РЕАКЦИИ НА РАСТЕНИЯТА КЪМ ЗАСУШАВАНЕ – МОЛЕКУЛЯРНА БИОЛОГИЯ, ФИЗИОЛОГИЯ И АГРОНОМИЧЕСКИ АСПЕКТИ

DROUGHT STRESS RESPONSES IN PLANTS – MOLECULAR BIOLOGY, PHYSIOLOGY AND AGRONOMICAL ASPECTS

Иван Йорданов[1], Детелин Стефанов[2], Василена Кръстева[2], Мария Гурманова[2], Василий Голцев*[2]
Ivan Yordanov[1], Detelin Stefanov[2], Vasilena Krasteva[2], Maria Gourmanova[2], Vasilij Goltsev*[2]

[1]Институт по физиология на растенията и генетика, Българска академия на науките, София 1113, България
Катедра по биофизика и радиобиология, Биологически факултет, Софийски университет „Св. Климент Охридски”, бул. „Драган Цанков” 8, 1164 София, България
[1]Institute of Plant Physiology and Genetics, Bulgarian Academy of Sciences, Sofia 1113, Bulgaria
[2]Department of Biophysics and Radiobiology, Faculty of Biology, *St. Kliment Ohridski* University of Sofia, 8, Dragan Tzankov Boulevard, 1164 Sofia, Bulgaria

Email: goltsev@biofac.uni-sofia.bg

Резюме

Абиотични фактори на средата, като засушаването, високата степен на засоляване, ектремните температури и химичното замърсяване, представляват сериозна заплаха за селското стопанство и водят до влошаване на условията на средата, в която се развиват растенията. Засушаването като стресов фактор се свързва с парниковия ефект, причинен от глобалното замърсяване на атмосферата. То е един от най-неблагоприятните стресови фактори, повлияващи биологията на растенията. Засушаването може да повиши засоляването на почвите на земята. Изясняването на физиологичните, биохимичните, биофизичните и молекулярнобиологичните отговори на растенията, които са обект на засушаване, е от важно значение за разбирането на механизмите, повишаващи резистентността към воден дефицит. Растенията, подложени на засушаване, използват широк спектър от промени в генната експресия и промени в клетъчния метаболизъм, водещи до промени в скоростта на растежа и добивите. Настоящият обзор е посветен на разглеждане на съвременните схващания за отговора на растенията на засушаването от ефектите на молекулярно ниво до екологични аспекти на засушаването.

Abstract

Abiotic stress factors, such as drought, high salinity, extreme temperatures and chemical pollution, are a serious threat to agriculture and lead to deterioration of the environmental conditions. Drought, which is connected to the greenhouse effect and caused by the global atmosphere pollution, can lead to high soil salinity worldwide. Drought is one of the most unfavourable environmental stress factors for the plants. The clarification of the physiological, biochemical, biophysical and molecular responses of the plants subjected to drought stress is of major importance for the understanding of the mechanisms plants use to increase their resistance to water deficit. Plants under drought stress employ a wide range of responses, from changes of the gene expression and cell metabolism to changes in both growth and yield rates. This is a review of the current knowledge of plant responses to water deficiency from molecular to ecological levels.

Ключови думи: засушаване, фотосинтеза, стрес, възкръсващи растения, хлорофилна флуоресценция.
Key words: drought, photosynthesis, resurrect plants, chlorophyll fluorescence.

Съкращения: 1-qP: налягане на възбуждането върху ФС2; A: скорост на фотосинтезата; ABA: абсцисиева киселина; ABS/CSm: поток абсорбирани фотони на реакционен център; A_{pot}: фотосинтетичен метаболитен потенциал; C_c: концентрация на CO_2 в хлоропласта; Chl: хлорофил; C_i: вътреклетъчна концентрация на CO_2; DF: забавена флуоресеценция; DGDG: дигалактозилдиацилглицерол; DW: сухо тегло; E: средно дневно изпарение; Fv/Fm (=φ_{Po}): максимална ефективност на PS II; φ_{Po}: максимален квантов добив на PSII; g_s: устична проводимост за CO_2; GSSG and GSH: окислен и редуциран глутатион; g_w: листна проводимост за водни пари; k_P/k_N: отношение на константите на фотохимични към нефотохимични процеси по време на фотосинтезата; M_d: маса на напълно изсушени листа;

MDA: малон диалдехид; M_f: свежо тегло на листа; MGDG: моногалактозилдиацилглицерол; M_t: маса на рехидратиран лист; MR: отразена модулирана светлина при 820 nm; NPQ: нефотохимично гасене; OEC: кислород-отделящ комплекс; P: тургорно налягане; PF: бърза флуоресценция; PSI and PSII: фотосистема 1 и 2; ψ: воден потенциал; π: осмотичен потенциал; RCs: фотосинтетични реакционни центрове; RC/CSm: активни реакционни центрове на единица напречно сечение; RuBP: рибулозобифосфат; ROS: активни кислородни форми; RWC: относително водно съдържание; SOD: супероксиддисмутаза; T: тотална транспирация на единица площ по време на растеж до прибиране на реколтата; TFs: транскрипционни фактори; Tmax: средно дневно изпаряване по време на растеж до прибиране на реколтата; TRo/CSm: уловен енергиен поток на единица напречно сечение; TR_0/RC: ефективност на улавянето на един реакционен център; t: потенциал, обусловен от междуклетъчното съдържимо; UV: ултравиолетова светлина; Vj: относителна вариабилна флуоресценция в точка J от индукционната крива на флуоресценцията; WUE: ефективност на използване на водата; Y: тотално сухо вещество на единица листна площ.

Abbreviations: 1-qP: excitation pressure on PSII; A: photosynthetic rate; ABA: abscisic acid; ABS/CSm: absorption flux per excited cross section; A_{pot}: photosynthetic metabolic potential; C_c: chloroplast CO_2 concentration; Chl: chlorophyll; C_i: intercellular CO_2 concentration; DF: delayed fluorescence; DGDG: digalactosyl diacyl glycerol; DW: dry weight; E: mean daily evaporation; Fv/Fm ($=\varphi_{Po}$): the maximal efficiency of PS II; $_{Po}$: maximal PSII quantum yield; g_s: stomatal conductance to CO_2; GSSG and GSH: oxidized and reduced glutathione; g_w: leaf conductance for water vapor; k_P/k_N: ratio photochemistry to nonphotochemistry constants; M_d: the mass after drying by removing all water; MDA: malonaldehyde; M_f: the mass of fresh plant material; MGDG: monogalactosyl diacyl glycerol; M_t: the mass when the material is fully hydrated; MR: modulated light reflection at 820nm; NPQ: non-photochemical quenching; OEC: oxygen evolving complex; P: turgor pressure; PF: prompt fluorescence; PSI and PSII: photosystem I and II, respectively; ψ: water potential; π: osmotic potential; RCs: photosynthetic reaction centers; RC/CSm: active RCs per CS; RuBP: ribulose bisphosphate; ROS: reactive oxygen species; RWC: relative water content; SOD: superoxide dismutase; T: total transpiration per area during growth to harvest; TFs: transcription factors; Tmax: mean daily free water evaporation for the same period; TRo/CSm: trapped energy flux per CS; TR_0/RC: trapping efficiency per reaction center; τ: matrix potential; UV: ultraviolet light; Vj: relative variable fluorescence at the J-step; WUE: water-use efficiency; Y: total dry matter mass per area.

1. Water and plants

Water is indispensable factor ensuring life on the Earth. The importance of water molecule for biosphere comes from its anomalous properties resulting from its dipole nature. Such dipole nature of low molecular weight water molecule ensured its liquid state because a high degree of cohesion and low viscosity that is originated from H-bonds (Schulze et al., 2005). Water facilitates many vital biological reactions by being a solvent, a transport medium and evaporative coolant (Bohnert et al., 1995). Dielectric constant of water allowed excellent salvation for mineral salts. Thus mineral ions needed for plant growth become available for metabolic uptake in the growing regions of all organs. Water is important environmental factor as a very effective heat buffer for organisms, ensuring freezing avoidance and transpiration cooling in plants (Schulze et al., 2005). Water does not interfere with photosynthesis in plants because of their radiation absorption – water does not absorb visible light.

The state of water could be simply described by **water potential**, ψ, a measure of energy required for to remove water molecules from any water containing system (measure of a difference in the chemical potentials, i.e. as a difference in free energy). The water potential tells us about the tendency of the water to move one direction or another. For historical reasons, the units used are those of pressure, pascals (Pa), which are dimensionally the same as free energy units, Jm^{-3} (Kramer and Boyer, 1995). Water potential in plant cell consist several components (Schultze et al., 2005):

$$(-)\psi = (-)\pi + (-)\tau + P \qquad (1)$$

where π is **osmotic potential**, τ is **matrix potential** and P (involving cell wall and tissue pressure, i.e. **turgor pressure**). In hydrated cell τ is zero, while in desiccated cells when water remains bound to cellular and subcellular components only. Water constitutes some 85~90% of the growing tissues of planes, and 5-15% of the mass of seeds (Grace, 1997). Simply the state of water in plants could be described as **relative water content**, RWC, i.e. the percentage of maximum water content that the tissue is capable of holding (Grace, 1997):

$$RWC= 100(M_f - M_d)/(M_t - M_d) \qquad (2)$$

Where M_f is the mass of **the fresh plant material**, M_t, is the mass when **the material is fully hydrated** by being placed in water in the dark until no further water can be absorbed (such a leaf is said to be fully turgid) and M_d is **the mass after drying by removing all water** in an oven at a reference temperature, often 80°C.

The relationship between the water potential and the water content is very important (Grace, 1997). As the leaf loses water, the cells reduce in volume and the solutes become more concentrated. At the same time, the pressure excreted by the walls declines. The relationship between the water potential and the water content differs markedly between species, and may influence the ecological range of the species. A **mesophyte plant** (a plant unable to grow in dry places) may show a small decline in water potential during decline in relative water content, but a xerophyte, normally growing in dry places shows a relatively large decline whilst still maintaining a positive turgor. Thus, **the xerophyte** is more able to extract water from the soil.

The main processes involving in adaptation of land plants to dry environment are generalized by Grace (1997) as follows: 1) highly reflective leaf surfaces; 2) stomata sunk into wells, or positioned within invaginations after leaf rolling; 3) reductions in leaf area per mass of plant; 4) leaves reduced in size; deep roots, or a large mass of root per mass of shoot; 5) modifications of stem or root to form water-storage organs; 6) ability to shed leaves during the driest periods to avoid water deficits; 7) diversity between **annual** and **perennial** plants;

Molecular biology of drought stress shows that it is unrealistic to consider that there is a single "gene for drought tolerance" because the plant response to drought is complex and diverse (see 4.6. and for reviews see Alpert and Oliver, 2002; Levitt, 1980; Walters et al., 2002).

2. Stress concept

The term **"plant stress"** is used by most authors in a very broad sense which justifies the establishment of unifying concept of plant stress. The original general stress for living organisms was developed by H. Selye (1936, 1956). Later Larcher (1987) summarized the stress concept of plants. He stated that the "every organism experiences stress although the way which it is expressed differs according to its level of organization. From the botanical point of view, he formulate stress as "state in which increasing demands made upon a plant leaf to an initial destabilization of functions, followed by normalization and improved resistance" and also "if the limit of tolerance are exceeded and the adaptive capacity is overworked, the result may be permanent damage or even death". According to Larcher (1987) stress contains both destructive and constructive elements and also stress is a selection factor as well as a driving force for improved resistance and adaptive evolution. The researchers differentiated tree phases of stress: reaction – immediately after its beginning, when the catabolism exceed anabolism; restituting or the phase of recovery and hardened.

Lichtenthaler (1988) extended the stress concept of plants by differentiating between **eu-srress** and **dis-stress**, in which case 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 has a negative effect on the plant and its development. A mild stress may activate cell metabolism, increase the physiological activity of plant, and does not cause any damaging effects even at long duration.

Strasser and coauthors (Tsimilli-Michael et al., 1996) developed an idea that the adaptation of plants to a continuously changing environment is approached as an expression of an **optimization strategy, dictated by the thermodynamic demand for minimal entropy production**. A logic bridge between the theoretical predictions of open system thermodynamics and the phenomenology of experimentally investigated aspects of the behavior of plants is established, in terms of the **JKB-Trilogy,** and further applied for the PS II of the photosynthetic apparatus. **Any living system is an open system**, with a complex structure, that functions as energy convertor. The actual performance of the system at a given time has been described by as determined by three terms (Strasser, 1988, pp. 333-337):

J - All energetic inputs,

K - Constellation of structural-conformational parameters that determine kinetic pathways for energy conservation and dissipation. This corresponds to the biochemical inventory and the conformation, i.e. to the hardware of the system and it is, therefore, an extensive parameter.

B - The established relative level of the energy flow through the system. B is an intensive parameter and can be regarded as an expression of the behavior of the system.

The chlorophyll *a* fluorescence kinetics, analyzed according to the theory of energy fluxes in biomembranes, lead to a constellation of structural and functional parameters, thus providing a quantification of the system behavior (Tsimilli-Michael et al., 1996).

There are various abiotic environment stresses that plants are subjected at natural conditions: water deficit stress, heat stress, salt and osmotic stress, oxidative stress, low temperature stress (cold and freezing), heavy metal stresses, as well as various combinations from these stresses.

3. Drought stress – mechanisms, types stress reactions, adjustments

3.1. Drought and desiccation

Water losses, i.e. dehydration could be considered as 'drought' and 'desiccation'. Hoekstra et al. (2001) are distinguished them on the basis of the critical water level. The tolerance to moderate dehydration can be considered as 'drought tolerance'. **Drought** is characterized with moisture content below which there is no bulk cytoplasmic water present [~23% water on a fresh weight basis, or $\sim 0.3 gH_2O.g_{DW}^{-1}$]. **Desiccation** generally refers to the tolerance of further dehydration, when the hydration shell of molecules is gradually lost.

3.2. Ecological classification of plants based to their adjustment to environment with different moisture

Plants dispose with great ability to spread in various water environments. On this base, plant could be classified by their adjustment to water quantity (Lambers et al., 2008). **Mesophyte** plant that typically grows without severe moisture stresses. **Hydrophyte** plants grow partly or wholly in water, while **hygrophyte** species typically occurring on permanently moist sites. **Xerophyte** plant that typically grows in dry environments. Other plants that are typical for dry environments are **succulent plant** with tissue of high degree of succulence. Succulence is thick fleshy state of herbaceous tissues due to high water content. It might seem that succulence could evolve with a few simple modifications such as increasing the volume of cortex and pith, reducing leaf size and number, and establishing mechanisms (spines or poisons) that protect stored water (Mauseth, 2004). Some desert plants, known as **phreatophytes**, produce extremely deep roots that tap the water table (Lambers et al., 2008). These plants generally have high rates of photosynthesis and transpiration with little capacity to restrict water loss or withstand drought. The representative group of 'true' desiccation tolerant plants in the sense of Hoekstra's and collaborators classification is so-called **'resurrect plants'.** Resurrection plant withstands complete dehydration and resumes functioning upon rehydration (Gaff ,1971). In opposite to typical vascular (**homoiohydric**) plants resurrection ones are defined as poikilohydric (for review see Scott, 2000; Proctor and Tuba, 2002; Bernacchia and Furini, 2004). **Poikilohydric plants** or plant parts (seeds, pollen) that can dry out without losing their capacity to function upon rehydration (Lambers et al., 2008). There are two strategies among **resurrection angiosperms**: 1) Those that lose chlorophyll and break down their chloroplasts upon drying (**poikilochlorophyllous**); 2) Those that retain some or all of their chlorophyll and chloroplast ultrastructure (**homoiochlorophyllous**).

3.3. Physical geography based classification of the types of drought

It is also possible to define drought as a natural event that causes negative effect on land, water resources and hydrological balance as a result of rain falling below the normal levels. Drought types are classified as: meteorological, agricultural, hydrologic and physiologic drought (Sade et al., 2011).

Meteorological drought is defined as the deviation of values from normal rainfall for a specific period (at least 30 years). These definitions are usually territorial and based on understanding of the regional climatology. **Agricultural drought** is defined as the absence of water needs of plant, seen during limitation of water resources and in moisture periods. In this kind of drought, falling period is more important than amount of precipitation. **Physiological drought** is defined as a state of water expressed by the water content limiting the plant production in the soil root zone. The expression physiological drought seems to be a better characteristic to specify the water deficiency for plants. During physiological drought, plant cannot use water in the soil because of the unsuitable formation.

4. Physiological and structural changes under drought

The plant response to stress involves complex network of reactions including changes in their macro- and microstructure, adjustment in plant metabolism and various physiological responses on different level of organization – cell, membrane, hormonal etc.

4.1. Drought stress and reactive oxygen species induced damages

Reactive oxygen species (ROS) can occur as by-products of regular cellular metabolism such as in photosynthesis. Stresses such as drought lead to their accelerated formation. Under water deficit conditions the main sites of ROS production in the plant cell are chloroplasts, mitochondria and microbodies (Mundree et al., 2002). In general, ROS (particularly superoxide and hydroxyl radicals) are damaging to essential cellular components such as DNA, proteins and lipids (Sudo et al., 2011). Plants have evolved complex protective mechanisms to prevent the damage initiated by free radicals. It includes antioxidant enzymes such as superoxide dismutase, catalases and peroxidases, and free radical scavengers such as carotenoids, ascorbate, tocopherols and oxidized and reduced glutathione (GSSG and GSH, respectively) (Price et al., 1994). However, in periods of more severe stress in desiccation-sensitive plants, the scavenging system becomes saturated by the increased rate of radical production, and damage is inevitable (Mundree et al., 2002).

4.2. Drought stress ion homeostasis and osmoprotectants

Drought and salinity impose an osmotic stress on plants by decreasing the chemical activity of water and causing loss of turgor within the cell (for review see Mundree et al., 2002). High intracellular concentrations of chloride and Na^+ ions are toxic to cell systems because they interfere with the hydrophobic-electrostatic forces which assist molecules to maintain their native state. Ion transporters create cell turgor, which is facilitated by high K^+. The generation of electrochemical gradients across membranes energizes the active transport of nutrients and ions into the cytoplasm, using membrane-bound H^+-co-transporters. The plant vacuole primarily maintains cellular turgor pressure along with other functions such as giving the cell shape and rigidity, increasing the cellular surface area to facilitate efficient photosynthesis and absorption of nutrients and storage of various compounds such as sugars, polysaccharides, organic acids, amino acids, pigment compounds and compounds that could be toxic to the cell if released into the cytoplasm (Taiz, 1992). The vacuole also plays a vital role in maintaining ion homeostasis between itself and the cytoplasm.

One of the mechanisms that plants use to combat the detrimental effects of water loss is to synthesize compatible solutes, such as polyols, sugars, amino acids, betaines and related compounds (Bohnert et al., 1996; Ramanjulu and Bartels, 2002). By definition compatible solutes are synthesized in response to osmotic stress and can occur at high intracellular concentrations without hindering normal cellular metabolism (Ramanjulu and Bartels, 2002). The properties of compatible solutes facilitate the maintenance of favorable turgor pressure during water stress and in addition may serve as protective agents by stabilizing proteins (Carpenter et al., 1990). Compatible solutes have also been shown to function as free radical scavengers, protecting DNA from the damaging effects of reactive oxygen species (Akashi et al., 2001).

4.3. Aquaporins

The capacity of **aquaporins** to transport small neutral solutes and/or gases, in addition to water, has raised the intriguing possibility that aquaporins may work as membrane channels with multiple functions (Tyerman et al., 2002) including their participation in drought stress response. Aquaporins exhibit a typically conserved structure with six membrane spanning domains linked by three extra- and two intracellular loops, the N- and C-terminal tails of the protein bathing in the cytosol (Fujiyoshi et al., 2002). The main aquaporin function is the dynamic control of the water permeability of plant cells and organs (Luu and Maurel, 2005). Such control occurs during development but also in response to external stimuli. In particular, plants can experience environmental conditions that are very challenging for their water status.

4.4. Drought stress and lipids

Along with proteins, lipids are the most abundant components of membranes and they play a role in the resistance of plant cells to environmental stresses (Kuiper, 1980; Suss and Yordanov, 1986). Strong water deficit leads to disturbance of the association between membrane lipids and proteins as well as to a decrease in the enzyme activity and transport capacity of the bilayer (Caldwell and Whitman, 1987; Poulson et al., 2002).

Drought stress provoked considerable changes in lipid metabolism such as *Brasica napris.* Strong drought stress results in a profound overall drop in MGDG/DGDG declined 3-fold while the relative part of MGDG was 12-fold lower (Benhassaine-Kesri et al., 2002).

4.5. Effects of hormones on desiccation tolerance

Abscisic acid (ABA) is known to be involved in the response to osmotic stress. ABA has been proposed to be an essential mediator in triggering plant responses to drought, salinity, and cold stresses. Endogenous ABA levels have been reported to increase as a result of water stress, and ABA induces stomatal closure in guard cells by activating Ca^{2+}, potassium (K^+), and anion channels (Leung and Giraudat, 1998). At present other plant hormones are considered as indirectly effectors to drought stress response.

4.6. Drought stress responsive gene expression

The physiological and biochemical changes in plants under particular stress conditions are related to altered gene expression. Onset of a stress triggers some (mostly unknown) initial sensors, which then activate cytoplasmic Ca^{2+} and protein signaling pathways, leading to stress-responsive gene expression and physiological changes (Bressan et al., 1998; Xiong et al., 2002). Responses to abiotic stress require the production of important metabolic proteins such as those involved in synthesis of osmoprotectants and of regulatory proteins operating in the signal transduction pathways, such as kinases or transcription factors, TFs. Given that most of these responses imply control of gene expression, TFs play a critical role in the abiotic stress response (Chaves and Oliveira, 2004). TFs are proteins with a DNA domain that binds to the *cis*-acting elements present in the promoter of a target gene. They induce (activators) or repress (repressors) the activity of the RNA polymerase, thus regulating gene expression. TFs can be grouped into families according to their DNA-binding domain (Riechmann et al., 2000). A group of genes controlled by a certain type of TF is known as a regulon. In the plant response to abiotic stresses, at least four different regulons can be identified: (1) the CBF/DREB regulon; (2) the NAC (NAM, ATAF and CUC) and ZF-HD (zinc-finger homeodomain) regulon; (3) the AREB/ABF (ABA-responsive element-binding protein/ABA-binding factor) regulon; and (4) the MYC (myelocytomatosis oncogene)/MYB (myeloblastosis oncogene) regulon. The first two regulons are ABA independent, and the last two are ABA dependent. It is explained below how these regulons are controlled and how TFs may be involved in the regulation of photosynthesis as a response to abiotic stress.

The emerging view of the salt-and drought-signaling network unequivocally supports a key and integrative function of members of the bZIP TFs in these regulatory networks (Golldack et al., 2011) and the potential of these factors to confer enhanced stress tolerance has been demonstrated repeatedly. A key regulator of salt stress adaptation, the group F bZIP TF bZIP24, was identified by differential screening of salt-inducible transcripts in *A. thaliana* and a halophytic *Arabidopsis*-relative model species (Yang et al., 2009).

Involvement of WRKY factors in plant salt adaptation was shown for WRKY25 and WRKY33 that increased salt tolerance (Jiang and Deyholos, 2009). In *A. thaliana*, wrky63 knock out mutants showed decreased sensitivity to ABA and drought (Ren et al., 2010). In these plants, the stomata closure and the expression of the AREB1/ABF2 TF were affected indicating involvement of WRKY factors in the ABA-dependent pathway of drought and salt adaptation (Ren et al., 2010).

NAC type proteins are not only involved in diverse processes as developmental programs, defense, and biotic stress responses (Olsen et al., 2005) but they also have a key function in abiotic stress tolerance inclusive drought and salinity. Thus, in rice ONAC5 and ONAC6 are transcriptionally induced by ABA, drought, and salt stress (Takasaki et al., 2010). ONAC5 and ONAC6 transcriptionally activate stress-inducible genes as OsLEA3 by direct binding to the promoter and they interact *in vitro* suggesting functional dimerization of these TFs (Takasaki et al., 2010). Interestingly, members of the NAC TF family are potential regulatory targets of the small RNA (miRNA) posttranscriptional silencing machinery (Rhoades et al., 2002; Guo et al., 2005).

5. Morphological adaptations to drought

Water deficit induces many morphological changes in desiccation-tolerant vascular plants, the most obvious of which is leaf folding. The folding of leaves during drying is not unique to resurrection plants and also occurs in desiccation-sensitive plants. Leaves of the desiccation-tolerant dicot *C. wilmsii*, which are fully expanded when watered, progressively curl inward during drying and become tightly folded so that only the abaxial surfaces of the older leaves in the outer whorl are exposed to the sun (Sherwin and Farrant, 1998). Leaf folding is thought to limit oxidative stress damage from UV radiation, and is an important morphological adaptation for surviving desiccation. Indeed, *C. wilmsii* plants do not survive desiccation in sunlight if the leaves are mechanically prevented from folding (Farrant et al., 2003).

In the desiccation-tolerant grass *S. stapfianus*, the leaf adaxial side, which is most exposed to sun radiation, is very rich in epicuticular waxes, whose main function is probably to reûect light, and to limit irradiation and heating of leaf tissues (Dalla Vecchia et al., 1998). During dehydration, this cuticular wax covering, together with the closure of stomata, helps to decrease the rate of water loss. This may also be an important protective mechanism for the thylakoid membranes, which are maintained in the chloroplasts and are particularly sensitive to light damage in water stress (Dalla Vecchia et al., 1998).

6. Photosynthesis and drought stress

Plant growth is affected by drought considerably before effects on photosynthesis are observed (Nonami and Boyer, 1990). The inhibition of photosynthesis in drought-stressed leaves is often relieved when these leaves are exposed to very high CO_2 concentration (e.g., Cornic et al., 1989) it is widely held that the photosynthetic apparatus is resistant to drought (Cornic and Massacci, 1996). However, when RWC falls below 70%, a cascade of physiological processes can be affected resulting in irreversible or slowly reversible damage to the photosynthetic apparatus (e.g., Kaiser, 1987; Cornic and Massacci, 1996). The occurrence of mild drought stress (i.e., RWC 70%) is the most common circumstance in nature (Smith et al., 2004).

Drought decreases photosynthetic rate, A, via decreased stomatal conductance to CO_2, g_s, and photosynthetic metabolic potential, A_{pot} (Lawlor and Tezara, 2009). Photosynthetic rate decreases as g_s falls. Low light during growth and drought did not impaired photosynthesis, but at high light an inhibition was observed (Lawlor and Tezara, 2009). At a given intercellular CO_2 concentration (C_i) A decreases, showing impaired metabolism (A_{pot}). The C_i and probably chloroplast CO_2 concentration (C_c), decreases and then increases. Photosystem activity is unaffected until very severe drought stress (Lawlor and Tezara, 2009). In intact leaves, redox poising of the electron transport chain in favor of Fd-dependent cyclic electron flow is created at reduced concentrations of oxygen and carbon dioxide (Bukhov and Carpentier, 2004). In nature, such situation is often observed under drought stress, which causes stomata closure (Wu et al., 1991). This provides preferential involvement of cyclic electron transport to the energization of the thylakoid membrane and, consequently, to the control of PSII photochemistry (Katona et al., 1992). Involvement of NAD(P)H dehydogenase into cyclic electron transport under conditions of moderate water stress cannot, however, be ruled out (Bukhov and Carpentier, 2004). The involvement of PSI-driven reactions in response to increased salinity seems more obvious in cyanobacteria and eukaryotic algae than in higher plants since the chloroplastic compartment in unicellular organisms is directly involved into cell defense against stress (Bukhov and Carpentier, 2004). Low A, together with photorespiration, which is maintained or decreased, provides a smaller sink for electron transport, causing overenergization of energy transduction. Despite increased non-photochemical quenching (NPQ), excess energy result in generation of ROS. Decreased ATP limits RuBP production by the Calvin cycle and thus A_{pot}. Rubisco activity is unlikely to determine A_{pot}. Sucrose synthesis is limited by lack of substrate and impaired enzyme regulation. With drought, photorespiration decreases relative to light respiration, and mitochondria consume reductant and synthesise ATP.

In contrast to C3 photosynthesis, the response of C4 photosynthesis to drought stress has been less well studied (Ghannoum, 2009). The key feature of C4 photosynthesis is the operation of a CO_2-concentrating mechanism in the leaves, which serves to saturate photosynthesis and suppress photorespiration in normal air. C4 photosynthesis is highly sensitive to drought stress. With declining leaf water status, CO_2 assimilation rate and stomatal conductance decrease rapidly and photosynthesis goes through three successive phases (Ghannoum, 2009). The initial, mainly stomatal phase may or may not be detected as a decline in assimilation rates depending on environmental conditions. This is because the CO_2-concentrating mechanism is capable of saturating C4 photosynthesis under relatively low intercellular CO_2 concentrations. This is followed by a mixed stomatal and non-stomatal phase and, finally, a mainly non-stomatal phase. The main non-stomatal factors include reduced activity of photosynthetic enzymes; inhibition of nitrate assimilation, induction of early senescence, and changes to the leaf anatomy and ultrastructure. Elevated CO_2 concentration alleviates the effect of water stress on plant productivity indirectly via improved soil moisture and plant water status as a result of decreased stomatal conductance and reduced leaf transpiration. It is suggested that there is a limited capacity for photorespiration or the Mehler reaction to act as significant alternative electron sinks under water stress in C4 photosynthesis. This may explain why C4 photosynthesis is equally or even more sensitive to water stress than its C3 counterpart in spite of the greater capacity and water use efficiency of the C4 photosynthetic pathway (Ghannoum, 2009).

CAM photosynthesis is closely related with succulence. Moreover, resurrect plant strategy to avoid drought stress is closely related with CAM metabolism, because many resurrect plants are CAM plants (Markovska et al., 1997), as well.

7. The poikilohydric strategy and photosynthesis during drought stress.

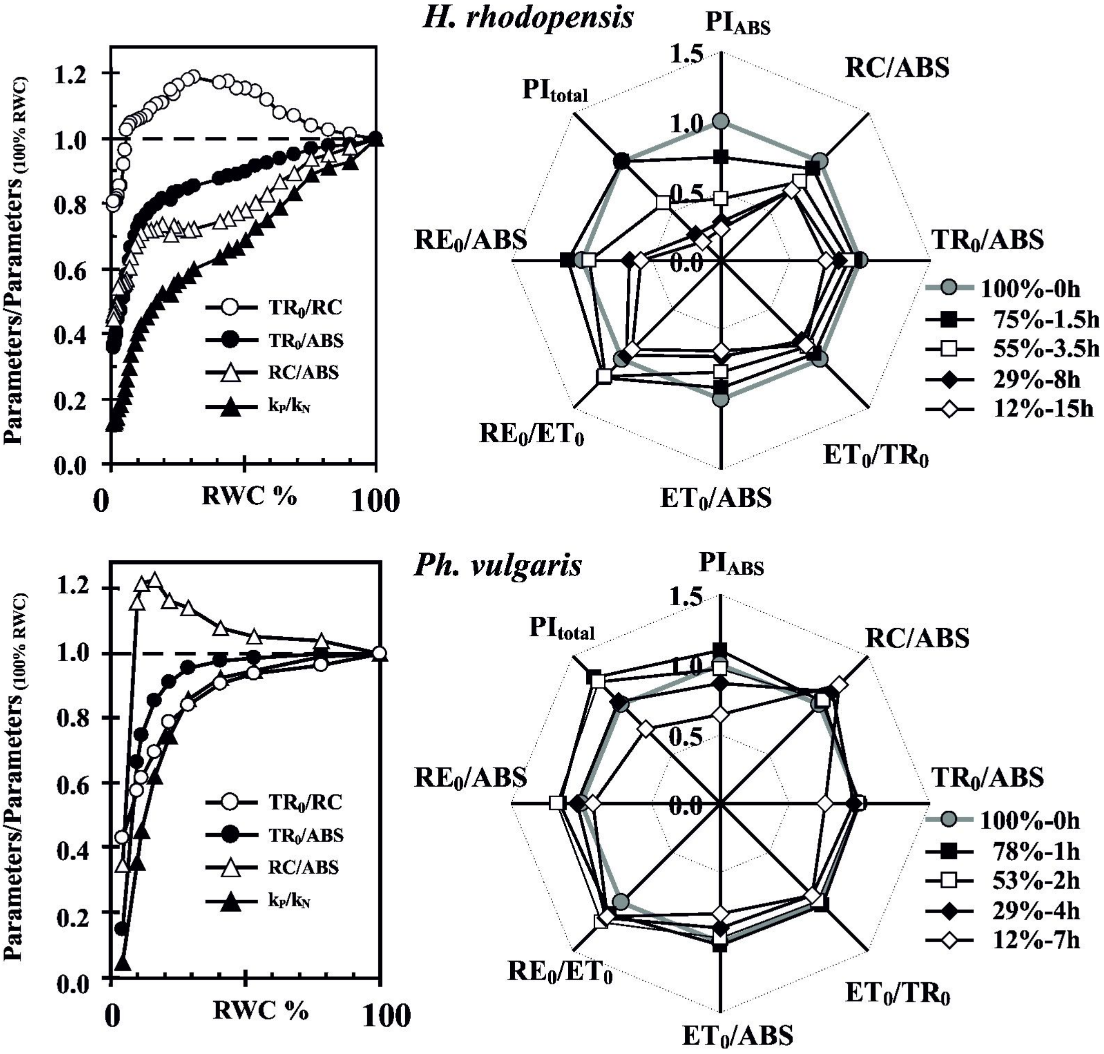
Poikilohydric plants can gain and lose water rapidly, and there is no control over water loss comparable to that in vascular plants (Proctor and Tuba, 2002). On rehydration, essentially normal metabolism returns within minutes or hours. The response of photosynthesis to cell water content appears to be substantially the same as in vascular plants (Proctor and Tuba, 2002 and references therein).

It was found that air-dried *H. rhodopensis* leaves could preserve up to 80% of their chlorophylls (Kimenov and Jordanov, 1974; Markovska et al., 1994). On this basis, *H. rhodopensis* is considered as a homoiochlorophyllous species that is able to retain its photosynthetic apparatus and chlorophylls in a recoverable form upon drought stress (Proctor and Tuba, 2002).

Haberlea expresses the ability for full recovery of photosynthesis after rehydration. Georgieva et al. (2005, 2007) showed that water loss influences fluorescence induction, thermoluminescence emission, far-red induced P700 oxidation and oxygen evolution in the leaves of *H. rhodopensis*. Moreover, all these parameters nearly returned to the control levels within a few days after rehydration. *Haberlea rhodopensis* shows a low rate of leaf net CO_2 uptake (4–6 $\mu molm^{-2}\ s^{-1}$) under saturating photosynthetic photon flux densities in normal air (Peeva and Cornic, 2009). Enhanced CO_2 uptake at saturating CO_2 and light lead to assumption that *H. rhodopensis* leaves has a very low mesophyll CO_2 conductance. Peeva and Cornic (2009) concludes that the main advantage of *H. rhodopensis* leaf in drought conditions is related to possibility of Haberlea leaf cells to avoid mechanical stress.

The changes in the CO_2 assimilation rate, chlorophyll fluorescence parameters, thermoluminescence, fluorescence imaging and electrophoretic characteristics of the chloroplast proteins were measured in control, moderately dehydrated (50% water content), desiccated (5% water content) and rehydrated plants (Georgieva et al., 2007). During the first phase of desiccation the net CO_2 assimilation decline was influenced by stomatal closure. Further lowering of net CO_2 assimilation was caused by both the decrease in stomatal conductance and in the photochemical activity of Photosystem II. Severe dehydration caused inhibition of quantum yield of PSII electron transport, disappearance of thermoluminescence B band and mainly charge recombination related to $S_2Q_A^-$ takes place.

On the basis of chlorophyll fluorescence analysis (see Strasser et al., 2004; Tsimilli-Michael et al., 2008; Strasser et al., 2010), the drought induced reaction of photosynthetic machinery could be monitored in *in vivo* plant systems. Using parameters of JIP-test (Strasser et al., 2004) a comparison between the strategies of photosynthetic machinery adaptation to low water content in detached leaves of desiccation-tolerant plant *Haberlea rhodopensis* and in drought-sensitive bean plant (*Phaseolus vulgaris*) was carried out. A new instrument (M-PEA), which measures simultaneously kinetics of prompt fluorescence (PF), delayed fluorescence (DF) and modulated light reflection at 820 nm (MR), was used to screen dark-adapted leaves of the resurrection plant *Haberlea rhodopensis* during their progressive drying, down to 1% relative water content (RWC), and after their re-watering. The results suggest that the desiccation tolerance of the photosynthetic machinery in *H. rhodopensis* is mainly based on mechanism(s) that lead to inactivation of photosystem II reaction centres (transformation to heat sinks), triggered already by a small RWC decrease. In details, detached *Haberlea* leaves (Fig. 1, left top panel), the decrease of the RWC results in inactivation of reaction centres. Similar observation was previously reported to cause a decrease of open RCs (Georgieva et al., 2005).



***Фиг. 1.** Параметри, количествено определящи структурните особености на фотосинтетичния апарат на тъмнинно адаптирани листа на Haberlea rhodopensis (горните панели) and Phaseolus vulgaris (долните панели) с различни нива на водно съдържание, предизвикани на тъмно. Параметрите (за подробности вж. Strasser et al., 2010), получени от JIP-тест, базиран на бързата фаза (OJIP) на индукционната крива на бързата флуоресценция, бяха нормализирани, използвайки като еталон съответните стойности при 100% RWC. В левите панели избраните параметри описват промените в структурата на ФС2, зависейки от RWC за всички измервания с различно водно съдържание в листата. Сивите части показват областите от RWC, при които намалението в RWC води до съществено понижение във фотосинтетичния капацитет на ФС2 до крайно инхибиране. Десните панели описват ефективностите на цялостната енергийна каскада – от абсорбция на светлината до редукция на крайните акцептори на електрони в акцепторната страна на ФС1 – и индексът на ефективност за избрани състояния на засушаване еднакви за двата вида растения (показани в панелите с продължителността на времето за засушаване)*

***Fig. 1.** Parameters quantifying the structure of the photosynthetic machinery of dark-adapted H. rhodopensis (top panels) and Ph. vulgaris (bottom panels) leaves that were at different water-content-states established in darkness. The parameters (for the their definition, see Strasser et al., 2010), derived by the JIP-test from the fast rise (OJIP) transients of the prompt fluorescence, were normalised using as reference the corresponding values at 100% RWC. In the left panels, selected parameters referring to the PSII structure are presented vs. the RWC, for all the measured water-content-states. The shaded areas indicate the RWC range in which RWC decrease results in a pronounced decrease of PSII photochemical capacity down to inhibition. The right panels depict the efficiencies for the whole energy cascade – from absorption up to the reduction of end electron acceptors at the PSI acceptor side – and the performance indexes, for selected water-content-states with about the same water content in both species (indicated in the panels together with the duration of drying time)*

The response to RWC decrease in beans (Fig. 1, bottom left panel) differs from that in haberlea. The difference concerning φ_{Po} (and k_P/k_N) behaviour is that the decrease occurs mainly for RWC below 40% RWC. However, the behaviour of TR_0/RC and RC/ABS is completely different. In the 100-10% RWC range, RC/ABS increases and TR_0/RC decreases progressively with the decrease of RWC. The antenna size decrease (equivalent to RC/ABS increase) indicates that antenna chlorophylls are the first to be degraded before the whole photosynthetic unit is damaged. The deviation of the k_P/k_N curve from the RC/ABS curve increases with the decrease of the RWC (especially for RWC below 30%); the deviation is much bigger than in the case of haberlea, meaning that the increase of k_N is more pronounced in beans.

The right panels of Fig. 1 depict the efficiencies (structural parameters) for the whole energy cascade – from absorption up to reduction of end electron acceptors at the PSI acceptor side – and the performance indexes (potentials governed by the structural parameters), for selected water-content-states with about the same RWC in both species (indicated in the panels together with the duration of drying-time); in these plots, the selected states are not in the range of extreme desiccation.

Comparison of the two patterns shows that the difference in the response of the two species to RWC decrease covers all the presented parameters and that the impact is more extended in haberlea than in beans. However, it should be pointed out that all the JIP-test parameters presented in Fig. 1 is on absorption basis. Therefore, Fig. 1 reveals that RWC decrease, which causes degradation of a fraction of Chl in bean leaves, affects less the structure and potentials of the non-degraded photosynthetic machinery than in haberlea, where it does not cause any degradation even down to 1% RWC; on the other hand, in the extreme desiccation range (shaded area in left panels) the structure and potentials of the non-degraded photosynthetic machinery is affected more in beans than in *Haberlea*.

8. Drought stress in combination with other environmental factors

8.1. Complex nature of dry environments

8.1.1. Drought stress combined with high temperature and high irradiation

Water-limited environments impose multiple limitations on the ability of plants to gain carbon. Lack of water is accompanied with unfavorable conditions such as high light and high temperature all interacting to increase plant stress (Smith et al., 2004). Smith et al. (2004) reviewed the traits commonly observed in dryland plants involve: 1) minimizing solar interception – vertical leaf orientation, midday wilting, paraheliotropism (leaf cupping), and pubescence (Smith et al., 1997); 2) leaf size can control leaf temperature independently of light interception and/or latent heat loss, and so many dryland plants; 3) traits affecting both light interception and canopy temperature – seasonal leaf polymorphism and deciduousness.

Drought stress would be the determinant factor in the distribution in evergreen and deciduous trees at low altitudes, whereas in shrubs and cushions at intermediate altitudes – at the treeline – or higher, it would be the temperatures and/or the combination of both stresses, moreover the light stress. These multiple stresses modulate the distribution and the seasonal and annual phenological patterns of plants are postulated.

There was found different behavior of plants in drought stress conditions depending from the manner of treatment. In opposite to field conditions, the results accepted from artificial conditions as for example treatment on detached leaves reveals controversial responses to combined treatment. The effects of drought and high temperature stresses on damaging mechanisms of both photosystems have been seldom mentioned, and both coordination between PS II and PS I and response of electron transfer components to two kinds of stresses were unclear (Qin et al., 2011). Detached leaves exposed to high temperature (42°C) under high irradiance (1200 $\mu molm^{-2}s^{-1}$ PFD) or drought (PEG-6000, 30%) under high temperature (42°C) the maximal efficiency of PS II (Fv/Fm) and absorbance at 820 nm decreased greatly in peanut leaves, accompanied by the increase of relative variable fluorescence at the J-step (Vj), the obvious decrease of absorption flux per excited CS (t = m) (ABS/CSm), trapped energy flux per CS (t = m) (TRo/CSm) and active RCs per CS (t = m) (RC/CSm) calculated from the chlorophyll fluorescence transient curve. The obvious increase of 1-qP and the xanthophyll cycle-dependent energy dissipation (NPQ) were also detected in peanut leaves under these stresses. Additionally, the activity of SOD decreased in peanut leaves under these stresses, accompanied by the increase of malonaldehyde (MDA) and permeability of plasma membrane. These results showed that severe photoinhibition of PS II and PS I in peanut leaves was induced by combined drought and high temperature stresses. However, K-step was not induced in the rapid chlorophyll induction curve, which implied that peanut oxygen evolving complex (OEC) was not sensitive to high temperature and drought stresses, and donor side of PS II reaction centers was more sensitive to high temperature and drought stresses relatively. The main factor caused the damage to peanut photosystems might be the accumulation of reactive oxygen species (ROS) induced by excess energy. First, the xanthophyll cycle could only dissipate part of excess energy; second, the water-water cycle could not dissipated energy efficiently under the studied stresses, which caused the accumulation of ROS greatly. Drought and high irradiance (1200 $\mu molm^{-2}s^{-1}$ PFD) did not induce significant changes in photosynthetic reactions in comparison to combined action of drought and heat stress or high temperature plus high irradiance treatments.

In the field, the response is species dependent (Rubio-Casal et al., 2010). *P. pinea* showed a high sensitivity to the combined effects of drought and high temperatures at the end of the drier and warmer summers. In addition, its net photosynthetic rate decreased with warmer temperatures. The photosynthetic apparatus of *J. phoenicea* showed a suboptimal state during summertime denoted as high chronic photoinhibition levels that increased with lower ψ.

8.1.2. Drought stress in cold environment

As in water-limited environments, architectural features of leaves and crowns in cold environments may reflect optimization of leaf energy balances as much as for sunlight interception for photosynthesis (Smith et al., 2004). Cool habitats in temperate and tropical latitudes occur often due to elevation effects, which also lead to lower ambient pressure and more rapid diffusion rates. More rapid diffusion, combined with lower water vapor holding capacities of cool air, cause water stress that affects photosynthesis in cold environments, irrespective of water supply (Smith and Geller, 1979; Leuschner, 2000).

In above mentioned study of Rubio-Casal et al. (2010) a species dependent response to combined stress treatment was found. In opposite to *P. pinea, J. oxycedrus* showed the lowest tolerance to chilling stress with its highest chronic photoinhibition levels during wetter and colder periods and its lower net photosynthetic rates at lower temperatures.

8.1.3. Drought and salinity stresses

Plants are often subjected to periods of soil and atmospheric water deficits accompanied by high soil salinity. Photosynthesis, together with cell growth, is among the primary processes to be affected by water or salt stress. When compared with drought, salt stress affected more genes and more intensely, possibly reflecting the combined effects of dehydration and osmotic stress in salt-stressed plants. Early responses to water and salt stress have been considered mostly identical (Munns, 2002). Drought and salinity share a physiological water deficit that attains, more or less intensely, all plant organs (Chaves et al., 2009). However, under prolonged salt stress plants respond in addition to dehydration to hyper-ionic and hyper-osmotic stress. Under salinity, in addition to water deficits, plants endure salt-specific effects.

9. Physiological indices for plant water relationships

Water quantity in crop plants is from great importance for predicting and management of crop yields. Many indices are introduced to estimate the level of drought stress.

9.1. Water-Use Efficiency (WUE)

Water-use efficiency (WUE) refers to the amount of water lost during the production of biomass or the fixation of CO_2 in photosynthesis (for details see Lambers et al., 2005). The **water-use efficiency of productivity** is the ratio between gain in biomass and loss of water during the production of that biomass. **The photosynthetic water-use efficiency** is the ratio between carbon gain in photosynthesis and water loss in transpiration, A/E. Other estimation of the **water-use efficiency** related with photosynthetic activity is the ratio of photosynthesis (A) and leaf conductance for water vapor A/g_w considered by Comstock & Ehleringer (1992) as **intrinsic water-use efficiency**.

9.2. Water and crop yield

De Wit (1958) showed that for dry, high-radiation climates, yield and transpiration were related as

$$Y/T = m/Tmax \qquad (3)$$

where Y = total dry matter mass per area, T = total transpiration per area during growth to harvest, and Tmax = mean daily free water evaporation for the same period. The constant m is related to water requirement (Kirkham, 2005)).

Equation 3 could be simplified for humid regions because, when water was not limiting, fluctuations in intercepted radiation, although reflected in transpiration and growth, would not affect appreciably the ratio T/Tmax. De Wit found under these conditions that

$$Y/T = n \qquad (4)$$

where n is a constant, gave a better description than does Equation 3. The value of m in Equation 3 can be approximated with Equation 3 from water use efficiency and mean daily evaporation (E):

$$m = (Y/T).E. \qquad (5)$$

Also, evaporation was used directly with no correction to free water evaporation.

The relationship between yield and transpiration as determined by Arkley (1963), who used data from Briggs and Shantz (1913). By Briggs and Shantz (1913) a close relation between transpiration and dry matter production was achieved. That is, dry matter is decreased by water deficits.

The relationship between evapotranspiration and dry-matter production may or may not be linear. This is partly because the fraction of evaporation that does not contribute to plant growth varies throughout the crop life cycle.

It is also necessary briefly look at the situation of an individual leaf. For a single leaf, the net assimilation, or net photosynthesis, increases with light intensity to the saturation point and then levels off. The transpiration rate will, however, increase linearly with radiation to a much higher intensity. Thus, the ratio between transpiration and photosynthesis will vary according to the radiation intensity. The high ratio occurring at extremely low radiation intensity is because transpiration has some value, whereas photosynthesis first has to compensate for the respiration. This high ratio is of little significance because of the low rates of both processes. The lowest ratio is observed only in the early morning and late afternoon.

10. Controlling water balance and irrigation

As it is observed in section 8, **soil management** is of great importance for control of water balance in plants. Plants, and for us it is especially crop plants, rely on the steady supply of soil water, flowing to the roots over the entire season (Ehlers and Goss, 2003). Therefore arable soils have to be conditioned to take in rainwater, the sole source of soil water, at a rate equal to the rainfall rate. Water supply from groundwater to crops will be important only in locations where the soils are characterized by a shallow water table. The main control is achieved at different levels such as: 1) controlling infiltration to avoid soil erosion; 2) controlling evaporation, because water flux to the soil surface is not limited by the hydraulic properties of the soil thus the rate of evaporation is governed more or less solely by external meteorological conditions.

Different approach to control water balance is to controlling water use by **crop management**. Crop rotation is a planned temporal sequence of crops in an arable field, often with each one being grown as a pure stand. The crops may be annual, biennial or perennial. Crops with a long growing season can consume the supply of soil water to a considerable depth, A large water use by the previous crop may negatively affect the water supply or the following crop. Controlled crop rotation is necessary to reduce drought effects.

Irrigation practice permits better crop growing. The earth's land area covers roughly 15 billion ha. That is around 29% of the total earth's surface. Only one tenth of the land area, namely 1.5 billion ha, is arable land. But on average the arable land area per person is limited by additional reasons. Now amounts of arable land area are just around 0.25 ha per person.

Irrigated agriculture presents a real contrast to rainfed agriculture. Irrigation is the human-based, artificial application of water to the soil for the purpose of facilitating plant growth and the development of yield. The **water requirement** is the unrestricted water use of a crop stand at a location without any shortages or limitations, and includes transpiration and soil evaporation. In other words, the crop is grown without water stress. Of course the daily water requirement varies during the season. The total water requirement of the crop is calculated at the end of the season. The benefit of irrigation will depend on climatic, crop and soil variables. The principal aim of irrigation in crop production is to supplement the soil water storage that relies on rainfall. Irrigation minimizes growth restrictions due to water shortage. Old methods of irrigation apply the water on the soil surface by **flooding**. These methods are simple and do not require sophisticated techniques. But there is an inherent danger of large, uncontrolled water losses. Nowadays, modern methods are available that minimize unproductive water losses. They were developed with the goal of feeding the irrigation water directly into the plant root system. The main methods reviewed in Ehler and Goss' book (Ehlers and Goss, 2003) are as follow: **controlled flooding**; **border strip irrigation**; **basin irrigation**; and **furrow irrigation**.

In conclusion, the study of intimate responses of plants to water deficit and the control of water balance in crops enhance good agriculture practice and increase the efficient supply of food resources for humans.

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ACKNOWLEDGEMENTS

Authors thank to Bulgarian National Science Fund, Project № DO 02-137 / 15.12.2008 for the financial support.

Статията е приета на 20.12.2011 г.
Рецензент – доц. д-р Златко Златев
E-mail: zl_zlatev@abv.bg