Invited Review

Title:

Drought stress and carbon assimilation in a warming climate: reversible and irreversible impacts

Author:

Urs Feller

Address:

Prof. em. Urs Feller

Institute of Plant Sciences and Oeschger Centre for Climate Change Research (OCCR)

University of Bern

Altenbergrain 21

CH-3013 Bern

Switzerland

E-Mail:

Urs.feller@ips.unibe.ch

Abstract

Global change is characterized by increased CO_2 concentration in the atmosphere, increasing average temperature and more frequent extreme events including drought periods, heat waves and flooding. Especially the impacts of drought and of elevated temperature on carbon assimilation are considered in this review. Effects of extreme events on the subcellular level as well as on the whole plant level may be reversible, partially reversible or irreversible. The photosynthetically active biomass depends on the number and the size of mature leaves and the photosynthetic activity in this biomass during stress and subsequent recovery phases. The total area of active leaves is determined by leaf expansion and senescence, while net photosynthesis per leaf area is primarily influenced by stomatal opening (stomatal conductance), mesophyll conductance, activity of the photosynthetic apparatus (light absorption and electron transport, activity of the Calvin cycle) and CO_2 release by decarboxylation reactions (photorespiration, dark respiration). Water status, stomatal opening and leaf temperature represent a "magic triangle" of three strongly interacting parameters. The response of stomata to altered environmental conditions is important for stomatal limitations. Rubisco protein is quite thermotolerant, but the enzyme becomes at elevated temperature more rapidly inactivated (decarbamylation, reversible effect) and must be reactivated by Rubisco activase (carbamylation of a lysine residue). Rubisco activase is present under two forms (encoded by separate genes or products of alternative splicing of the pre-mRNA from one gene) and is very thermosensitive. Rubisco activase was identified as a key protein for photosynthesis at elevated temperature (non-stomatal limitation). During a moderate heat stress Rubisco activase is reversibly inactivated, but during a more severe stress (higher temperature and/or longer exposure) the protein is irreversibly inactivated, insolubilized and finally degraded. On the level of the leaf, this loss of photosynthetic activity may still be reversible when new Rubisco activase is produced by protein synthesis. Rubisco activase as well as enzymes involved in the detoxification of reactive oxygen species or in osmoregulation are considered as important targets for breeding crop plants which are still productive under drought and/or at elevated leaf temperature in a changing climate.

Contents

1.   Introduction

The continuous increase in atmospheric CO_2 concentration and the rise in mean ambient temperature are well known facts in the course of global change (IPCC, 2012; Knutti et al., 2016). Additionally climate change models predict more frequent and more severe extreme events such as drought phases or heat waves (Schär et al., 2004; Fuhrer et al. 2006; Mittal et al., et a., 2014; Fischer and Knutti, 2015; Teskey et al., 2015). Drought as well as elevated ambient temperature may cause considerable impacts on crop plants by disturbing essential physiological functions including photosynthesis, mineral nutrient acquisition, long-distance transport via xylem and phloem, interactions between organs as well as yield quantity and quality (Loreto and Centritto, 2008; Gilgen and Buchmann, 2009; Ji et al., 2010; Jentsch et al., 2011; Cottee et al., 2014; Molina-Rueda and Kirby, 2015; Ramya et al., 2015; Xu et al., 2015).

Drought (Yordanov et al., 2000; Gilgen et al., 2010; Aranjuelo et al., 2011; Aimar et al., 2014) and heat (Haldimann and Feller, 2005; Sharkey, 2005; Fu et al., 2008; Chen et al., 2014; Cottee et al., 2014; Feng et al., 2014) as well as interactions between these two environmental stresses (Valladeres and Pearcy, 1997; Xu and Zhou, 2006; De Boeck et al., 2007; Grigorova et al., 2011, 2012; Vile et al., 2012; Balla et al., 2014; Jagadish et al., 2014; Sekmen et al., 2014) must be considered for a comprehensive evaluation of carbon assimilation in the course of global change. Leaf temperature is often elevated in drought-stressed plants, since ambient temperature is also high and cooling by transpiration is less efficient when stomata are less open or epicuticular waxes are produced (Gallé and Feller, 2007; Gallé et al., 2007; Aharoni et al., 2004; Reynolds-Henne et al., 2010).

Some negative effects of an abiotic stress phase on plants are reversible during a subsequent recovery phase, while other effects are not or only partially reversible (Loreto and Centritto, 2008; Damour et al., 2009; Mathur et al., 2011; Rodriguez-Dominguez, 2012; Wimmer and Eichert, 2013; Kuhn et al., 2015). All activities must be integrated over space (including the various organs) and over time (including stress and recovery phases) to evaluate the overall performance of a plant (Xu et al., 2013; Bollig and Feller, 2014). Therefore the reversibility of damages is a key aspect in this context and is the focus of this review. Throughout stress and recovery phases, the photosynthetically active biomass per plant and the net CO_2 assimilation rate per biomass unit are key parameters (Morales et al., 2014; Sanchez et al., 2015). Leaf expansion and leaf senescence are relevant for the photosynthetically active biomass per plant (Luna-Flores et al., 2015; Chen et al., 2015a; Marquez-Garcia et al., 2015).

The question, to which extent impacts of extreme environmental conditions are reversible, is relevant on the level of enzymes, on the level of organs and also on the level of whole plants (Feller et al., 1998; Haldimann et al., 2008; Gilgen and Feller, 2014). While an enzyme may be transiently inactivated by elevated temperature and may be reactivated after the stress phase (reversible inactivation), it may be irreversibly damaged and degraded during a more severe stress phase leading to an irreversible loss of this protein. In the latter case, new enzyme molecules may be produced and become active already during the stress phase or during the recovery phase as long as compartmentation and basic cellular functions including gene expression and protein synthesis are maintained (Fu et al., 2008; Cartagena et al., 2015; Chen et al., 2014; Liu et al., 2014; Wang et al., 2015). During the stress phase, protein synthesis is important for the adaptation of the metabolism, especially for the formation of protective proteins such as dehydrins (Close, 1997; Volaire and Lelievre, 2001; Vaseva et al., 2014) or enzymes involved in the detoxification of reactive oxygen species (Ahmed et al., 2015; Jain et al., 2015) and in the production of compatible solutes and secondary metabolites (Jain et al., 2015; Simova-Stoilova et al., 2015).

2.   Photosynthetically active leaf area

The photosynthetically active leaf area is an important parameter for individual plants and depends on the number and size of active leaves (Fig. 1). Leaf emergence and expansion increase the active leaf

area, while senescence decreases it (Ebdon and Petrovic, 1998; Munne-Bosch and Alegre, 2004; Lee et al., 2012; Pantin et al., 2012; Turner et al., 2012; Blösch et al., 2015; Esmaeilzade-Moridani et al, 2015; Marquez-Garcia et al., 2015). The area of a leaf may be decreased under drought as compared to unstressed plants by a negatively influenced leaf expansion during leaf development or to some extent by shrinkage (Burling et al., 2013; Scoffoni et al., 2014) of previously expanded leaves as a consequence of water loss (Fig. 1 A, B, C). While the minor loss of leaf area caused by shrinkage is in general reversible when mature leaves become again fully turgid after improving the water status of the plant by rainfall or re-watering, the decreased area of mature leaves caused by negative effects on leaf expansion cannot be reversed after leaf expansion when secondary cell walls are synthesized. A smaller number of young leaves may be produced under drought (Fig. 1 A, C) or senescence may start earlier in older leaves (Fig. 1 A, D). Often senescence in such leaves is atypical and characterized by an incomplete degradation of chlorophylls and proteins and by a poor nitrogen remobilization (Fig. 2, C, D, E). Phloem transport and the nitrogen status of leaves are affected by drought, since the source/sink network is altered (Borrell et al., 2001; Feller et al., 2015). Especially lowered sink strength in young leaves and reproductive organs contributes to these changes. Vegetative storage proteins may accumulate in senescing legume leaves under drought when nitrogen export capacity is limited (Lee et al., 2014). Beyond a certain point, leaf senescence becomes irreversible and this leaf biomass is lost for the plant (Figs. 1 D, 2 C, D, E). Besides the onset and the velocity of leaf senescence, mechanisms involved in the catabolism of leaf constituents may be altered under abiotic stresses (Thoenen et al., 2007; Feller et al., 2008; Simova-Stoilova et al., 2010). In general, photosynthetic capacity declines before other cellular functions (e.g. respiration, intermediary metabolism associated with nutrient remobilization) are lost as summarized previously (Hörtensteiner and Feller, 2002; Feller et al., 2008). Deciduous trees exposed to severe drought may shed the leaves in summer and produce new leaves several weeks later when the water status of the trees in improved (Haldimann et al., 2008). Since these newly formed leaves are shed again in fall, the investment in these leaves is not paid back by photosynthetic activity and will finally weaken the trees. It might be helpful to consider such responses to drought for genotype selection or breeding.

Young leaves may again be produced more rapidly during a recovery phase following the drought period (Blösch et al., 2015). In this case the drought effects are not reversible on the level of already senesced leaves (irreversible loss of these leaves), but are partially reversible on the level of the whole plant (loss of mature leaves and production of new leaves). Newly emerging leaves may be positioned differently in previously stressed plants than in unstressed control plants (Fig. 2 C, D). Often new leaves are produced from axillary buds in previously stressed dicotyledonous plants and not at the shoot apex as in control plants. Even closely related species (e.g. the two forage grasses *Digitalis glomerata* with pronounced senescence in older leaves and *Lolium perenne* with marked effects on leaf expansion) may differ in their senescence and leaf expansion patterns under the same drought conditions (Blösch et al., 2015). Although new leaves are formed after a stress period, canopy architecture is affected and overall shoot biomass is decreased (Gilgen et al., 20010; Blösch et al., 2015).

Light interception and rate of photosynthesis can be also influenced via the spatial orientation of leaves including movement of turgid leaves (e. g. in legumes), leaf curling (e. g. in maize and other cereals) and wilting as illustrated in Figs. 1 A, B and 2 A, B (Save et al., 1993; Werner et al., 1999; Biskup et al., 2007). Lower leaves in a dense stand may be exposed under drought to a higher photon flux density than the same leaves of non-stressed plants, since less photons are absorbed by leaves at the top of the plant. These changes are at least in early stress phases reversible (Fig. 2 A, B). After re-watering (e. g. rainfall in fields), leaf rolling can be reversed within minutes to hours.

3.   Drought effects on stomata and on leaf temperature

Depending on the plant species and on other environmental conditions stomatal (density, size and opening of stomates) or non-stomatal limitations (e.g. mesophyll conductance, metabolic limitations) are more relevant under drought (Jones, 1998; Medrano et al., 2002; Damour et al., 2009; Signarbieux and

Feller, 2011; Garruna-Hernandez et al., 2014; Greer, 2015). The relevance of non-stomatal limitations (e.g. mesophyll conductance) was reported by several groups (Loreto et al., 1992; Flexas et al., 2002; Morison and Lawson, 2007). Ambient temperature, air humidity, photon flux density, stomatal opening and air convection affect the temperature in the mesophyll (Feller, 2006; Reynolds-Henne et al., 2010; Carvalho et al., 2015). Various regions of the same leaf may differ considerably in their actual temperatures (Reynolds-Henne et al., 2010; Gilgen and Feller, 2014; Feller and Vaseva, 2014). Furthermore, stomatal control may indirectly affect xylem embolism and influence as a consequence drought responses in a complex manner (Jones and Sutherland, 1991).

Leaf temperature strongly depends on photon flux density. The temperatures in shaded and fully sun-exposed leaves from the same plant may differ by more than 10 °C (Feller, 2006). Leaf temperature changes within seconds when sun-exposed leaves are shadowed or vice versa. From the macroscopic world we expect a sunrise in the morning, perhaps a cloud during the day and finally a romantic sunset in the evening, but no rapid changes in a wide range. However, for leaf cells the situation is different, since even in fully sun-exposed plants in stands (with a leaf area index considerably above 1.0) a high percentage of leaves is shadowed by other leaves (Collinson et al., 1996; Liu et al., 2008). Photon flux density may change very rapidly during the day as a consequence of altered spatial arrangements (e. g. angle of the sun relative to crop plants, especially when grown in rows as for cereals). Oscillations in leaf temperature were detected in several plant species after transferring leaves from darkness to light (Feller, 2006; Reynolds-Henne et al., 2010; Feller and Vaseva, 2014). These oscillations can be explained by a rapid heating of previously darkened leaves (within seconds) followed by a slow start of cooling by stomatal opening (within minutes). The lowered leaf temperature may again cause partial closure of stomata within minutes, decrease cooling efficiency by transpiration and lead to a temperature increase again. These assumptions as well as a trade-off between abscisic acid-induced closure and heat-induced opening of stomata were confirmed by measuring stomatal aperture (Reynolds-Henne et al., 2010; Feller and Vaseva, 2014).

The reversible stomatal closure initiated by root signals (i.e. abscisic acid) in plants grown on soil with a low water potential (Davies and Zhang, 1991; Li et al., 2000; Schroeder et al., 2001; Wilkinson and Davies, 2002; Chaves et al., 2009; Pinheiro and Chaves, 2011) or by the CO_2 concentration in the leaf (Vavasseur and Raghavendra, 2005) is well known. Besides the reversible regulation of stomatal opening, transpiration and leaf temperature may be affected by the deposition of cuticular waxes or by the formation of stomatal plugs in a less reversible or even irreversible manner (Stockey and Ko, 1986; Kozlowski and Pallardy, 2002; Gallé and Feller, 2007; Zhu et al., 2014). The enhanced deposition of cuticular waxes was found to be correlated with an improved drought tolerance (Aharoni et al., 2004; Yang et al., 2011).

Leaf temperature, water status and stomatal opening are interconnected in a complex manner (Valladares and Pearcy, 1997; Feller, 2006; Reynolds-Henne et al., 2010; Feller and Vaseva, 2014; Teskey et al., 2015). Increased abscisic acid levels cause closure of stomates and reduce leaf cooling by transpiration. However, drastically increased temperature may cause stomatal opening and allow better leaf cooling despite the fact that soil and leaf water potentials are low and abscisic acid levels are increased (Feller, 2006; Reynolds-Henne et al., 2010).

Powerful infrared cameras are available in these days and are suitable to investigate the response of different species or of different varieties of a species to abiotic stresses (Jones, 1999; Jones et al., 2002; Price et al., 2002; Moller et al., 2007; Jones et al., 2009; Reynolds-Henne et al., 2010; Feller and Vaseva, 2014; Gilgen and Feller, 2014). Thermography allows a good spatial and temporal resolution of canopy temperatures, is suitable for investigations in the laboratory as well as for studies in the field and can serve as an indicator for stomatal functioning (Jones, 1999; Jones et al., 2002; Price et al., 2002; Moller et al., 2007; Jones et al., 2009; Feller and Vaseva, 2014).

A temperature sensor is often included in modern equipment for the analysis of net CO_2 assimilation based on infrared gas analysis and/or for the analysis of fluorescence parameters (Haldimann and Feller, 2005; Gallé et al, 2007). Leaf temperature can be accurately registered with such built-in sensors during

the physiological measurements. However, the equipment itself may considerably influence leaf temperature by affecting air convection, photon flux density, air humidity at the leaf surface or CO_2 concentration in a cuvette. The temperature of an undisturbed leaf may change within a few seconds after placing the leaf in the equipment, while the status of the photosynthetic apparatus may still depend mainly on leaf temperature before starting the analyses and may then also respond to the altered conditions. Therefore caution is recommended when using such temperature data. Additional measurements with a contact-free infrared thermometer and avoiding shadowing are highly recommended just before starting the physiological analyses and perhaps also afterwards to identify such effects (Feller, 2006; Gallé and Feller, 2007; Gallé et al., 2007; Feller and Vaseva, 2014). Alternatively, pictures from a thermal camera (infrared camera) can be very helpful (Reynolds-Henne et al., 2010; Gilgen and Feller, 2014; Feller and Vaseva, 2014). Gas exchange measurements at steady state after a sufficiently long adaptation period in a cuvette with a controlled environment would eliminate or at least drastically reduce this problem.

4.   Impacts on Rubisco and Rubisco activase

Various key components of the photosynthetic machinery including membranes, photosystem II and enzymes in the Calvin cycle were considered as limiting components at elevated temperature (Feller et al., 1998; Crafts-Brandner and Salvucci, 2000, 2004; Salvucci et al., 2001; Salvucci and Crafts-Brandner, 2004; Sharkey, 2005; Hozain et al., 2010; Yan et al., 2011; Carmo-Silva et al., 2012; Xu et al., 2013). Rubisco activase was identified as a key protein for the thermotolerance of photosynthesis and was therefore investigated by several groups in more detail (Salvucci et al., 2001; Sharkey, 2005; Portis et al., 2008; Kaiser et al., 2015). It must be borne in mind that the component which is reversibly inactivated by moderately increased temperature is not necessarily identical with the component becoming irreversibly damaged after a marked increase in leaf temperature (Crafts-Brandner and Salvucci, 2004; Sharkey, 2005; Xu et al., 2013). Furthermore, an improved thermotolerance of photosystem II was observed in plants exposed to drought or heat (Haldimann and Feller, 2005; Oukarroum et al., 2009). This is an example for an adaptation of the photosynthetic apparatus to abiotic stresses related to global change.

Rubisco and Rubisco activase are matching pairs (Li et al., 2005). Solanaceae are different from non-Solanaceae, since charged residues allow proper interactions between Rubisco and Rubisco activase from Solanaceae, but not when one of the two proteins derives from non-Solanaceae (Li et al., 2005; Wachter et al., 2013). Such interactions must be borne in mind for genetic engineering Rubisco activase in crop plants.

As mentioned above, CO_2 fixation by Rubisco (Fig. 3) was found to be highly sensitive to elevated temperature, while photosynthetic electron transport was still functional under these conditions (Feller et al., 1998; Sharkey, 2005). Rubisco protein is quite stable at elevated temperature and under drought, but Rubisco activity can be reversibly decreased by accelerated inactivation (decarbamylation) and less effective reactivation by Rubisco activase (Law and Crafts-Brandner, 1999; Crafts-Brandner and Salvucci, 2000, 2004; Kim and Portis, 2006). Key processes involved in reversible and irreversible drought and heat effects are summarized in Fig. 3. Rubisco activase was identified as a key enzyme for photosynthesis during a heat phase and a subsequent recovery phase (Feller et al., 1998; Salvucci et al., 2001; Carmo-Silva et al., 2012; Yamori et al., 2012). The formation of oligomers was identified as a key process in determining thermal stability of the two Rubisco activase isoforms (Keown and Pearce, 2014). Recently this enzyme was described as a "multiple responder to abiotic stresses" (Chen at al., 2015b).

Rubisco activase is a nuclear-encoded stromal protein present under two forms with different properties (Salvucci et al., 2006; Portis et al., 2008; Carmo-Silva and Salvucci, 2016).The longer redox-regulated α-isoform and the shorter β-isoform of rubisco activase are in some plants encoded in the same gene and are synthesized on two mRNAs produced from the same pre-mRNA by alternative splicing as illustrated in Fig. 3, process 2b (Werneke et al., 1989; Salvucci et al., 2003). In other plant species the two isoforms are encoded in separate genes (Fig. 3, processes 2a and 2c; Salvucci et al., 2003; Yin et al., 2014).The longer redox-regulated α-isoform contains at the C-terminus an extension with two cysteine

residues which are absent in the shorter β-isoform (Portis, 2003). These two residues can be reduced via the thioredoxin system (Portis, 2003). The α-isoform of Rubisco activase can be reversibly inactivated by two mechanisms: It may be inactivated/reactivated by oxidation/reduction of the two cysteine residues near the C-terminus via the thioredoxin system (Zhang and Portis, 1999; Portis, 2003) and may additionally be inactivated by direct effects of the moderately elevated temperature (Keown and Pearce, 2014) as schematically shown in Fig. 3 (processes 5 and 6). The shorter β-isoform missing the two cysteine residues is also sensitive to moderately elevated temperature, but is not regulated by redox reactions mediated by the thioredoxin system. Only the shorter β-isoform of Rubisco activase was detected in tobacco, while the longer α-isoform with the C-terminal extension containing two cysteine residues was absent (Zhang et al., 1999; Carmo-Silva and Salvucci, 2013). It must be borne in mind that no regulation via the thioredoxin system is possible when the α-isoform is absent (Carmo-Silva and Salvucci, 2013).

Furthermore, interactions with chaperonin-60 beta may protect Rubisco activase to some extent during heat stress (Salvucci, 2008). A further temperature increase may lead to irreversible damages such as cross-linking Rubisco activase subunits, partial denaturation and finally to proteolysis (Feller et al., 1998). For these Rubisco activase molecules the heat effect is irreversible, but for the cell it may still be reversible when transcription and translation are still functional allowing the synthesis of new Rubisco activase subunits.

Heat tolerance of Rubisco activase from various plant species varies in a wide range (Salvucci and Crafts-Brandner, 2004). A good correlation between Rubisco activase properties and the temperature optimum for photosynthesis was reported (Salvucci and Crafts-Brandner, 2004; Kurek et al., 2007; Kumar et al., 2009). These findings clearly demonstrate that there is a potential for more thermotolerant Rubisco activases. Therefore Rubisco activase was considered as a key protein for breeding plants with a higher heat and /or drought tolerance in a changing climate (Kurek et al., 2007; Parry et al., 2011; Mueller-Cajar et al., 2014; Pinheiro et al., 2014; Singh et al., 2014; Zhang et al., 2015). Fukuyama et al. (2012) reported that in rice overexpressing Rubisco activase CO_2 assimilation rate is decreased. In these plants Rubisco quantity is decreased most likely by "post-transcriptional mechanisms" (Fukayama et al., 2012). These findings together with the aspects mentioned above indicate that the interactions between Rubisco activity and Rubisco activase are highly complex and represent a challenge for breeding genotypes with a better performance under abiotic stress.

5.   Reactive oxygen species and protection of chloroplast constituents

The production and the detoxification of reactive oxygen species (ROS) are important processes in plants exposed to drought and/or heat (Mittler and Zilinskas, 1994; Munne-Bosch et al., 2001; Mittler, 2002; Apel and Hirt, 2004; Reddy et al., 2004; Locato et al., 2008, 2009; Simova-Stoilova et al., 2009; Snider et al., 2010; Osorio et al., 2011; Xu et al., 2013). ROS production is increased under abiotic stresses (energy dissipation) and as a consequence cellular constituents including proteins and membrane lipids may be damaged (Mittler, 2002). Therefore ROS detoxification by enzymes (Xiao et al., 2008 ; Bian and Jiang, 2009; Fan et al., 2012; Salazar-Parra et al., 2012 ; Demeter et al., 2014; Sekmen et al., 2014; Song et al., 2014) or low molecular-weight compounds (Mittler, 2002) is essential for the functionality of leaf cells under abiotic stress. The xanthophyll cycle represents a plastid-specific ROS detoxification mechanism (Gallé et al., 2007; Haldimann et al., 2008; de la Rosa-Manzano et al., 2015), while other ROS detoxifying systems (e. g. superoxide dismutases) are present in several subcellular compartments (Locato et al., 2009; Simova-Stoilova et al., 2009; Snider et al., 2010; Song et al., 2014). The accumulation and compartmentation of some metabolites (expecially of ROS scavengers and of compatible solutes such as proline, betain or glycinebetaine which are also important for osmoregulation) help to protect cells from damages caused by heat or drought and to maintain basic cellular functions (Hormaetxe et al., 2007; Wang et al., 2010; Albert et al., 2012; Hu et al., 2013; Wujeska et al., 2013: AbdElgawad et al., 2015; Grant et al., 2015). Such protective effects were recently reported in detail for phenolic compounds (Farfan-Vignolo and Asard, 2012; Wegener et al., 2015), α-tocopherol (Munne-

Bosch and Alegre, 2000; Farfan-Vignolo and Asard, 2012) and for isoprene production/emission (Velikova et al., 2005 ; Velikova, 2008; Centritto et al., 2014 ; Seco et al., 2015 ; Vanzo et al., 2015). Advantages of drought acclimation for improved plant performance were reported by Selote et al. (2004).

Additional protective proteins are essential for the proper functionality of cellular constituents (especially of enzyme and membrane proteins) and for basic cellular functions. Chaperones, heat shock proteins, aquaporins (involved in trans-membrane transport of water and other small molecules such as CO_2) and dehydrins belong to this category (Close, 1997; Volaire and Lelievre, 2001; Park et al., 2003; Salvucci, 2008; Xiao et al., 2009; Grigorova et al., 2011; Liu et al., 2014; Vaseva et al., 2014; Moshelion et al., 2015; Wang et al., 2015).

Most of the protective enzymes and solutes mentioned above are not directly involved in photosynthesis, but are relevant for maintaining the metabolism in chloroplasts as well as in other subcellular compartments in a functional state (Vassileva et al, 2009; Grigorova et al., 2012). Such protective mechanisms are relevant for stress phases, but may also be relevant for the performance of plants after a stress period by influencing the velocity and the degree of recovery (Gallé and Feller, 2007; Gallé et al., 2007; Vassileva et al., 2011).

6.   Net CO_2 assimilation

The decrease in net CO_2 assimilation during a heat period is initially reversible, but depending on the leaf temperature reached and the duration of the stress it may be only partially reversible or even irreversible (Haldimann and Feller, 2004, 2005; Haldimann et al., 2008; Vassileva et al., 2009; Cano et al., 2014; Zwicke et al., 2015). The performance of a crop depends on the processes during a stress period as well as during the pre-stress phase and during a subsequent recovery phase after the stress period. Therefore the integral performance during the whole season is relevant for a comprehensive evaluation of a species or of a genotype. Net photosynthesis does not only depend on photosynthetic electron transport and Calvin cycle activity, since carbon losses via decarboxylation processes also contribute to the overall performance (Wingler et al., 1999; Haupt-Herting et al., 2001; Noctor et al., 2002; Bai et al., 2008; Rivero et al., 2009; Vassileva et al., 2009, 2011). The impact of heat and drought on respiration is also crucial for the carbon balance and should be considered when comparing genotypes (Flexas et al., 2006; Vassileva et al., 2011).

For net carbon assimilation on the whole plant level the export via the phloem and the further utilization of assimilates are relevant besides photosynthetic performance of leaves (Lipiec et al., 2013). The supply of roots with energy in the form of organic solutes is equally important as the supply of other shoot parts like expanding leaves or maturing fruits and seeds (Lipiec et al., 2013). Non-metabolized solutes with a good mobility in the phloem represent suitable tools to investigate drought effects on long-distance transport via xylem and phloem (Feller at al., 2015). A CO_2 emission by sink organs such as roots, stems or fruits are not easily detected with standard equipment and are not often addressed in experiments with drought-stressed plants. However, these processes may be highly relevant in plants subjected to abiotic stresses. The paradigm that deep rooting is important for drought tolerance of plants was recently questioned (Grieder et al., 2014; Nippert and Holdo, 2015), but large cortical cells in maize roots (Chimungu et al., 2014) and lateral root development (smaller number and increased length) were found to be well correlated with drought tolerance (Zhan et al., 2015).   Leaf CO_2 assimilation and stomatal conductance were considerably increased in maize lines with large root cortical cells compared to lines with smaller ones (Chimungu et al., 2014). In field experiments with grasslands at various altitudes no shift to deeper water uptake depth was observed under drought (Prechsl et al., 2015). Drought effects on root morphology and physiology remain to be further elucidated in the context of overall performance and net CO_2 assimilation.

Analytical limitations make it extremely difficult to identify drought and heat impacts on the level of whole plants. Sophisticated equipment with infrared gas analyzer (IRGA) technique allows sensitive measurements of net CO_2 assimilation on a leaf area basis, while the analyses of net CO_2 assimilation on a per organ or on a per plant basis are more difficult to handle and less often included in research programs (Signarbieux and Feller, 2012). For a comprehensive analyses of plant performance CO_2 assimilation in all above-ground plant parts and CO_2 release in all below- and above-ground parts throughout the day must be considered as illustrated in Fig. 1, although direct measurements are usually not feasible. Measurements on the second fully expanded leaf from the top may underestimate drought or heat impacts in cereals with an anticipated senescence of older leaves (Marquez-Garcia et al., 2015). In comparison with unstressed control plants, plant architecture can be considerably influenced by an abiotic stress period and also afterwards during the recovery phase (Fig. 2). Furthermore, it must be considered that CO_2 assimilation may – especially in plants subjected to severe stress - vary in a wide range throughout the day (Haldimann et al., 2008).

7.   Conclusions

Adaptation and mitigation are keywords for transdisciplinary approaches in the context of global change and include aspects of plant physiology and agronomy (Swart et al., 2014). Since various plant species are affected differently by abiotic stresses, competition in plant communities (e.g. in grasslands or forests) may be altered under drought or heat and influence species composition (Gilgen et al., 2010; AbdeElgawad et al., 2015; Zwicke et al., 2015). Especially a shift in favor of weeds and invasive species may cause serious problems (Gilgen et al., 2010; Godoy et al., 2011). Root activities and the supply of the roots with shoot-borne assimilates play most likely a key role in this context, although they are not easily accessible in experiments (Gilgen and Feller, 2013, 2014).

A complex regulation network must be analyzed to identify metabolic adaptations in a comprehensive manner (Fortunati et al., 2008; Centritto et al., 2011; Vaseva and Feller, 2013; Jagadish et al., 2014; Zwicke et al., 2015). Several key proteins involved in drought or heat stress tolerance were identified and studies including modern proteomics may allow a deeper insight into regulatory mechanisms and may allow to identify additional key players in plant stress responses (Priest et al., 2014 ; Song et al., 2014 ; Simova-Stoilova et al., 2015). Besides the identification of relevant genes, post-transcriptional processes must be borne in mind and may represent additional challenges for breeding programs focused on abiotic stress responses. Alternative splicing in pre-mRNA processing was - in some species - identified in the synthesis of Rubisco activase (Wernecke et al., 1989; Salvucci et al., 2003) and in 1-pyrroline-5-carboxylate synthetase (Kesari et al., 2012). These two enzymes are highly relevant in leaves of drought-stressed plants or in leaves exposed to elevated temperature. Natural antisense transcripts were identified as possible post-transcriptional regulatory elements for the synthesis of dehydrins (LEA proteins), a group of proteins playing a role in the tolerance of drought, cold and other abiotic stresses (Feller and Vaseva, 2014). Such processes involving pre-mRNA or RNA are interesting in the context of evolution on one hand and indicate that responses to abiotic stresses may be regulated at various levels including many players and representing a challenge for breeding crop plants with suitable properties in a changing climate.

The response of different genotypes of the same crop species to drought or heat periods may vary in wide range (Vassileva et al., 2009, 2011, 2012; Erice et al., 2010, 2011; Yin et al., 2010 ; Parry et al., 2011; Prior et al., 2011; Cao et al., 2014 ; Habash et al., 2014; Topbjerg et al., 2014; Acuna-Galinda et al., 2015 ; Lopes et al., 2015; Wani et al., 2015; Wehner et al., 2015). This is the basis for breeding of crop varieties with a better performance under abiotic stresses. Of course such breeding programs cannot be restricted to the few aspects covered in this review, since the whole plant must finally perform well. Evaluation and breeding of crop genotypes with improved properties under abiotic stresses include constitutive criteria (e.g. properties of Rubisco and of Rubisco activase; density, size and shape of stomata), genes for stress-related proteins (e.g. dehydrins, aquaprins, chaperonins, enzymes involved in ROS detoxification or in the accumulation of compatible solutes) and the regulatory network on the whole

plant (e.g. phytohormones) or at the cellular level (e.g. regulation of gene expression, modification of membrane properties, protein modification, proteolysis). Infrared cameras allow non-invasive analyses of aerial plant parts (thermography) and can be used for high high-throughput comparisons of many genotypes in selection and breeding programs to identify varieties with a better performance under heat and/or drought (Jones, 1999; Jones et al., 2002; Price et al., 2002; Moller et al., 2007; Jones et al., 2009). A close collaboration between geneticists, physiologists and agronomists must be envisaged in order to address stress tolerance in a comprehensive manner including stress and recovery periods and considering from the beginning problematic side effects of improvements. The more frequent and more severe extreme events as predicted by climate models (Fischer and Knutti, 2015; Knutti et al., 2016) will be a challenge and also cause some pressure for the scientists involved (Parry et al., 2011).

Acknowledgements

References

AbdElgawad, H., De Vos, D., Zinta, G., Domagalska, M.A., Beemster, G.T.S., Asard, H., 2015. Grassland species differentially regulate proline concentrations under future climate conditions: an integrated biochemical and modelling approach. New Phytol., 208, 354-369.

Acuna-Galindo, M.A., Mason, R.E., Subramanian, N.K., Hays, D.B., 2015. Meta-analysis of wheat QTL regions associated with adaptation to drought and heat stress. Crop Sci. 55, 477-492.

Aharoni, A., Dixit, S., Jetter, R., Thoenes, E., van Arkel, G., Pereira, A., 2004. The SHINE clade of AP2 domain transcription factors activates wax biosynthesis, alters cuticle properties, and confers drought tolerance when overexpressed in Arabidopsis. Plant Cell, 16, 2463-2480.

Ahmed, I.M., Nadira, U.A., Bibi, N., Cao, F.B., He, X.Y., Zhang, G.P., Wu, F.B., 2015. Secondary metabolism and antioxidants are involved in the tolerance to drought and salinity, separately and combined, in Tibetan wild barley. Environ. Exp. Bot. 111, 1-12.

Aimar, D., Calafat, M., Andrade, A.M., Carassay, L., Bouteau, F., Abdala, G., Molas, M.L., 2014. Drought effects on the early development stages of *Panicum virgatum* L.: Cultivar differences. Biomass & Bioenergy 66, 49-59.

Albert, B., Le Cahérec, F., Niogret, M.-F., Faes, P., Avice, J.-C., Leport, L., Bouchereau, A., 2012. Nitrogen availability impacts oilseed rape (*Brassica napus* L.) plant water status and proline production efficiency under water-limited conditions. Planta 236, 659-676.

Apel, K., Hirt, H., 2004. Reactive oxygen species: Metabolism, oxidative stress, and signal transduction. Annu. Rev. Plant Biol. 55, 373-399.

Aranjuelo, I., Molero, G., Erice, G., Avice, J.-C., Nogués, S., 2011. Plant physiology and proteomics reveals the leaf response to drought in alfalfa (*Medicago sativa* L.). J. Exp. Bot. 62, 111-123.

Bai, J., Xu, D.H., Kang, H.M., Chen, K., Wang, G., 2008. Photoprotective function of photorespiration in *Reaumuria soongorica* during different levels of drought stress in natural high irradiance. Photosynthetica 46, 232-237.

Balla, K., Bencze, S., Bonis, P., Arendas, T., Veisz, O., 2014. Changes in the photosynthetic efficiency of winter wheat in response to abiotic stress. Centr. Eur. J. Biol. 9, 519-530.

Bian, S.M., Jiang, Y.W., 2009. Reactive oxygen species, antioxidant enzyme activities and gene expression patterns in leaves and roots of Kentucky bluegrass in response to drought stress and recovery. Sci. Hortic. 120, 264-270.

Biskup, B., Scharr, H., Schurr, U., Rascher, U., 2007. A stereo imaging system for measuring structural parameters of plant canopies. Plant Cell Environ. 30, 1299-1308.

Blösch, R.M., Riesen, O., Feller, U., 2015. Extended drought periods in grasslands: impacts on the number of photosynthetically active leaves and on leaf senescence in grass and clover species. International Journal of Energy and Environment 9, 147-155.

Bollig, C., Feller, U., 2014. Impacts of drought stress on water relations and carbon assimilation in grassland species at different altitudes. Agric. Ecosyst. Environ. 188, 212-220.

Borrell, A., Hammer, G., Van Oosterom, E., 2001. Stay-green: A consequence of the balance between supply and demand for nitrogen during grain filling? Ann. Appl. Biol. 138, 91-95.

Burling, K., Cerovic, Z. G., Cornic, G., Ducruet, J. M., Noga, G., Hunsche, M., 2013. Fluorescence-based sensing of drought-induced stress in the vegetative phase of four contrasting wheat genotypes. Env. Exp. Bot. 89, 51-59.

Cano, J.F., Lopez, R., Warren, C.R., 2014. Implications of the mesophyll conductance to CO_2 for photosynthesis and water-use efficiency during long-term water stress and recovery in two contrasting Eucalyptus species. Plant Cell Environ. 37, 2470-2490.

Cao, X., Jia, J.B., Zhang, C., Li, H., Liu, T.X., Jiang, X.N., Polle, A., Peng, C.H., Luo, Z.B., 2014. Anatomical, physiological and transcriptional responses of two contrasting poplar genotypes to drought and re-watering. Physiol. Plant. 151, 480-494.

Carmo-Silva, A.E., Gore, M.A., Andrade-Sanchez, P., French, A.N., Hunsaker, D.J., Salvucci, M.E., 2012. Decreased CO_2 availability and inactivation of Rubisco limit photosynthesis in cotton plants under heat and drought stress in the field. Env. Exp. Bot. 83, 1-11.

Carmo-Silva, A.E., Salvucci, M.E., 2013. The regulatory properties of Rubisco activase differ among species and affect photosynthetic induction during light transitions. Plant Physiol. 161, 1645-1655.

Carmo-Silva, A.E., Salvucci, M.E., 2016. The regulatory properties of Rubisco activase differ among species and affect photosynthetic induction during light transitions. Plant Physiol. 161, 1645-1655.

Cartagena, J.A., Seki, M., Tanaka, M., Yamauchi, T., Sato, S., Hirakawa, H., Tsuge, T., 2015. Gene expression profiles in Jatropha under drought stress and during recovery. Plant Mol. Biol. Reporter 33, 1075-1087.

Carvalho, D.R.A., Torre, S., Kraniotis, D., Almeida, D.P.F., Heuvelink, E., Carvalho, S.M.P., 2015. Elevated air movement enhances stomatal sensitivity to abscisic acid in leaves developed at high relative air humidity. Front. Plant Sci. 6, 383.

Centritto, M., Brilli, F., Fodale, R., Loreto, F., 2011. Different sensitivity of isoprene emission, respiration and photosynthesis to high growth temperature coupled with drought stress in black poplar (*Populus nigra*) saplings. Tree Physiol. 31, 275-286.

Centritto, M., Haworth, M., Marino, G., Pallozzi, E., Tsonev, T., Velikova, V., Nogues, I., Loreto, F., 2014. Isoprene emission aids recovery of photosynthetic performance in transgenic *Nicotiana tabacum* following high intensity acute UV-B exposure. Plant Sci. 226, 82-91.

Chaves, M.M., Flexas, J., Pinheiro, C., 2009. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Ann. Bot. 103, 551-560.

Chen, K.M., Li, H.W., Chen, Y.F., Zheng, Q., Li, B., Li, Z.S., 2015a. TaSCL14, a Novel Wheat (*Triticum aestivum* L.) GRAS Gene, Regulates Plant Growth, Photosynthesis, Tolerance to Photooxidative Stress, and Senescence. J. Genet.Genomics, 42, 21-32.

Chen, W.L., Yang, W.J., Lo, H.F., Yeh, D.M., 2014. Physiology, anatomy, and cell membrane thermostability selection of leafy radish (*Raphanus sativus* var. oleiformis Pers.) with different tolerance under heat stress. Sci. Hort. 179, 367-375.

Chen, Y., Wang, X.M., Zhou, L., He, Y., Wang, D., Qi, Y.H., Jiang, D.A., 2015b. Rubisco activase is also a multiple responder to abiotic stresses in rice. Plos One 10: e0140934.

Chimungu, J.G., Brown, K.M., Lynch, J.P., 2014. Large root cortical cell size improves drought tolerance in maize. Plant Physiol. 166, 2166-U1471.

Close, T.J., 1997. Dehydrins: A commonality in the response of plants to dehydration and low temperature. Physiol. Plant. 100, 291-296.

Collinson, S.T., AzamAli, S.N., Chavula, K.M., Hodson, D.A., 1996. Growth, development and yield of bambara groundnut (*Vigna subterranea*) in response to soil moisture. J. Agric. Sci. 126, 307-318

Cottee, N.S., Wilson, I.W., Tan, D.K.Y., Bange, M.P., 2014. Understanding the molecular events underpinning cultivar differences in the physiological performance and heat tolerance of cotton (*Gossypium hirsutum*). Funct. Plant Biol. 41, 56-67.

Crafts-Brandner, S.J., Salvucci, M.E., 2000. Rubisco activase constrains the photosynthetic potential of leaves at high temperature and CO_2. P. Natl. Acad. Sci. USA 97, 13430-13435.

Crafts-Brandner, S.J., Salvucci, M.E., 2004. Analyzing the impact of high temperature and CO_2 on net photosynthesis: Biochemical mechanisms, models and genomics. Field Crops Res. 90, 75-85.

Damour, G., Vandame, M., Urban, L., 2009. Long-term drought results in a reversible decline in photosynthetic capacity in mango leaves, not just a decrease in stomatal conductance. Tree Physiol. 29, 675-684.

Davies, W.J., Zhang, J.H., 1991. Root signals and the regulation of growth and development of plants in drying soil. Annu. Rev. Plant Physiol. Plant Mol. Biol. 42, 55-76.

De Boeck, H.J., Lemmens, C.M.H.M., Gielen, B., Bossuyt, H., Malchair, S., Carnol, M., Merckx, R., Ceulemans, R., Nijs, R., 2007. Combined effects of climate warming and plant diversity loss on above- and below-ground grassland productivity. Env. Exp. Bot. 60, 95-104.

De la Rosa-Manzano, E., Andrade, J.L., Garcia-Mendoza, E., Zotz, G., Reyes-Garcia, C., 2015. Photoprotection related to xanthophyll cycle pigments in epiphytic orchids acclimated at different light microenvironments in two tropical dry forests of the Yucatan Peninsula, Mexico. Planta 242, 1425-1438.

Demeter, Z., Kanalas, P., Mathe, C., Cseke, K., Szollosi, E., M-Hamvas, M., Jambrik, K., Kiss, Z., Meszaros, I., 2014. Osmotic stress responses of individual white oak (*Quercus* section, *Quercus* subgenus) genotypes cultured in vitro. J. Plant Physiol. 171, 16-24.

Ebdon, J.S., Petrovic, A.M., 1998. Morphological and growth characteristics of low- and high-water use Kentucky bluegrass cultivars. Crop Sci. 38, 143-152.

Erice, G., Louahlia, S., Irigoyen, J.-J., Sanchez-Diaz, M.-D., Avice, J.-C., 2010. Biomass partitioning, morphology and water status of four alfalfa genotypes submitted to progressive drought and subsequent recovery. J. Plant Physiol. 167, 114-120.

Erice, G., Louahlia, S., Irigoyen, J.J., Sanchez-Diaz, M., Alami, I.T., Avice, J.-C., 2011. Water use efficiency, transpiration and net CO_2 exchange of four alfalfa genotypes submitted to progressive drought and subsequent recovery. Environ. Exp. Bot. 72, 123-130.

Esmaeilzade-Moridani, M., Kamkar, B., Galeshi, S., Ghaderifar, F., Da Silva, J.A.T., 2015. Leaf expansion and transpiration responses of millet species to soil water deficit. Pedosphere, 25, 834-843.

Fan, W.J., Zhang, M., Zhang, H.X., Zhang, P., 2012. Improved tolerance to various abiotic stresses in transgenic sweet potato (*Ipomoea batatas*) expressing spinach betaine aldehyde dehydrogenase. Plos One, 7, e37344.

Farfan-Vignolo, E.R., Asard, H., 2012. Effect of elevated CO_2 and temperature on the oxidative stress response to drought in *Lolium perenne* L. and *Medicago sativa* L. Plant Physiol. Biochem. 59, 55-62.

Feller, U., 2006. Stomatal opening at elevated temperature: an underestimated regulatory mechanism. Gen. Appl. Plant Physiol. XXXII (special issue), 19-31.

Feller, U., Anders, I., Mae, T., 2008. Rubiscolytics: fate of Rubisco after its enzymatic function in a cell is terminated. J. Exp. Bot. 59, 1615-1624.

Feller, U., Anders, I., Wei, S., 2015. Effects of PEG-Induced Water Deficit in Solanum nigrum on Zn and Ni Uptake and Translocation in Split Root Systems. Plants 4, 284-297 .

Feller, U., Crafts-Brandner, S.J., Salvucci, M.E., 1998. Moderately high temperatures inhibit ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activase-mediated activation of Rubisco. Plant Physiol. 116, 539-546.

Feller, U., Vaseva, I.I., 2014. Extreme climatic events: impacts of drought and high temperature on physiological processes in agronomically important plants
Front. Environ. Sci. 2: 39.

Feng, B., Liu, P., Li, G., Dong, S.T., Wang, F.H., Kong, L.A., Zhang, J.W., 2014. Effect of heat stress on the photosynthetic characteristics in flag leaves at the grain-filling stage of different heat-resistant **winter wheat varieties. J. Agr. Crop Sci. 200, 143-15.**

Fischer, E.M., Knutti, R., 2015. Anthropogenic contribution to global occurrence of heavy-precipitation and high temperature extremes. Nature Clim. Change 5, 560-564.

Flexas, J., Bota, J., Escalona, J.M., Sampol, B., Medrano, H., 2002. Effects of drought on photosynthesis in grapevine under field conditions: an evaluation of stomatal and mesophyll limitations. Funct. Plant Biol. 29, 461-471.

Flexas, J., Bota, J., Galmes, J., Medrano, H., Ribas-Carbo, M., 2006. Keeping a positive carbon balance under adverse conditions: responses of photosynthesis and respiration to water stress. Physiol. Plant. 127, 343-352.

Fortunati, A., Barta, C., Brilli, F., Centritto, M., Zimmer, I., Schnitzler, J.P., Loreto, F., 2008. Isoprene emission is not temperature-dependent during and after severe drought-stress: a physiological and biochemical analysis. Plant J. 55, 687-697.

Fu, J.M., Momcilovic, I., Clemente, T.E., Nersesian, N., Trick, H.N., Ristic, Z., 2008. Heterologous expression of a plastid EF-Tu reduces protein thermal aggregation and enhances CO_2 fixation in wheat (*Triticum aestivum*) following heat stress. Plant Mol. Biol. 68, 277-288.

Fuhrer, J., Beniston, M., Fischlin, A., Frei, C., Goyette, S., Jasper, K., Pfister, C., 2006. Climate risks and their impact on agriculture and forests in Switzerland. Clim. Change 79, 79-102.

Fukayama, H., Ueguchi, C., Nishikawa, K., Katoh, N., Ishikawa, C., Masumoto, C., Hatanaka, T., Misoo, S., 2012. Overexpression of rubisco activase decreases the photosynthetic CO2 assimilation rate by reducing rubisco content in rice leaves. Plant Cell Physiol. 53, 976-986.

Gallé, A., Feller, U., 2007. Changes of photosynthetic traits in beech saplings (*Fagus sylvatica*) under severe drought stress and during recovery. Physiol. Plant. 131, 412-421.

Gallé, A., Haldimann, P., Feller, U., 2007. Photosynthetic performance and water relations in young pubescent oak (*Quercus pubescens*) trees during drought stress and recovery. New Phytol. 174, 799-810.

Garruna-Hernandez, R., Orellana, R., Larque-Saavedra, A., Canto, A., 2014. Understanding the physiological responses of a tropical crop (*Capsicum chinense* Jacq.) at high temperature. Plos One 9, e111402.

Gilgen, A.K., Buchmann, N., 2009. Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. Biogeosciences 6, 2525-2539.

Gilgen, A.K., Feller, U., 2013. Drought stress alters solute allocation in broadleaf dock (*Rumex obtusifolius*). Weed Sci. 61, 104-108.

Gilgen, A.K., Feller, U., 2014. Effects of drought and subsequent rewatering on *Rumex obtusifolius* leaves of different ages: reversible and irreversible damages. J. Plant Interact. 9, 75-81.

Gilgen, A.K., Signarbieux, C., Feller, U., Buchmann, N., 2010. Competitive advantage of *Rumex obtusifolius* L. Might increase in intensively managed temperate grasslands under drier climate. Agric. Ecosyst. Environ. 135, 15-23.

Godoy, O., de Lemos, J.P., Valladares, F., 2011. Invasive species can handle higher leaf temperature under water stress than Mediterranean natives. Environ. Exp. Bot. 71, 207-214.

Grant, O.M., Tronina, L., Garcia-Plazaola, J.I., Esteban, R., Pereira, J.S., Chaves, M.M., 2015. Resilience of a semi-deciduous shrub, *Cistus salvifolius*, to severe summer drought and heat stress. Funct. Plant Biol. 42, 219-228.

Greer, D.H., 2015. Seasonal changes in the photosynthetic response to CO_2 and temperature in apple (*Malus domestica* cv. 'Red Gala') leaves during a growing season with a high temperature event. Funct. Plant Biol. 42, 309-324.

Grieder, C., Trachsel, S., Hund, A., 2014. Early vertical distribution of roots and its association with drought tolerance in tropical maize. Plant Soil 377, 295-308.

Grigorova, B., Vaseva, I.I., Demirevska, K., Feller, U., 2011. Expression of selected heat shock proteins after individually applied and combined drought and heat stress. Acta Physiol. Plant. 33, 2041-2049.

Grigorova, B., Vassileva, V., Klimchuk, D., Vaseva, I., Demirevska, K., Feller, U., 2012. Drought, high temperature, and their combination affect ultrastructure of chloroplasts and mitochondria in wheat (*Triticum aestivum* L.) leaves. J. Plant Interact. 7, 204-213.

Habash, D.Z., Baudo, M., Hindle, M., Powers, S.J., Defoin-Platel, M., Mitchell, R., Saqi, M., Rawlings, C., Latiri, K., Araus, J.L., Abdulkader, A., Tuberosa, R., Lawlor, D.W., Nachit, M.M., 2014. Systems responses to progressive water stress in durum wheat. Plos One 9, e108431.

Haldimann, P., Feller, U., 2004. Inhibition of photosynthesis by high temperature in oak (*Quercus pubescens* L.) leaves grown under natural conditions closely correlates with a reversible heat-dependent reduction of the activation state of ribulose-1,5-bisphosphate carboxylase/oxygenase. Plant Cell Environ. 27, 1169-1183.

Haldimann, P., Feller, U., 2005. Growth at moderately elevated temperature alters the physiological response of the photosynthetic apparatus to heat stress in pea (*Pisum sativum* L.) leaves. Plant Cell Environ. 28, 302-317.

Haldimann, P., Gallé, A., Feller, U., 2008. Impact of an exceptionally hot dry summer on photosynthetic traits in oak (*Quercus pubescens*) leaves. Tree Physiol. 28, 785-795.

Haupt-Herting, S., Klug, K., Fock, H.P., 2001. A new approach to measure gross CO_2 fluxes in leaves. Gross CO_2 assimilation, photorespiration, and mitochondrial respiration in the light in tomato under drought stress. Plant Physiol. 126, 388-396.

Hormaetxe, K., Becerril, J.M., Hernandez, A., Esteban, R., Garcia-Plazaola, J.I., 2007. Plasticity of photoprotective mechanisms of *Buxus sempervirens* L. leaves in response to extreme temperatures. Plant Biol. 9, 59-68.

Hörtensteiner, S., Feller, U., 2002. Nitrogen metabolism and remobilization during senescence. J. Exp. Bot. 53, 927-937.

Hozain, M.I., Salvucci, M.E., Fokar, M., Holaday, A.S., 2010. The differential response of photosynthesis to high temperature for a boreal and temperate *Populus* species relates to differences in Rubisco activation and Rubisco activase properties. Tree Physiol. 30, 32-44.

Hu, B., Simon, J., Rennenberg, H., 2013. Drought and air warming affect the species-specific levels of stress-related foliar metabolites of three oak species on acidic and calcareous soil. Tree Physiol. 33, 489-504.

IPPC, 2012. Summary for Policymakers, in: Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change, eds C.B. Field, V. Barros, T.F. Stocker, D. Qin, D.J. Dokken, K.L. Ebi et al. (Cambride: Cambridge University Press), 1-19.

Jagadish, K.S.V., Kadam, N.N., Xiao, G., Melgar, R.J., Bahuguna, R.N., Quinones, C., Tamilselvan, A., Prasad, P.V.V., 2014. Agronomic and physiological responses to high temperature, drought, and elevated CO_2 interactions in cereals. In: Advances in Agronomy, Vol. 127, D.L. Sparks, ed., pp 111-156.

Jain, R., Chandra, A., Venugopalan, V.K., Solomon, S., 2015. Physiological changes and expression of SOD and P5CS genes in response to water deficit in sugarcane. Sugar Tech. 17, 276-282.

Jentsch, A., Kreyling, J., Elmer, M., Gellesch, E., Glaser, B., Grant, K., et al., 2011. Climate extremes initiate ecosystem-regulating functions while maintaining productivity. J. Ecol. 99, 689-702.

Ji, X.M., Shiran, B., Wan, J.L., Lewis, D.C., Jenkins, C.L.D., Condon, A.G., Richards, R.A., Dolferus, R., 2010. Importance of pre-anthesis anther sink strength for maintenance of grain number during reproductive stage water stress in wheat. Plant Cell Environ. 33, 926-942.

Jones, H.G., 1998. Stomatal control of photosynthesis and transpiration. J. Exp. Bot. 49, 387-398.

Jones, H.G., 1999. Use of thermography for quantitative studies of spatial and temporal variation of stomatal conductance over leaf surfaces. Plant Cell Environ. 22, 1043-1055.

Jones, H.G., Serraj, R., Loveys, B.R., Xiong, L.Z., Wheaton, A., Price, A.H., Adam, H., 2009. Thermal infrared imaging of crop canopies for the remote diagnosis and quantification of plant responses to water stress in the field. Funct. Plant Biol. 36, 978-989.

Jones, H.G., Stoll, M., Santos, T., de Sousa, C., Chaves, M.M., Grant, O.M., 2002. Use of infrared thermography for monitoring stomatal closure in the field: application to grapevine. J. Exp. Bot. 53, 2249-2260.

Jones, H.G., Sutherland, R.A., 1991. Stomatal control of xylem embolism. Plant Cell Environ. 14, 607-612.

Kaiser, M.E., Morales, A.; Harbinson, J.; Kromdijk, J.; Heuvelink, E.; Marcelis, L.F.M., 2015. Dynamic photosynthesis in different environmental conditions. J. Exp. Bot. 66, 2415-2426.

Keown, J.R., Pearce, F.G., 2014. Characterization of spinach ribulose-1,5-bisphosphate carboxylase/oxygenase activase isoforms reveals hexameric assemblies with increased thermal stability. Biochem. J. 464, 413-423.

Kesari, R., Lasky, J.R., Villamor, J.G., Maarais, D.L.D., Chen, Y.J.C., Liu, T.W., Lin, W., Juenger, T.E., Verslues, P.E., 2012. Intron-mediated alternative splicing of *Arabidopsis* P5CS1 and its association with natural variation in proline and climate adaptation. Proc. Natl. Acad. Sci. U.S.A. 109, 9197-9202.

Kim, K.M., Portis, A.R., 2006. Kinetic analysis of the slow inactivation of Rubisco during catalysis: Effects of temperature, O_2 and Mg^{++}. Photosynthesis Res. 87, 195-204.

Knutti R., Rogelj, J., Sedlacek, J., Fischer, E.M., 2016. A scientific critique of the two-degree climate change target. Nature Geosci. 9, 13-19.

Kozlowski, T.T., Pallardy, S.G., 2002. Acclimation and adaptive responses of woody plants to environmental stresses. Bot. Rev. 68, 270-334.

Kuhn, A.R., Grill, S., Baumgarten, M., Ankerst, D.P., Matyssek, R., 2015. Daily growth of European beech (*Fagus sylvatica* L.) on moist sites is affected by short-term drought rather than ozone uptake. Trees-Structure and Function, 29, 1501-1519.

Kumar, A., Li, C.S., Portis, A.R., 2009. *Arabidopsis thaliana* expressing a thermostable chimeric Rubisco activase exhibits enhanced growth and higher rates of photosynthesis at moderately high temperatures. Photosynthesis Res. 100, 143-153.

Kurek, I., Chang, T.K., Bertain, S.M., Madrigal, A., Liu, L., Lassner, M.W., Zhu, G.H., 2007. Enhanced thermostability of *Arabidopsis* Rubisco activase improves photosynthesis and growth rates under moderate heat stress. Plant Cell 19, 3230-3241.

Law, R.D., Crafts-Brandner, S.J., 1999. Inhibition and acclimation of photosynthesis to heat stress is closely correlated with activation of ribulose-1,5-bisphosphate carboxylase/oxygenase. Plant Physiol. 120, 173-182.

Lee, S., Seo, P.J., Lee, H.J., Park, C.M., 2012. A NAC transcription factor NTL4 promotes reactive oxygen species production during drought-induced leaf senescence in *Arabidopsis.* Plant J. 70, 831-844.

Lee, B.-R., Lee, D.-G., Avice, J.-C., Kim, T.-H., 2014. Characterization of vegetative storage protein (VSP) and low molecuar proteins induced by water deficit in stolon of white clover. Biochem. Biophys. Res. Commun.443, 229-233.

Li, C.H., Salvucci, M.E., Portis, A.R., 2005. Two residues of rubisco activase involved in recognition of the rubisco substrate. J. Biol. Chem. 280, 244864-24869.

Li, J.X., Wang, X.Q., Watson, M.B., Assmann, S.M., 2000. Regulation of abscisic acid-induced stomatal closure and anion channels by guard cell AAPK kinase. Science 287, 300-303.

Lipiec, J., Doussan, C., Nosalewicz, A., Kondracka, K., 2013. Effect of drought and heat stress on plant growth and yield: a review. Intern. Agrophys. 27, 463-477.

Liu, S.H., Wang, J., Cong, B.L., Huang, X.H., Chen, K.S., Zhang, P.Y., 2014. Characterization and expression analysis of a mitochondrial heat-shock protein 70 gene from the Antarctic moss *Pohlia nutans.* Polar Biol. 37, 1145-1155.

Liu, X., Jin, H., Wang, G.H., Herbert, S.J., 2008. Soybean yield physiology and development of high-yielding practices in Northeast China. Field Crops Res. 105, 157-171.

Locato, V, Gadaleta, C., De Gara, L., De Pinto, M.C., 2008. Production of reactive species and modulation of antioxidant network in response to heat shock: A critical balance for cell fate. Plant Cell Environ. 31, 1606-1619.

Locato, V., de Pinto, M.C., De Gara, L., 2009. Different involvement of the mitochondrial, plastidial and cytosolic ascorbate-glutathione redox enzymes in heat shock responses. Physiol. Plant. 135, 296-306.

Lopes, M.S., El-Basyoni, I., Baenziger, P.S., Singh, S., Royo, C., Ozbek, K., Aktas, H., Ozer, E., Ozdemir, F., Manickavelu, A., Ban, T., Vikram, P., 2015. Exploiting genetic diversity from landraces in wheat breeding for adaptation to climate change. J. Exp. Bot. 66, 3477-3486.

Loreto, F., Centritto, M., 2008. Leaf carbon assimilation in a water-limited world. Plant Biosyst. 142, 154-161.

Loreto, F., Harley, P.C., Dimarco, G., Sharkey, T.D., 1992. Estimation of mesophyll conductance to CO_2 flux by 3 different methods. Plant Physiol. 98, 1437-1443.

Luna-Flores, W., Estrada-Medina, H., Morales-Maldonado, E., Alvarez-Rivera, O., 2015. Plant stress by water deficit: a review. Chilean J. Agric. Anim. Sci. 31, 61-69.

Marquez-Garcia, B., Shaw, D., Cooper, J.W., Karpinska, B., Quain, M.D., Makgopa, E.M., Kunert, K., Foyer, C.H., 2015. Redox markers for drought-induced nodule senescence, a process occurring after drought-induced senescence of the lowest leaves in soybean (*Glycine max*). Ann. Bot. 116, 497-510.

Mathur, S., Allakhverdiev, S.I., Jajoo, A., 2011. Analysis of high temperature stress on the dynamics of antenna size and reducing side heterogeneity of Photosystem II in wheat leaves (*Triticum aestivum*). Biochim. Biophys. Acta-Bioenergetics, 1807, 22-29.

Medrano, H., Escalona, J.M., Bota, J., Gulias, J., Flexas, J., 2002. Regulation of photosynthesis of C-3 plants in response to progressive drought: Stomatal conductance as a reference parameter. Ann. Bot. 89, 895-905.

Mittal, N., Mishra, A., Singh, R., Kumar, P., 2014. Assessing future changes in seasonal climatic extremes in the Ganges river basin using an ensemble of regional climate models. Clim. Change 123, 273-286.

Mittler, R., 2002. Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci. 7, 405-410.

Mittler, R., Zilinskas, B.A., 1994. Regulation of pea cytosolic ascorbate peroxidase and other antioxidant enzymes during the progression of drought stress and following recovery from drought. Plant J. 5, 397-405.

Molina-Rueda, J.J., Kirby, E.G., 2015. Transgenic poplar expressing the pine GS1 a show alterations in nitrogen homeostasis during drought. Plant Physiol. Biochem. 94, 181-190.

Moller, M., Alchanatis, V., Cohen, Y., Meron, M., Tsipris, J., Naor, A., Ostrovsky, V., Sprintsin, M., Cohen, S., 2007. Use of thermal and visible imagery for estimating crop water status of irrigated grapevine. J. Exp. Bot. 58, 827-838.

Morales, L.V., Coopman, R.E., Rojas, R., Escandon, A.B., Flexas, J., Galmes, J., Garcia-Plazaola, J.I., Gago, J., Cabrera, H.M., Corcuera, L.J., 2014. Acclimation of leaf cohorts expanded under light and water stresses: an adaptive mechanism of Eucryphia cordifolia to face changes in climatic conditions? Tree Physiol. 34, 1305-1320.

Morison, J.I.L., Lawson, T., 2007. Does lateral gas diffusion matter? Plant Cell Environ. 30, 1072-1085.

Moshelion, M., Halperin, O. Wallach, R., Oren, R., Way, D.A., 2015. Role of aquaporins in determining transpiration and photosynthesis in water-stressed plants: crop water-use efficiency, growth and yield. Plant Cell Environ. 38, 1785-1793.

Mueller-Cajar, O., Stotz, M., Bracher, A., 2014. Maintaining photosynthetic CO_2 fixation via protein remodelling: the Rubisco activases. Photosynth. Res. 119, 191-201.

Munne-Bosch, S. Alegre, L., 2000. The significance of beta-carotene, alpha-tocopherol and the xanthophyll cycle in droughted *Melissa officinalis* plants. Aust. J. Plant Physiol. 27, 139-146.

Munne-Bosch, S., Alegre, L., 2004. Die and let live: Leaf senescence contributes to plant survival under drought stress. Funct. Plant Biol. 31, 203-216.

Munne-Bosch, S., Jubany-Mari, T., Alegre, L., 2001. Drought-induced senescence is characterized by a loss of antioxidant defenses in chloroplasts. Plant Cell Environ. 24, 1319-1327.

Nippert, J.B., Holdo, R.M., 2015. Challenging the maximum rooting depth paradigm in grasslands and savannas. Funct. Ecol. 29, 739-745.

Noctor, G., Veljovic-Jovanovic, S., Driscoll, S., Novitskaya, L., Foyer, C.H., 2002. Drought and oxidative load in the leaves of c-3 plants: A predominant role for photorespiration? Ann. Bot. 89, 841-850.

Osorio, M.L., Osorio, J., Vieira, A.C., Goncalves, S., Romano, A., 2011. Influence of enhanced temperature on photosynthesis, photooxidative damage, and antioxidant strategies in *Ceratonia siliqua* L. seedlings subjected to water deficit and rewatering. Photosynthetica, 49, 3-12.

Oukarroum, A., Schansker, G., Strasser, R.J., 2009. Drought stress effects on photosystem I content and photosystem II thermotolerance analyzed using Chl a fluorescence kinetics in barley varieties differing in their drought tolerance. Physiol. Plant. 137, 188-199.

Pantin, F., Simmoneau, T., Muller, B., 2012. Coming of leaf age: control of growth by hydraulics and metabolics during leaf ontogeny. New Phytol. 196, 349-366.

Park, S.H., Jun, S.S., An, G.H., Hong, Y.N., Park, M.C., 2003. A comparative study on the protective role of trehalose and LEA proteins against abiotic stresses in transgenic Chinese cabbage (*Brassica campestris*) overexpressing CaLEA or otsA. J. Plant Biol. 46, 277-286.

Parry, M.A.J., Reynolds, M., Salvucci, M.E., Raines, C., Andralojc, P J., Zhu, X.G., Price, G.D., Condon, A.G., Furbank, R.T., 2011. Raising yield potential of wheat. Ii. Increasing photosynthetic capacity and efficiency. J. Exp. Bot. 62, 453-467.

Pinheiro, C., Guerra-Guimaraes, L., David, T.S., Vieira, A., 2014. Proteomics: State of the art to study Mediterranean woody species under stress. Environ. Exp. Bot. 103, 117-127.

Pinheiro, C., Chaves, M.M., 2011. Photosynthesis and drought: can we make metabolic connections from available data? J. Exp. Bot. 62, 869-882.

Portis A.R., 2003. Rubisco activase-Rubisco's catalytic chaperone. Photosynth. Res. 75, 11-27.

Portis, A.R., Li, C.S., Wang, D.F., Salvucci, M.E., 2008. Regulation of Rubisco activase and its interaction with Rubisco. J. Exp. Bot. 59, 1597-1604.

Prechsl, U.E.; Burri, S; Gilgen, A.K.; Kahmen, A.; Buchmann, N., 2015.No shift to a deeper water uptake depth in response to summer drought of two lowland and sub-alpine C3-grasslands in Switzerland. .Oecologia 177 (1): 97-111.

Price, A.H., Cairns, J.E., Horton, P., Jones, H.G., Griffiths, H., 2002. Linking drought-resistance mechanisms to drought avoidance in upland rice using a QTL approach: progress and new opportunities to integrate stomatal and mesophyll responses. J. Exp. Bot. 53, 989-1004.

Priest, H.D., Fox, S.E., Rowley, E.R., Murray, J.R., Michael, T.P., Mockler, T.C., 2014. Analysis of global gene expression in *Brachypodium distachyon* reveals extensive network plasticity in response to abiotic stress. Plos One 9, e87499.

Prior, S.A., Runion, G.B., Marble, S.C., Rogers, H.H., Gilliam, C.H., Torbert, H.A., 2011. A review of elevated atmospheric CO_2 effects on plant growth and water relations: Implications for horticulture. Hortscience 46, 158-162.

Ramya, K.T., Jain, N., Ramya, P., Singh, P.K., Aroral, A., Singh, G.P., Prabhu, K.V., 2015. Genotypic variation for normalized difference vegetation index and its relationship with grain yield in wheat under terminal heat stress. Indian Journal of Genetics and Plant Breeding, 75, 174-182.

Reddy, A.R., Chaitanya, K.V., Vivekanandan, M., 2004. Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. J. Plant Physiol. 161, 1189-1202.

Reynolds-Henne, C.E., Langenegger, A., Mani, J., Schenk, N., Zumsteg, A., Feller, U., 2010. Interactions between temperature, drought and stomatal opening in legumes. Environ. Exp. Bot. 68, 37-43.

Rivero, R.M., Shulaev, V., Blumwald, E., 2009. Cytokinin-dependent photorespiration and the protection of photosynthesis during water deficit. Plant Physiol. 150, 1530-1540.

Rodriguez-Dominguez, C.M., Ehrenberger, W., Sann, C., Ruger, S., Sukhorukov, V., Martin-Palomo, M.J., Diaz-Espejo, A., Cuevas, M.V., Torres-Ruiz, J.M., Perez-Martin, A., Zimmermann, U., Fernandez, J.E., 2012. Concomitant measurements of stem sap flow and leaf turgor pressure in olive trees using the leaf patch clamp pressure probe. Agricultural Water Management, 114, 50-58.

Salazar-Parra, C., Aguirreolea, J., Sanchez-Diaz, M., Irigoyen, J.J., Morales, F., 2012. Climate change (elevated CO_2, elevated temperature and moderate drought) triggers the antioxidant enzymes' response of grapevine cv. Tempranillo, avoiding oxidative damage. Physiol. Plant. 144, 99-110.

Salvucci, M.E., 2008. Association of Rubisco activase with chaperonin-60 beta: a possible mechanism for protecting photosynthesis during heat stress. J. Exp. Bot. 59, 1923-1933.

Salvucci, M.E., Crafts-Brandner, S.J., 2004. Relationship between the heat tolerance of photosynthesis and the thermal stability of Rubisco activase in plants from contrasting thermal environments. Plant Physiol. 134, 1460-1470.

Salvucci, M.E., DeRidder, B.P., Portis, A.R., 2006. Effect of activase level and isoform on the thermotolerance of photosynthesis in *Arabidopsis*. J. Exp. Bot. 57, 3793-3799.

Salvucci, M.E., Osteryoung, K.W., Crafts-Brandner, S.J., Vierling, E., 2001. Exceptional sensitivity of Rubisco activase to thermal denaturation in vitro and in vivo. Plant Physiol. 127, 1053-1064.

Salvucci, M.E., van de Loo, F.J., Stecher, D., 2003. Two isoforms of Rubisco activase in cotton, the products of separate genes not alternative splicing. Planta 216, 736-744.

Sanchez, E., Scordia, D., Lino, G., Arias, C., Cosentino, S.L., Nogues, S., 2015. Salinity and water stress effects on biomass production in different *Arundo donax* L. clones. Bioenergy Res. 8, 1461-1479.

Save, R., Penuelas, J., Marfa, O., Serrano, L., 1993. Changes in leaf osmotic and elastic properties and canopy structure of strawberries under mild water-stress. Hortscience, 28, 925-927.

Schär, C., Vidale, P. L., Luthi, D., Frei, C., Haberli, C., Liniger, M.A., Appenzeller, C., 2004. The role of increasing temperature variability in European summer heat waves. Nature 427, 332-336.

Schroeder, J.I., Kwak, J.M., Allen, G.J., 2001. Guard cell abscisic acid signalling and engineering drought hardiness in plants. Nature 410, 327-330.

Scoffoni, C., Vuong, C., Diep, S., Cochard, H., Sack, L., 2014. Leaf shrinkage with dehydration: Coordination with hydraulic vulnerability and drought tolerance. Plant Physiol. 164, 1772-1788.

Seco, R., Karl, T., Guenther, A., Hosman, K.P., Pallardy, S.G., Gu, L.H., Geron, C., Harley, P., Kim, S., 2015. Ecosystem-scale volatile organic compound fluxes during an extreme drought in a broadleaf temperate forest of the Missouri Ozarks (central USA). Global Change Biol. 21, 3657-3674.

Sekmen, A.H., Ozgur, R., Uzilday, B., Turkan, I., 2014. Reactive oxygen species scavenging capacities of cotton (*Gossypium hirsutum*) cultivars under combined drought and heat induced oxidative stress. Environ. Exp. Bot. 99, 141-149.

Selote, D.S., Bharti, S., Khanna-Chopra, R., 2004. Drought acclimation reduces $O_2\cdot$ accumulation and lipid peroxidation in wheat seedlings. Biochem. Biophys. Res. Commun. 314, 724-729.

Sharkey, T.D., 2005. Effects of moderate heat stress on photosynthesis: Importance of thylakoid reactions, Rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. Plant Cell Environ. 28, 269-277.

Signarbieux, C., Feller, U., 2011. Non-stomatal limitations of photosynthesis in grassland species under artificial drought in the field. Environ. Exp. Bot. 71, 192-197.

Signarbieux, C., Feller, U., 2012. Effects of an extended drought period on physiological properties of grassland species in the field. J. Plant Res. 125, 251-261.

Simova-Stoilova, L., Demirevska, K., Petrova, T., Tsenov, N., Feller, U., 2009. Antioxidative protection and proteolytic activity in tolerant and sensitive wheat (*Triticum aestivum* L.) varieties subjected to long-term field drought. Plant Growth Regul. 58, 107-117.

Simova-Stoilova, L., Vaseva, I., Grigorova, B., Demirevska, K., Feller, U., 2010. Proteolytic activity and cysteine protease expression in wheat leaves under severe soil drought and recovery. Plant Physiol. Biochem. 48, 200-206.

Simova-Stoilova, L.P., Romero-Rodriguez, M.C., Sanchez-Lucas, R., Navarro-Cerrillo, R.M., Medina-Aunon, J.A., Jorrin-Novo, J.V., 2015. 2-DE proteomics analysis of drought treated seedlings of *Quercus ilex* supports a root active strategy for metabolic adaptation in response to water shortage. Front. Plant Sci. 6, 627.

Singh, J., Pandey, P., James, D., Chandrasekhar, K., Achary, V.M.M., Kaul, T., Tripathi, B.C., Reddy, M.K., 2014. Enhancing C3 photosynthesis: an outlook on feasible interventions for crop improvement. Plant Biotech. J. 12, 1217-1230.

Snider, J.L., Oosterhuis, D.M., Kawakami, E.M., 2010. Genotypic differences in thermotolerance are dependent upon prestress capacity for antioxidant protection of the photosynthetic apparatus in *Gossypium hirsutum*. Physiol. Plant. 138, 268-277.

Song, M.Z., Fab, S.L., Pang, C.Y., Wei, H.L., Yu, S.X., 2014. Genetic analysis of the antioxidant enzymes, methane dicarboxylic aldehyde (MDA) and chlorophyll content in leaves of the short season cotton (*Gossypium hirsutum* L.). Euphytica 198, 153-162.

Stockey, R.A., Ko, H., 1986. Cuticle micromorphology of *Araucaria dejussieu*. Bot. Gaz. 147, 508-548.

Swart, R., Biesbroek, R., Lourenço T.C., 2014. Science *of* adaptation to climate change and science *for* adaptation. Front. Environ. Sci. 2, 29.

Teskey, R., Wertin, T., Bauweraerts, I., Ameye, M., McGuire, M.A., Steppe, K., 2015. Responses of tree species to heat waves and extreme heat events. Plant Cell Environ. 38, 1699-1712.

Thoenen, M., Herrmann, B., Feller, U., 2007. Senescence in wheat leaves: Is a cysteine endopeptidase involved in the degradation of the large subunit of Rubisco? Acta Physiol. Plant. 29, 339-350.

Topbjerg, H.B., Kaminski, K.P., Markussene, B., Korup, K., Nielsen, K.L., Kirk, H.G., Andersen, M.N., Liu, F.L., 2014. Physiological factors affecting intrinsic water use efficiency of potato clones within a dihaploid mapping population under well-watered and drought-stressed conditions. Sci. Hort. 178, 61-69.

Turner, L.R., Holloway-Phillips, M.M., Rawnsley, R.P., Donaghy, D.J., Pembleton, K.G., 2012. The morphological and physiological responses of perennial ryegrass (*Lolium perenne* L.), cocksfoot (*Dactylis glomerata* L.) and tall fescue (*Festuca arundinacea* Schreb.; syn. *Schedonorus phoenix* Scop.) to variable water availability. Grass Forage Sci. 67, 507-518.

Valladares, F., Pearcy, R.W., 1997. Interactions between water stress, sun-shade acclimation, heat tolerance and photoinhibition in the sclerophyll *Heteromeles arbutifolia*. Plant Cell Environ. 20, 25-36.

Vanzo, E., Jud, W., Li, Z.R., Albert, A., Domagalska, M.A., Ghirardo, A., Niederbacher, B., Frenzel, J., Beemster, G.T.S., Asard, H., Rennenberg, H., Sharkey, T.D., Hansel, A., Schnitzler, J.P., 2015. Facing the future: Effects of short-term climate extremes on isoprene-emitting and nonemitting poplar. Plant Physiol. 169, 560-+.

Vaseva, I.I., Anders, I., Feller, U., 2014. Identification and expression of different dehydrin subclasses involved in the drought response of *Trifolium repens*. J. Plant Physiol. 171, 213-224.

Vaseva, I.I., Feller, U., 2013. Natural antisense transcripts of *Trifolium repens* dehydrins. Plant Signaling & Behavior 8:12, e27674.

Vassileva, V., Demirevska, K., Simova-Stoilova, L., Petrova, T., Tsenov, N., Feller, U., 2012. Long-term field drought affects leaf protein pattern and chloroplast ultrastructure of winter wheat in a cultivar-specific manner. J. Agr. Crop Sci. 198, 104-117.

Vassileva, V., Signarbieux, C., Anders, I., Feller, U., 2011. Genotypic variation in drought stress response and subsequent recovery of wheat (*Triticum aestivum* L.). J. Plant Res. 124, 147-154

Vassileva, V., Simova-Stoilova, L., Demirevska., Feller, U., 2009. Variety-specific response of wheat (*Triticum aestivum* L.) leaf mitochondria to drought stress. J. Plant Res. 122, 445-454.

Vavasseur, A., Raghavendra, A.S., 2005. Guard Cell metabolism and CO_2 sensing. New Phytol. 165, 665-682.

Velikova, V., Pinelli, P., Loreto, F. 2005. Consequences of inhibition of isoprene synthesis in *Phragmites australis* leaves exposed to elevated temperatures. Agric. Ecosyst. Environ. 106, 209-217.

Velikova, V.B., 2008. Isoprene as a tool for plant protection against abiotic stresses. J. Plant Interact. 3, 1-15.

Vile, D., Pervent, M., Belluau, M., Vasseur, F., Bresson, J., Muller, B., Granier, C., Simonneau, T., 2012. Arabidopsis growth under prolonged high temperature and water deficit: independent or interactive effects. Plant Cell Environ. 35, 702-718.

Volaire, F., Lelievre, F., 2001. Drought survival in *Dactylis glomerata* and *Festuca arundinacea* under similar rooting conditions in tubes. Plant Soil 229, 225-234.

Wachter, R.M., Salvucci, M.E., Carmo-Silva, A.E., Barta, C.,Genkov, T., Spreitzer, R.J., 2013. Activation of interspecies-hybrid Rubisco enzymes to assess different models for the Rubisco-Rubisco activase interaction. Photosynth. Res. 117, 557-566.

Wang, A.Q., Yu, X.H., Mao, Y., Liu, Y., Liu, G.Q., Liu, Y.S., Niu, X.L., 2015. Overexpression of a small heat-shock-protein gene enhances tolerance to abiotic stresses in rice. Plant Breeding, 134, 384-393.

Wang, G.P., Hui, Z., Li, F., Zhao, M.R., Zhang, J., Wang, W., 2010. Improvement of heat and drought photosynthetic tolerance in wheat by overaccumulation of glycinebetaine. Plant Biotechnol. Rep. 4, 213-222.

Wani, S.H., Sah, S.K., Sagi, L., Solymosi, K., 2015. Transplastomic plants for innovations in agriculture. A review. Agronomy for Sustainable Development, 35, 1391-1430.

Wegener, C.B., Jansen, G., Jurgens, H.U., 2015. Bioactive compounds in potatoes: Accumulation under drought stress conditions. Functional Foods in Health and Disease, 5, 108-116.

Wehner, G.G., Balko, C.C., Enders, M.M., Humbeck, K.K., Ordon, F.F., 2015. Identification of genomic regions involved in tolerance to drought stress and drought stress induced leaf senescence in juvenile barley. BMC Plant Biology, 15, 125.

Werneke J.M., Chatfield, J.M., Ogren, W.L., 1989. Alternative messenger-RNA splicing generates the 2 Ribulosebisphosphate carboxylase oxygenase activase polypeptides in spinach and *Arabidopsis*. Plant Cell 1, 815-825.

Werner, C., Correia, O., Beyschlag, W., 1999. Two different strategies of Mediterranean macchia plants to avoid photoinhibitory damage by excessive radiation levels during summer drought. Acta Oecol.-Int. J. Ecol. 20, 15-23

Wilkinson, S., Davies, W.J., 2002. ABA-based chemical signalling: the co-ordination of responses to stress in plants. Plant Cell Environ. 25, 195-210.

Wimmer, M.A., Eichert, T., 2013. Review: Mechanisms for boron deficiency-mediated changes in plant water relations. Plant Sci. 203, 25-32.

Wingler, A., Quick, W.P., Bungard, R.A., Bailey, K.J., Lea, P.J., Leegood, R.C., 1999. The role of photorespiration during drought stress: An analysis utilizing barley mutants with reduced activities of photorespiratory enzymes. Plant Cell Environ. 22, 361-373.

Wujeska, A., Bossinger, G., Tausz, M., 2013. Responses of foliar antioxidative and photoprotective defence systems of trees to drought: a meta-analysis. Tree Physiol. 33, 1018-1029.

Xiao, X.W., Xu, X., Yang, F., 2008. Adaptive responses to progressive drought stress in two *Populus cathayana* populations. Silva Fennica, 42, 705-719.

Xiao, X.W., Yang, F., Zhang, S., Korpelainen, H., Li, C.Y., 2009. Physiological and proteomic responses of two contrasting *Populus cathayana* populations to drought stress. Physiol. Plant. 136, 150-168.

Xu, J., Duan, X.G., Yang, J., Beeching, J.R., Zhang, P., 2013. Enhanced reactive oxygen species scavenging by overproduction of superoxide dismutase and catalase delays postharvest physiological deterioration of cassava storage roots. Plant Physiol. 161, 1517-1528.

Xu, Z.Z., Jiang, Y.L., Zhou, G.S., 2015. Response and adaptation of photosynthesis, respiration, and antioxidant systems to elevated CO_2 with environmental stress in plants. Front. Plant Sci. 6, 701.

Xu, Z.Z., Zhou, G.S., 2006. Combined effects of water stress and high temperature on photosynthesis, nitrogen metabolism and lipid peroxidation of a perennial grass *Leymus chinensis*. Planta 224, 1080-1090.

Yamori, W., Masumoto, C., Fukayama, H., Makino, A., 2012. Rubisco activase is a key regulator of non-steady-state photosynthesis at any leaf temperature and, to a lesser extent, of steady-state photosynthesis at high temperature. Plant J. 71, 871-880.

Yan, K., Chen, P., Shao, H., Zhang, L., Xu, G., 2011. Effects of short-term high temperature on photosynthesis and photosystem II performance in Sorghum. J. Agr. Crop Sci. 197, 400-408.

Yang, J., Ordiz, M.I., Jaworski, J.G., Beachy, R.N., 2011. Induced accumulation of cuticular waxes enhances drought tolerance in *Arabidopsis* by changes in development of stomata. Plant Physiol. Biochem. 49, 1448-1455.

Yin, Z., Meng, F., Song, H., Wang, X., Xu, X., Yu, D., 2010. Expression and quantitative trait loci analysis of two genes encoding Rubisco activase in soybean. Plant Physiol. 152, 1625-1737.

Yin, Z., Zhang, Z., Deng, D., Chao, M., Gao, Q., Wang, Y., Yang, Z., Bian, Y., Hao, D., Xu, C. 2014. Characterization of Rubisco activase genes in maize: An α-isoform gene functions alongside a β-isoform gene. Plant Physiol. 164, 2096-2106.

Yordanov, I., Velikova, V., Tsonev, T., 2000. Plant responses to drought, acclimation, and stress tolerance. Photosynthetica 38, 171-186.

Zhan, A., Schneider, H., Lynch, J.P., 2015. Reduced lateral root branching density improves drought tolerance in maize. Plant Physiol. 168, 1603-U885.

Zhang, M.R., Li, X.J., Yang, Y.M., Luo, Z., Liu, C., Gong, M., Zou, Z.R., 2015. An acidified thermostabilizing mini-peptide derived from the carboxyl extension of the larger isoform of the plant Rubisco activase. J. Biotechnol. 212, 116-124.

Zhang, N., Portis, A.R., 1999. Mechanism of light regulation of Rubisco: A specific role for the larger Rubisco activase isoform involving reductive activation by thioredoxin-f. Proc. Natl. Acad. Sci. USA. 96, 9438-9443.

Zhu, L., Guo, J.S., Zhu, J., Zhou, C., 2014. Enhanced expression of EsWAX1 improves drought tolerance with increased accumulation of cuticular wax and ascorbic acid in transgenic *Arabidopsis*. Plant Physiol. Biochem. 75, 24-35.

Zwicke, M., Picon-Cochard, C., Morvan-Bertrand, A., Prud'homme, M.-P., Volaire, F., 2015. What functional strategies drive drought survival and recovery of perennial species from upland grassland? Ann. Bot. 116, 1001-1015.
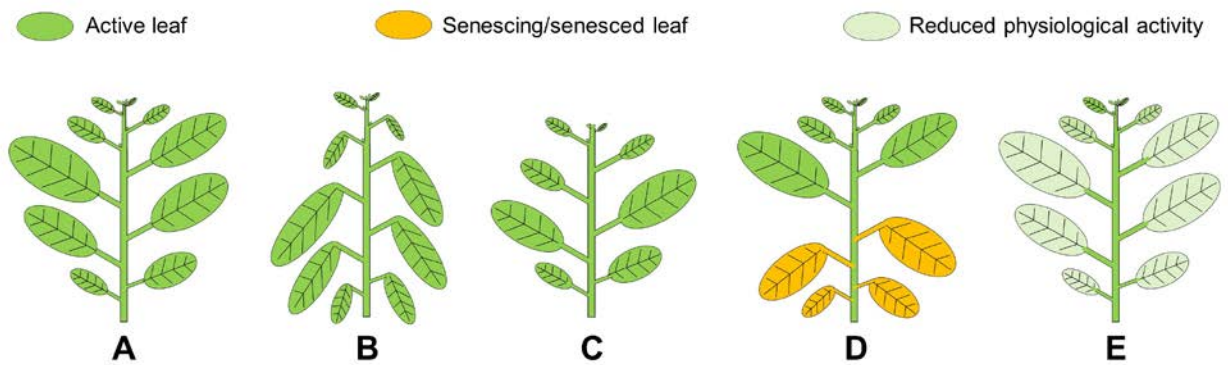
Fig. 1. Scheme representing drought effects on assimilatory capacity. As compared to control plants (A), the assimilatory capacity can be decreased by leaf orientation, rolling or wilting (B), by a reduced formation of new leaves (C), by an anticipated and often atypical leaf senescence (D) and by a decreased physiological activity of leaves (E).
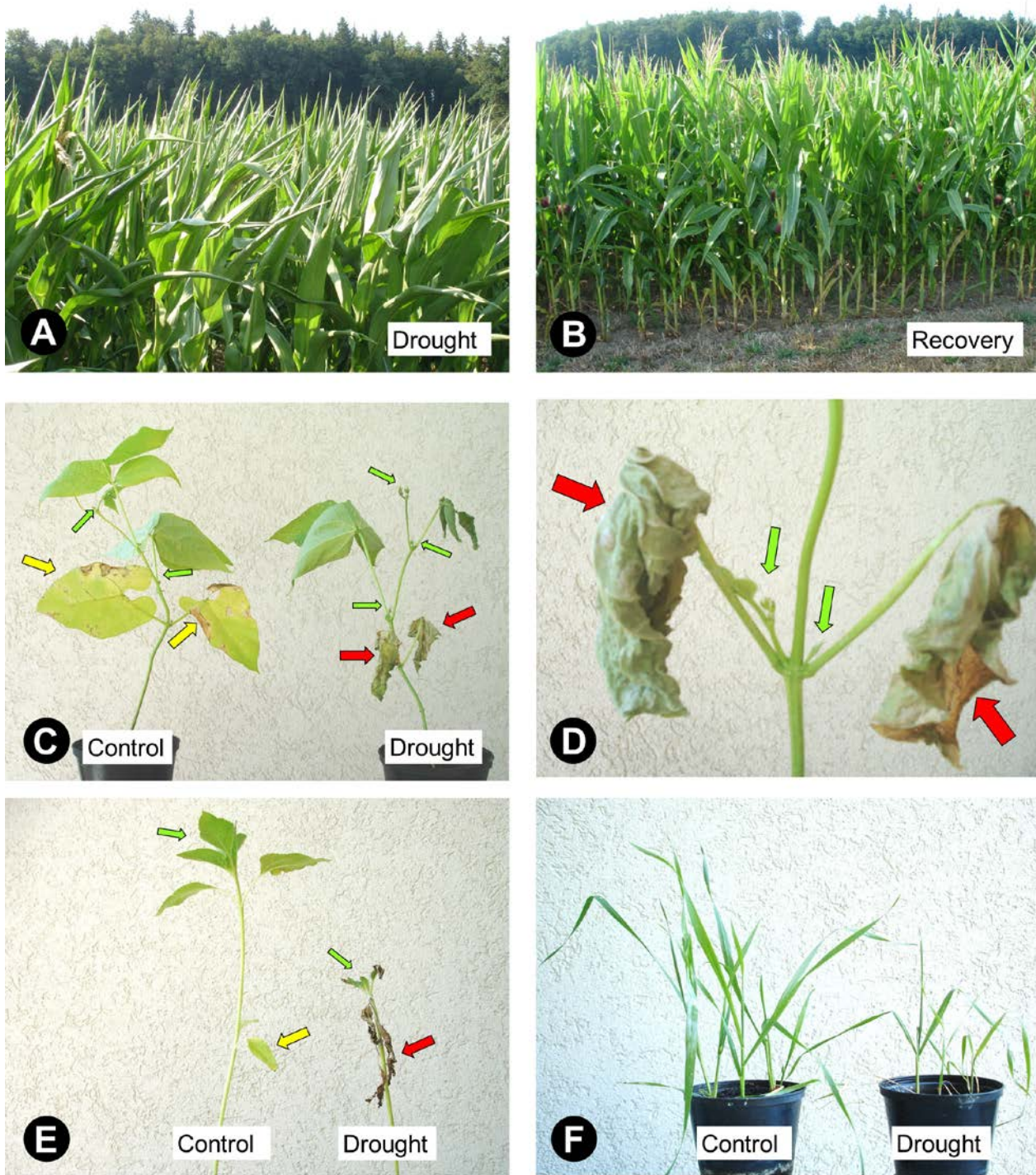
Fig. 2. Impact of severe drought on various crop plants. Leaf rolling is a response to an extended drought period (A) and is reversible during a subsequent recovery phase (B). Several processes affect the active leaf area in dwarf beans (C, D) and in sunflower plants (E): formation of new leaves (green arrows), regular senescence (yellow arrows) and atypical senescence with incomplete chlorophyll and protein catabolism (red arrows). The number of active leaves is decreased in wheat plants exposed to drought (F).
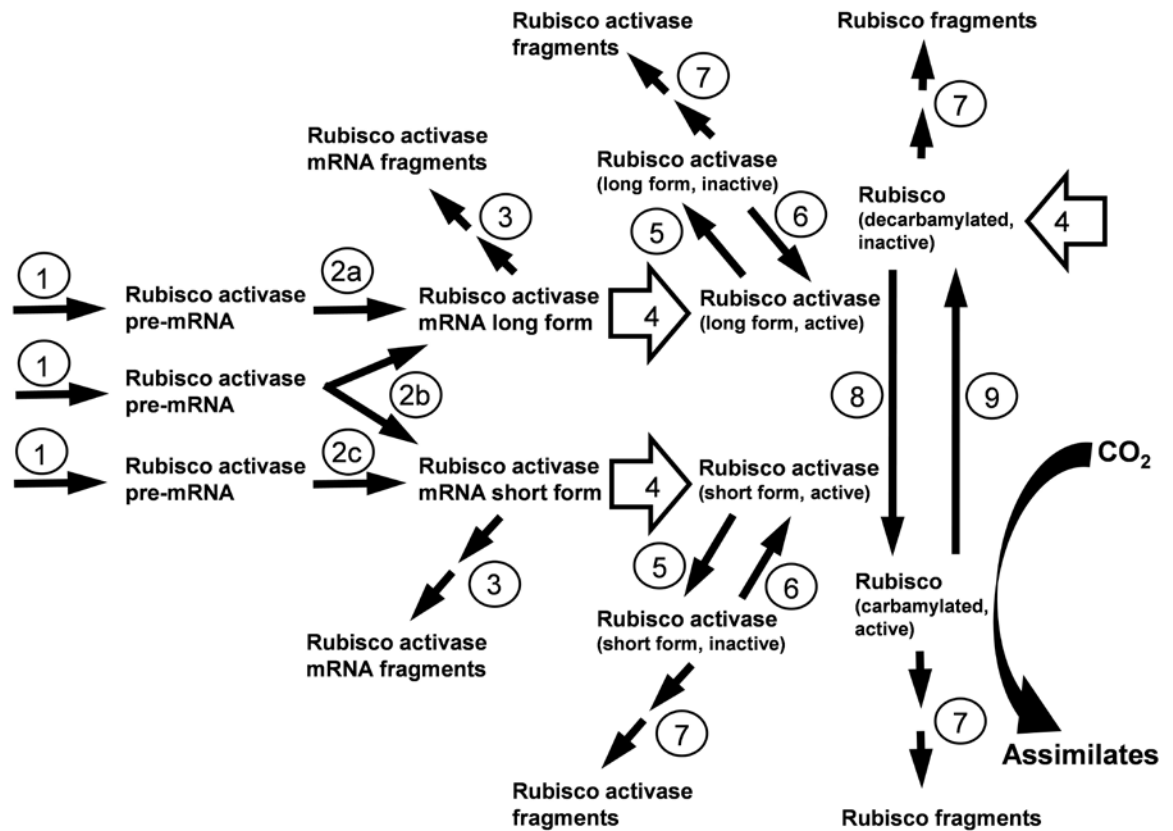
Fig. 3. Steps involved in the heat-induced down-regulation of Rubisco activase and Rubisco activities. The following processes are involved in the control of Rubisco activity and finally also of CO_2 assimilation: transcription of various Rubisco activase genes (1), splicing of pre-mRNA for the longer α-isoform (2a) and the shorter β-isoform (2c) of Rubisco activase, alternative splicing of pre-mRNA for the synthesis of the longer α-isoform as well as the shorter β-isoform (2b), mRNA degradation (3), protein synthesis by translation of various mRNAs (4), reversible inactivation of Rubisco activase (5), reactivation of Rubisco activase (6), irreversible inactivation and degradation of Rubisco activase and of Rubisco (7), Rubisco carbamylation catalyzed by Rubisco activase (8) and spontaneous inactivation of Rubisco ("fallover") and decarbamylation (9).