



Review

Drought stress and carbon assimilation in a warming climate: Reversible and irreversible impacts[☆]



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ABSTRACT

Global change is characterized by increased CO₂ 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 CO₂ 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.

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Contents

1. Introduction.....	85
2. Photosynthetically active leaf area.....	85
3. Drought effects on stomata and on leaf temperature.....	87
4. Impacts on Rubisco and Rubisco activase.....	87
5. Reactive oxygen species and protection of chloroplast constituents.....	89
6. Net CO ₂ assimilation.....	89
7. Conclusions.....	90
Acknowledgements.....	90
References.....	90

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1. Introduction

The continuous increase in atmospheric CO₂ concentration and the rise in mean ambient temperature are well known facts in the course of global change (IPPC, 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., 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 (Valladares 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 et al., 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 CO₂ 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. 1A–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 rewatering, 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. 1A, C) or senescence may start earlier in older leaves (Fig. 1A, 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. 2C–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 is 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. 2C, 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 over-

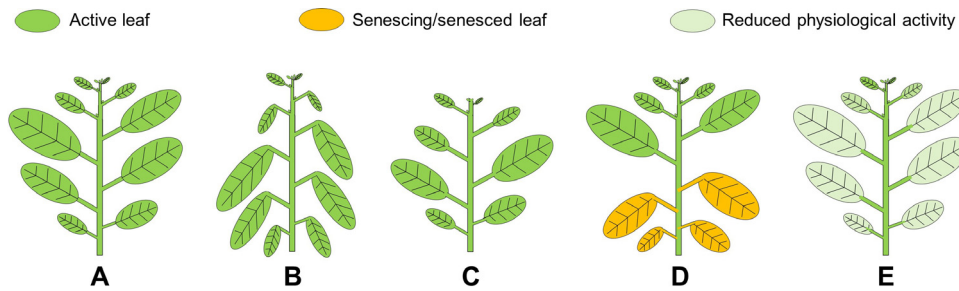


Fig. 1. Scheme representing drought effects on assimilatory capacity. As compared to control plants (A), the assimilatory capacity can be decreased by leaf orientation, rolling or wilting (B), by a reduced formation of new leaves (C), by an anticipated and often atypical leaf senescence (D) and by a decreased physiological activity of leaves (E).

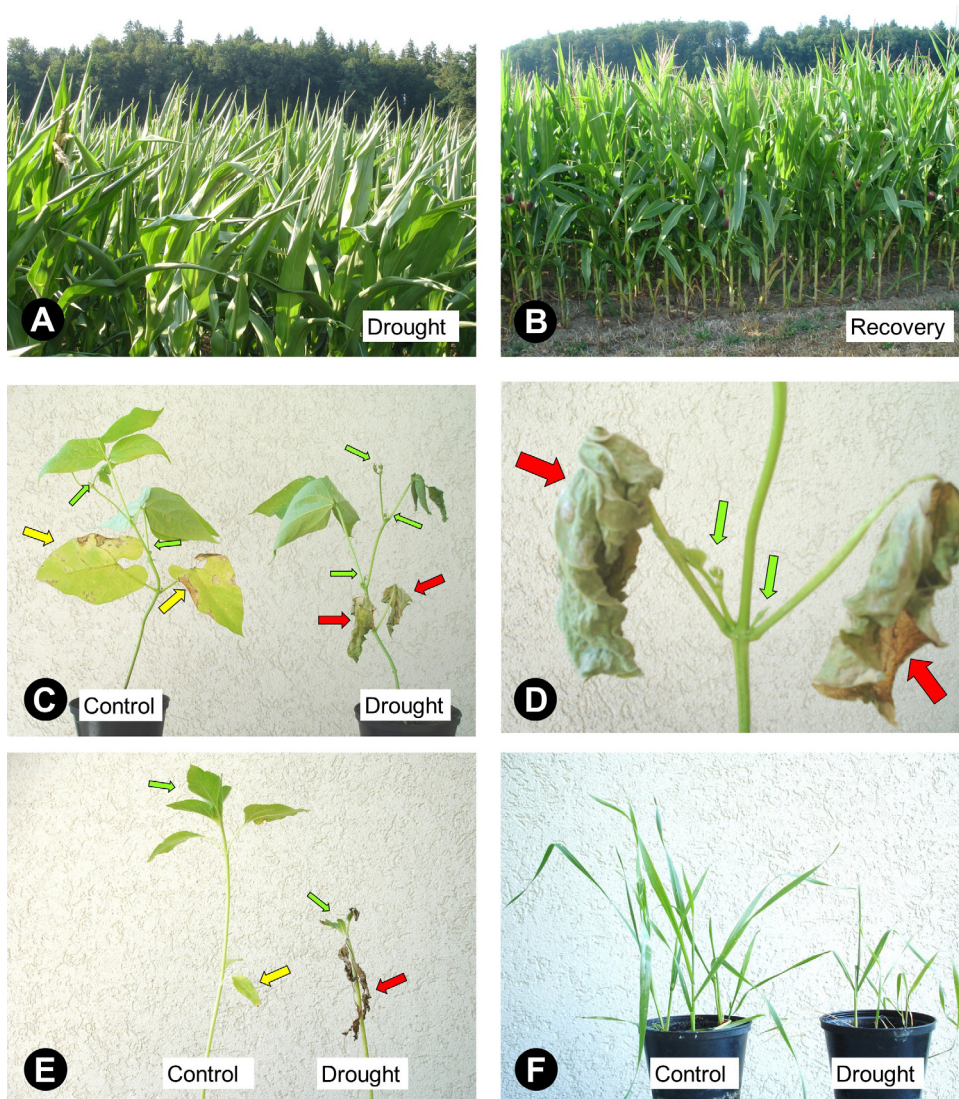


Fig. 2. Impact of severe drought on various crop plants. Leaf rolling is a response to an extended drought period (A) and is reversible during a subsequent recovery phase (B). Several processes affect the active leaf area in dwarf beans (C, D) and in sunflower plants (E): formation of new leaves (green 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).

all shoot biomass is decreased (Gilgen et al., 2010; 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. 1A, B and 2A, 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. 2A, 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 CO₂ 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; Kozłowski 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 poten-

tials 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 CO₂ 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 CO₂ 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 et al., 2004; 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).

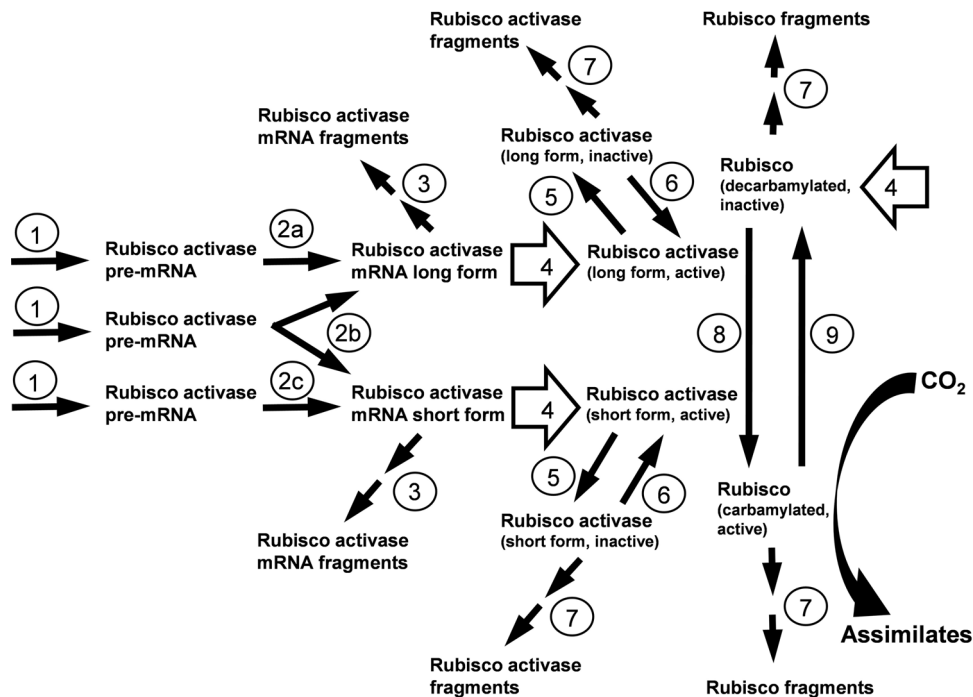


Fig. 3. Steps involved in the heat-induced down-regulation of Rubisco activase and Rubisco activities. The following processes are involved in the control of Rubisco activity and finally also of CO₂ assimilation: transcription of various Rubisco activase genes (1), splicing of pre-mRNA for the longer 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).

Such interactions must be borne in mind for genetic engineering Rubisco activase in crop plants.

As mentioned above, CO₂ 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 et 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 and Portis, 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). Fukayama et al. (2012) reported that in rice overexpressing Rubisco activase CO₂ 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 (especially of ROS scavengers and of compatible solutes such as proline, betaine 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 CO₂) 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 CO₂ assimilation

The decrease in net CO₂ 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 et al., 2015). A CO₂ 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 CO₂ 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 CO₂ 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 CO₂ assimilation on a leaf area basis, while the analyses of net CO₂ 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 CO₂ assimilation in all above-ground plant parts and CO₂ 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 CO₂ 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; AbdElgawad 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 (Werneke 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-Galindo 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, aquaprinins, 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-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).

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