa) showed symptoms of moderate oxidative stress, such as increase in SOD activity and contents of oxidized proteins and monodehydroascorbate (MDA). Severe water deficit caused decreases in all antioxidant activities (APOX, DHAR, GR, CAT) (Iturbe-Ormaetxe *et al.* 1998).

A drought-tolerant maize strain responded with significant increase in contents of antioxidants to water deficit, whereas a susceptible strain maintained a lower protection from oxidants (Pastori and Trippi 1992). In drying acorns of *Q. robur*, a loss in viability was associated with a significant reduction in antioxidative defences and appearance of free radicals (Hendry *et al.* 1992).

H_2O_2 is a strong oxidant that can initiate localised oxidative damage leading to disruption of metabolic function and losses of cellular integrity at sites where it accumulates (Foyer *et al.* 1997). H_2O_2 can diffuse relatively long distances causing changes in the redox status of surrounding cells and tissues where at relatively low concentrations it initiates an antioxidative response. Overexpression of GR in chloroplasts doubles the concentrations of Asc and glutathione (GSH) in leaves and confers increased resistance to oxidative stress (Foyer *et al.* 1997). CAT and POX are two major systems for the enzymatic removal of H_2O_2 in plants (Willekens *et al.* 1995). SOD catalyses dismutation of $O_2^{\bullet}$ to H_2O_2 and O_2. The activities of enzymes APOX, DHAR, and oxidised glutathione (GSSG) reductase participating in the Halliwell-Asada pathway, which removes H_2O_2 in cyanobacteria, chloroplasts, and root nodules, were largely depressed by water deficit (Dalton *et al.* 1986, Moran *et al.* 1994).

Moran *et al.* (1994) showed that water deficit led to pronounced decrease in the activity of CAT, DHAR, and glutathione reductase, but resulted in the increase of non-specific peroxidase and SOD. APOX and MDHAR acted in a cyclic manner to remove H_2O_2 that did not accumulate in stressed leaves. Drought caused a decrease in the content of reduced glutathione and an increase in that of vitamin E. Carotenoids and vitamin E are the main lipid soluble antioxidants of plant cells. In stressed leaves the content of carotenoids decreased weakly whereas that of vitamin E significantly increased.

H_2O_2 and other active oxygen species $OH^{\bullet}$, $^1O_2$, and $O_2^{-\bullet}$ may be responsible for the lipid peroxidation (Whetten and Sederoff 1995, Douglas 1996). Oxidation of lipids and proteins from leaves was enhanced two- to three-fold under stress and both processes were highly correlated. Augmented contents of catalytic metals and their decompartmentation occurring during water deficit are responsible for the oxidative damage observed *in vivo*. H_2O_2 can inactivate various Calvin-cycle enzymes (Asada and Takahashi 1987) and is involved in metal-catalysed oxidation systems, marking proteins for degradation (Levine *et al.* 1990).

Severe water deficit (-1.9 MPa) almost completely inhibited P_N, decreased the level of Chls, β-carotene, neoxanthin, and lutein, and caused further conversion of violaxanthin (Vx) to zeaxanthin (Zx), suggesting thus a damage to the photosynthetic apparatus. There were consistent decreases in antioxidants and pyridine nucleotides, and accumulation of catalytic Fe, malondialdehyde, and oxidised proteins (Iturbe-Ormaetxe *et al.* 1998).

Mittler and Zilinskas (1994) showed an increased production of mRNA for APOX and SOD and enhanced enzymatic activity of these proteins in drought-stressed pea plants. Catalase activity was also increased. These observations support the idea that both the Mehler reaction and photorespiration are important metabolic pathways for dissipation of radiant energy when the flux of CO_2 into the leaves of herbaceous plants is limited under drought (Foyer and Harbinson 1994).

The photoproduction of MDA radical was greatly enhanced by high irradiance, water stress, and suppression of the photosynthetic reactions. This is a sensitive endogenous probe of oxidative stress in leaf tissues: increased MDA contents indicate either increased oxidation of ascorbate or decreased efficiency of ascorbate regeneration, or a combination of both (Heber *et al.* 1996).

Schwanz *et al.* (1996) suggests that growth in elevated CO_2 might reduce oxidative stress to which leaf tissues are normally exposed and enhance metabolic flexibility to encounter increased stress by increases in antioxidative capacity.

Mechanisms of acclimation and stress tolerance

Plants adapt several ways to respond to environmental stresses. For plants grown in such conditions it is important to create physiological mechanisms of stress resistance in terms of stress avoidance or stress tolerance as discussed by Blum (1988). At the cellular level, plants attempt to alleviate the damaging effects of stress by altering their metabolism. Major alterations in patterns of gene expression occur at early stages of stresses. Some of these changes may provide a long-term protection against stress damage. If stress persists longer, more dramatic effects are visible in plant phenotype.

According to Bohnert and Shen (1999) a nearly universal reaction under stress (*e.g.*, water deficit) is the accumulation of "compatible solutes", many of which are osmolytes (*i.e.*, metabolites whose high cellular concentration increases the osmotic potential significantly) considered to lead to osmotic adjustment. These observations indicate that "compatible solutes" may have other functions as well, namely to protect enzyme and membrane structure and to scavenge radical oxygen species. Plant transformation leading to the presence of "compatible solutes" has resulted in significant increases in whole plant tolerance to osmotic stress.

Among the amino acid-based compounds a protection of cytoplasmic structure is ascribed mainly to "compatible solutes" proline and betaine. Proline alleviates the negative effect of NaCl on CO_2 fixation maintaining or restoring the otherwise depressed RuBPCO activity (Fedina *et al.* 1993). Cytoplasmic osmoregulation by increased amounts of betains occurs particularly under long drastic drought (Rhodes and Hanson 1993).

The extent of accumulation of proline in four tobacco cultivars correlated positively with their drought tolerance (van Rensburg *et al.* 1993). Ultrastructural investigations showed that drought-tolerant cultivars mobilised during water deficit the storage of starch more than the drought-sensitive cultivars.

When photosynthesis is inhibited, as it is at low water content, the radiant energy absorbed by the plant can exceed the level that this process is capable to dissipate in an orderly fashion. This results in excess excitation energy with potentially photoinhibitory effects (Biehler and Fock 1996). One of the principal mechanisms employed by plants to prevent or alleviate damage to the PSA is non-photochemical Chl fluorescence quenching (q_N) (Krause and Weis 1991, Ruban and Horton 1995). In this mechanism excess radiant energy is dissipated as heat in the light-harvesting antenna of PS2. This dissipation is under complex influence of photosynthetic events at the chloroplast level and it is primarily controlled by the trans-thylakoid pH gradient, ΔpH (Gounaris *et al.* 1984, Al-Khatib and Wiest 1990).

Deltoro *et al.* (1998) suggest that desiccation induces a Zx+Ax-mediated photoprotective mechanism in *Frullania dilatata* (desiccation intolerant). They propose that when CO_2 fixation and therefore ATP consumption are decreased at low RWC, the functioning electron flow gives rise to an acidification of the thylakoid lumen that induces Zx and Ax syntheses. The interaction of lumen acidity with de-epoxidised xanthophylls enhances q_N at low RWC. This model is consistent with the postulated function of de-epoxidised xanthophylls in the modulation of thermal energy dissipation (Demmig-Adams and Adams 1992) and with the requirement of a pH gradient for Zx synthesis and other forms of PS2 regulation involved in photoprotection (Bratt *et al.* 1995, Ruban and Horton 1995). The photoprotective process results in the diversion of energy away from the reaction centres (Adams and Demmig-Adams 1995, Ruban and Horton 1995). This pre-emptive avoidance mechanism aids photosynthetic recovery when water becomes available to plants, since it helps to prevent irrevocable damage to the photosynthetic apparatus during desiccation. The larger xanthophyll pool, in addition to the ability to form higher concentrations of Ax+Zx, would be consistent with a larger requirement for dissipation of absorbed photons (Logan *et al.* 1996). There are, however, experimental results that do not support the statement that xanthophyll cycle plays a major or specific role in the direct energy dissipation of absorbed radiant energy. Schindler and Lichtenthaler (1994) demonstrated by kinetic measurements of leaves of maple and *aurea* tobacco that Zx accumulation and the decline in F_v and F_v/F_m ratio under high irradiance (1000-2000 μmol m^{-2} s^{-1}) are not linearly correlated. The strongest decline in F_v parameters occurred only after 10 min (while Zx formation proceeds within 2 to 5 min) of irradiation, and was associated with only minor changes in Zx content. Thus under such conditions Zx formation and loss of Chl fluorescence are two independent high irradiance driven processes and the protective effect is more probably due to a separation of the LHC2 from RC of PS2 by the formed Zx. The presumed function of Zx in energy dissipation may be of the secondary order (Horton and Ruban 1992, Ruban *et al.* 1992).

Besides the above-mentioned mechanisms of energy dissipation, there are also other ways. For example, the energy dissipation at closed stomata can occur *via* ATP and NADPH, which are used for other metabolic processes, and they are obviously important mechanisms of tolerance and protection against water stress and photooxidative damage (Lichtenthaler 1996).

Concluding remarks

The literature analysed in this review shows the complexity of drought tolerance and supports the statements of many authors that the flexibility of cell metabolism and its fast acclimation to changes in environmental conditions is a first essential step in stress avoidance. The wider the range of adaptation capacity of plants, the better they are protected against various stresses. The changes in program of plant development are always associated with changes in their physiological program and activity. Drought affects photosynthetic mechanisms at both photochemical and biochemical (metabolic) levels. Stomatal control explains most of the observed decrease in leaf photosynthesis in plants submitted to mild drought. Changes in the complement of proteins and lipids also occur in thylakoid membranes of plants exposed to drought. Cytokinin induced stimulation of protein synthesis substantially alleviates the negative effects of water deficit on plants (Chernyadev 1997).

In spite of intensive investigation of the problem of drought, many of its aspects remain to be explored. Water deficit induces expression of particular genes and this is associated in most cases with adaptive responses of stressed plants. The functions of many of them are still not established. Therefore the main research challenge is to identify key stress responsive proteins, which one among the hundreds of proteins induced by stress provides stress resistance. As Ingram and Bartels (1996) mentioned, one of valuable approaches may be to identify the metabolic steps that are most sensitive to drought. Such approach can at least begin to elucidate which gene products are of primary importance.

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